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METHODS OF ACCOUNTING FOR
MATERNAL EFFECTS IN THE
ESTIMATION AND PREDICTION
OF GENETIC PARAMETERS

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ABSTRACT

Maximum likelihood techniques for estimating variance components have desirable features. Nevertheless, the use of maximum likelihood methods for estimating variance components from unbalanced data is difficult. Moreover, additional complications arise in the context of maternal effects models. In this thesis, procedures for generating maximum likelihood estimates of variance components in a maternal effects model are derived for the case of unbalanced data. A hierarchical design where by each sire is mated to several dams is used, there being observations on parents and offspring. The special structure of the data together with the assumption that the sires and the dams are unrelated is exploited in order to obtain explicit expressions for the inverse and the determinant of the variance-covariance matrix of the observations, which arises in the likelihood function and the partial derivatives thereof. Algorithms are proposed to generate the likelihood function and its partial derivatives which are required for constrained and unconstrained optimization of the function. As an illustration, the procedures are applied to weaning weight data of sheep and 8-week weights of pigs. The procedures are extended to estimate variance components in a multiple-trait setting.

Provided the relevant genetic variances and covariances are known, best linear unbiased prediction techniques can be used to predict direct and maternal genetic values. Predicting direct and maternal genetic values of all animals is not difficult since this is a special case of a multiple-trait evaluation. However, if the objective is to eliminate the influence of the maternal effect so that selection is for direct genetic merit, predictions are required for the direct genetic values of all animals of interest and the maternal genetic values of just their dams. Although no analysis is carried out using actual data, best linear unbiased prediction equations for predicting direct genetic values of all animals and the maternal genetic values of their dams are derived.

In the process, the rapid method of inverting the relationship matrix is modified to enable the inversion of the variance-covariance matrix of the genetic effects. The requirements that have to be satisfied in order to generate the correct inverse are given.

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CHAPTER 1. INTRODUCTION

In mammalian species, maternal effects are those differences between progeny performances that are attributable to differences in maternal environment provided by dams during gestation and the pre-weaning period in the life of the progeny. Although a maternal effect contributes an environmental component to progeny performance, variation between dams in maternal performance may arise from either genetic or environmental causes. The expression of the maternal genetic effect which only occurs if an animal subsequently becomes a dam, lags behind the expression of the direct genetic effect by one generation. Thus, in writing a model to describe the performance of a progeny, the genetic component can be subdivided into the direct genetic effect of the progeny and the maternal genetic effect of the dam. Several studies have indicated that the variation in the genetic component of maternal effects can be substantial and that a genetic correlation between direct and maternal effects may exist. Maternal environmental variability is assumed to be caused by non-genetic differences that are common to certain members of families such as full-sibs and maternal half-sibs.

Legates (1972) made a distinction between the terms maternal effects and maternal influences. Maternal effects are the measured phenotypic expressions arising from influences of the mother on a trait measured in her offspring, apart from the direct influence of the genes she transmits. The factors which condition the expression of the maternal effects are the maternal influences. He subdivided maternal influences into pre-natal and post-natal factors. The pre-natal factors are associated with the uterine influences of the mother which result from the genotype of the mother and also from environmental influences on her which are mediated to her offspring in-utero. Post-natal maternal influences arise from the influence of the mother on her offspring following parturition. Legates considers lactational output to be a major factor while factors such as temperament and maternal

instinct are important. According to Robison (1972) cytoplasm of the egg is another factor other than the intra-uterine environment and post-natal environment that is responsible for the maternal influence. However there is little evidence regarding the role of cytoplasmic effects on maternal performance.

Information on the magnitudes of genetic variation of maternal effects and the sign and magnitude of the correlation between direct and maternal genetic effects is, for certain traits essential in the planning of optimal breeding programmes and also for predicting a reliable response from selection. The prediction of genetic gain becomes complicated in the presence of maternal effects. Hanrahan (1976) examined the influence of maternal effects on the relative efficiency of progeny and performance test selection. He concluded that progeny testing is very inefficient for selection purposes when the traits considered are influenced by maternal effects. Van Vleck, St.Louis and Miller (1977) presented an equation to predict expected response to selection when traits under selection are affected maternally. Robison (1981) made suggestions for altering management plans to increase efficiency of selection in the presence of maternal effects.

Although selection for genetic gain in the direct and maternal genetic components is possible, the large negative genetic correlation that may exist between these components has indicated that simultaneous improvement of direct and maternal genetic effects by selection, could be difficult. For example, selection for direct effects lower the maternal ability of the dams that nurture the offspring in succeeding generations.

Best linear unbiased procedures [Henderson (1963)] can be used to predict the direct and maternal genetic effects of animals, provided that the genetic and environmental variances and possible covariances are known. In this thesis, procedures for generating maximum likelihood estimates of the relevant variance components are derived for the case of unbalanced data, the usual situation in animal breeding. These procedures will be applied to

weaning weight data from sheep and pigs. The methods will also be extended to estimate the variance components in a multiple-trait setting. The use of the best linear unbiased procedure to predict direct genetic effects of a set of animals and the maternal genetic effects of their dams is demonstrated. In the process, the rapid method of inverting the relationship matrix [Henderson (1975a,1976); Quaas (1975,1976,1984)] will be modified to enable the inversion of the variance-covariance matrix of the direct and maternal genetic effects.

CHAPTER 2. LITERATURE REVIEW

2.1. Estimation of variance components

Estimation of variance components is an important area in animal breeding. The proportion of the additive genetic variance is used to assess the potential for genetic improvement by selection. In addition, estimates of variance components are required for predicting (most often) the breeding values of candidates for selection.

2.1.1. Balanced data

Traditionally, variance components have been estimated from balanced data (equal number of observations in each sub-class) by the analysis of variance (ANOVA) method. This method involves computing mean squares in the analysis of variance and equating these mean squares to their expected values. The estimators resulting from this method have explicit expressions and computation is not difficult.

ANOVA estimators of variance components obtained from balanced data have several optimal properties. Graybill and Hultquist (1961) showed that the estimators obtained by this method (ANOVA) for a random model with balanced data are best quadratic unbiased (BQUE), a property of the estimators that is not dependent on normality assumptions. A best quadratic unbiased estimator is the quadratic form of observations which is unbiased and which, from among all such quadratic forms has minimum sampling variance. Albert (1976) showed that ANOVA estimators obtained from balanced data are BQUE for mixed models. Further Graybill and Wortham (1956), Graybill and Hultquist (1961), Seely (1971) and Albert (1976) showed that, if the data are normally distributed ANOVA estimators are best unbiased estimators (BUE). That is, of all unbiased estimators, ANOVA estimators have the smallest sample variance. Anderson, Henderson, Pukelsheim and

Searle (1984) showed that ANOVA estimators are BLUE under arbitrary kurtosis. As a result of these optimal properties, the analysis of variance method is popular for estimating variance components when data are balanced. A shortcoming of the method is the fact that it can lead to negative estimates of variance components. It has been suggested that when negative estimators arise, these could be truncated to zero, but when this is done, the method of estimation is no longer unbiased.

2.1.2. Unbalanced data

Most of the early published work on estimation of variance components has dealt with random models with balanced data. Henderson (1953) was the first to develop alternative methods of estimation to handle mixed models with unbalanced data. In his study, he proposed three methods of estimating variance components, which subsequently became to be known as Henderson's Method 1, Method 2 and Method 3, respectively.

2.1.2.1. Henderson's methods

Henderson's Method 1 involves computing sums of squares as in the standard analysis of variance of the corresponding case for balanced data, equating the sums of squares to their expectations under the assumptions of a random effects model and then solving the resultant linear equations in the unknown variance components. Although this method is computationally simple, it leads to biased estimates if any of the effects in the model, other than the general mean, are fixed. Therefore Method 1 is not appropriate for mixed models.

In Method 2, the fixed effects of the model are estimated by the method of least squares (computing as though random effects are fixed), and then Method 1 is used on the data that has been corrected for the fixed effects. Henderson, Searle and Shaeffer (1974) proved that Henderson's Method 2 is invariant for a wide

class of models including the mixed models where there are no interactions between fixed and random effects and also for the models that do not have nesting of fixed and random effects within each other.

Henderson's Method 3, which is also known as the method of fitting constants, involves computing reductions in sums of squares due to fitting different models. Each computed reduction in sums of squares is equated to its expected value under the assumption of the full model. For example,

$$\underline{y} = \underline{X}_1 \underline{\beta}_1 + \underline{e} \quad (2.1)$$

is a sub model of

$$\underline{y} = \underline{X}_1 \underline{\beta}_1 + \underline{X}_2 \underline{\beta}_2 + \underline{e} \quad (2.2)$$

where

\underline{y} is the vector of observations;

$\underline{\beta}' = (\underline{\beta}'_1, \underline{\beta}'_2)$ and the elements of $\underline{\beta}_1$ and $\underline{\beta}_2$ are unknown fixed or random effects;

$\underline{X} = (\underline{X}_1, \underline{X}_2)$ and \underline{X}_1 and \underline{X}_2 are known matrices; and

\underline{e} is the vector of residuals.

If $R(\underline{\beta}_1)$ and $R(\underline{\beta}_1, \underline{\beta}_2)$ are the reductions due to fitting (2.1) and (2.2), respectively, the difference of the expectations under the model (2.2) is the reduction due to fitting $\underline{\beta}_2$ after fitting $\underline{\beta}_1$, which is denoted by $R(\underline{\beta}_2 | \underline{\beta}_1)$. If $\underline{\beta}$ in the model

$$\underline{y} = \underline{X} \underline{\beta} + \underline{e} \quad (2.3)$$

is partitioned into $\underline{\beta}_1$ and $\underline{\beta}_2$ in such a way that $\underline{\beta}_2$ contains only random effects, $E[R(\underline{\beta}_2 | \underline{\beta}_1)]$ would not involve any fixed effects. Therefore, by a proper choice of the sub models, one can obtain unbiased estimates of variance components. Also, even if the elements in $\underline{\beta}_1$ are correlated with the elements of $\underline{\beta}_2$, no correlated terms appear in $E[R(\underline{\beta}_2 | \underline{\beta}_1)]$.

Henderson's Method 3 has the disadvantage that it is computationally difficult. Obtaining reductions in sums of squares as well as the coefficients of variance components in the expectations of the reductions can involve the inversion of matrices with order equal to the number of random effects in the data. In animal breeding studies, in particular, this could be very large and as a consequence the computing is difficult.

All three methods of Henderson are based on the single optimality criterion of unbiasedness. Except in the case of balanced data, estimators obtained from Henderson's methods do not have minimum variance properties. In the case of balanced data, these methods yield ANOVA estimates of variance components.

2.1.2.2. Maximum likelihood and restricted maximum likelihood methods

Hartley and Rao (1967) initiated the current revived interest in the use of the maximum likelihood (ML) method for estimating variance components. Earlier, this method had been rejected by Bush and Anderson (1963) for the reason that the procedure is computationally difficult.

With the ML method, the likelihood function of the observations are maximized over the entire sample space in order to obtain estimates of variance components and fixed effects simultaneously. Combined estimation of the fixed effects and the variance components by the method of ML involves the numerical solution of a nonlinear optimization problem. Non-negativity constraints can also be imposed.

Hartley and Rao (1967) established the large sample optimality properties, such as consistency and asymptotic efficiency, for the ML estimators. Harville (1977) comments that Hartley and Rao were the first to attempt an asymptotic theory that would be appropriate for the complicated analysis of variance models. However, Hartley and Rao imposed a restriction that the

number of observations in a particular level of any random factor should stay below some universal factor. This limited the applicability of the results of Hartley and Rao. Miller (1973,1977) developed an asymptotic theory which does not exclude the models of usual interest, although it is similar to that presented by Hartley and Rao. Searle (1971) derived a general expression for obtaining the large-sample variances of ML estimators, although explicit expressions for the variance components do not exist.

However, in practice, the maximum likelihood procedure has not generally been used to estimate variance components because of the computation difficulties involved. The estimation of variance components by ML does not take account of the loss in degrees of freedom that results from estimating the fixed effects of the model. Also, these estimators are derived under the assumption of a particular distributional form, the most popular being normality.

By extending an idea of Thompson (1962), Patterson and Thompson (1971) developed the restricted maximum likelihood (REML) method for estimating variance components in which, unlike ML, the loss in degrees of freedom from estimating the fixed effects of the model is taken into account. In this method, the likelihood is partitioned into two components where one of which is entirely free of fixed effects. Maximization of the likelihood over this portion leads to restricted maximum likelihood estimators of variance components. This is equivalent to saying that the likelihood of a set of error contrasts is maximized. An error contrast is defined as a linear function of the observation vector \underline{y} , say $\underline{a}'\underline{y}$, where \underline{a} does not involve any unknown parameters, and $E(\underline{a}'\underline{y}) = 0$, so that $\underline{a}'\underline{X} = \underline{0}$. Patterson and Thompson (1971) state that no information is lost by basing the estimates of the variance components on the likelihood of error contrasts.

The REML estimators are free of the fixed effects of the model as well as being invariant to them. Anderson (1979) demonstrated that in general, solutions to REML equations with balanced data are identical to ANOVA estimators. Corbeil and Searle (1976a) showed the same result for special cases (the 1-way random, the 2-way nested random and the 2-way crossed classification mixed, with or without interactions). This is a useful property because of the optimal properties of ANOVA estimates of variance components for balanced data.

There are several iterative numerical algorithms which can be used to compute ML and REML estimates of variance components. The method of steepest ascent and the Newton Raphson procedures are the most common algorithms used. Fisher's method of scoring is another method that has been used in applications. The Newton Raphson procedure can be expected to locate an optimum in a relatively few iterations provided the starting values are sufficiently close to the optimum. Also, it may converge to a point which is not a local or global optimum, if the starting value does not lie in a small neighbourhood of the optimum. The extended Newton Raphson procedure which, under special circumstances is identical to the steepest ascent method [Powell (1970)], overcomes this problem. Apart from the methods mentioned above, there are numerous other algorithms which can be used [see Harville (1977)]. Harville (1977) comments that there is no iterative routine for ML or REML that will be satisfactory for every application.

There are routines that have been developed especially for estimating variance components by ML or REML method. Amongst these is the routine that uses a transformation called a W transformation which was developed by Hemmerle and Hartley (1973) for ML estimation. Corbeil and Searle (1976b) extended the W transformation to estimate variance components by the REML method. Henderson (1973a) demonstrated that the same solution as that of ML can be obtained by solving the mixed model equations proposed by Henderson (1950) and then later derived by Henderson, Kempthorne, Searle and Von Krosigk (1959). He also showed that

the mixed model equations can be used to compute the large-sample variances of the maximum likelihood estimators by using the method explained by Searle (1971).

2.1.2.3. Quadratic estimation of variance components

Townsend and Searle (1971) derived best quadratic unbiased estimators (BQUE) of variance components for the 1-way classification random model with zero mean and normally distributed errors, for unbalanced data. Previously the estimation of variance components from unbalanced data was usually carried out using Henderson's methods. For the vector \underline{y} , normally distributed with zero mean and variance-covariance matrix \underline{V} , Townsend's and Searle's BQUE of a variance component, σ^2 , was the quadratic form $\underline{y}'\underline{A}\underline{y}$, where \underline{A} was determined so that $2\text{tr}(\underline{A}\underline{V}\underline{A}\underline{V})$ is minimized, subject to $\sigma^2 = \text{tr}(\underline{A}\underline{V})$ ("tr" denoting the trace of a matrix). For balanced data, these estimators reduce to ANOVA estimators. La Motte (1973) extended the best quadratic unbiased estimation to a general linear model. Noting that, except for special cases, BQEs do not necessarily have uniformly minimum variance, he considered "best" as a local property. He showed that, in addition to the lower bounds, the "locally best" estimators have other useful analytical properties.

the

Rao (1970) introduced the minimum norm quadratic unbiased estimation (MINQUE) procedure for estimating heteroscedastic variances. Rao (1971a, 1972) studied the optimization problems which occur in MINQUE theory and used this method to determine minimum norm quadratic unbiased estimators of variance components. In the MINQUE approach, a linear function of the variance components, $\underline{a}'\underline{g}^2$, is estimated as a quadratic form $\underline{y}'\underline{A}\underline{y}$ where the choice of \underline{A} depends on the following criteria:

(1) $\underline{y}'\underline{A}\underline{y}$ is an unbiased estimate of $\underline{a}'\underline{g}^2$. That is,

$$E(\underline{y}'\underline{A}\underline{y}) = \underline{a}'\underline{\sigma}^2.$$

Since for a general linear model as in (2.3), the expected value of $\underline{y}'\underline{A}\underline{y}$ is given as

$$E(\underline{y}'\underline{A}\underline{y}) = \underline{\beta}'\underline{X}'\underline{A}\underline{X}\underline{\beta} + \text{tr}(\underline{A}\underline{V})$$

where \underline{V} is the variance-covariance matrix of \underline{y} , $\underline{y}'\underline{A}\underline{y}$ will be an unbiased estimator of $\underline{a}'\underline{\sigma}^2$ for all $\underline{\beta}$ and $\underline{\sigma}^2$ if and only if

$$\underline{X}'\underline{A}\underline{X} = \underline{0}$$

and

$$\underline{a}'\underline{\sigma}^2 = \text{tr}(\underline{A}\underline{V});$$

- (2) $\underline{y}'\underline{A}\underline{y}$ is translation invariant. A quadratic form is said to be translation invariant if it is unaffected by changes in the vector of fixed effects. Thus $\underline{y}'\underline{A}\underline{y}$ is translation invariant if

$$\underline{y}'\underline{A}\underline{y} = (\underline{y} - \underline{X}\underline{\beta})'\underline{A}(\underline{y} - \underline{X}\underline{\beta})$$

which implies that

$$\underline{A}\underline{X} = \underline{0}; \text{ and}$$

- (3) $\underline{y}'\underline{A}\underline{y}$ minimizes a suitable norm. Rao (1971a) minimized the Euclidian norm of $\underline{Z}'\underline{A}\underline{Z} - \underline{\Delta}$, where $\underline{\Delta}$ is a suitable diagonal matrix and demonstrated that this is equivalent to the problem of determining \underline{A} such that $\text{tr}(\underline{A}\underline{V}\underline{A}\underline{V})$ is minimized.

La Motte (1973) noted that Rao's minimum norm quadratic estimators are best quadratic estimators at $\underline{\theta}_0$, where $\underline{\theta}_0$ is determined by the choice of the norm minimized.

Rao (1971b) minimized the variance of a quadratic form of the observations in a linear model to obtain locally best unbiased estimators (MIVQUE) of variance components. La Motte (1973)

presented the general approach for such estimation. When the variables are normally distributed, MIVQUE is identical to the MINQUE under the Euclidian norm mentioned earlier.

2.2. Estimation of variance and covariance components:

Maternal effects models

The biometrical aspects of maternal effects were first developed by Dickerson (1947). He utilized path coefficient diagrams to demonstrate the relationship between the individual phenotype and the genetic influences which affect phenotype directly (direct effects) and indirectly (through maternal environment).

2.2.1. Equating covariances between relatives to their expected values

The use of covariances between relatives is the most common method of estimating maternal genetic variances. The usual method in the past has been that of making general statements about the maternal influence by comparing correlations observed in various relationships. For example, maternal half-sibs versus paternal half-sibs; and dam-offspring versus sire-offspring. Koch and Clark (1955) used path coefficient diagrams between different relatives to assess the importance of maternal effects on economically important characters in beef cattle.

Willham (1963) examined the theoretical compositions of covariances between specific relatives in the presence of maternal effects. He expressed the phenotypic observation of animal X, whose dam is animal W, as

$$P_x = g_{Ox} + g_{mW} + e_{Ox} + e_{mW} \quad (2.4)$$

where

g_{Ox} is the direct effect of the genotype of x;

g_{mW} is the maternal effect on X caused by the genotype of animal's dam W;

e_{OX} is the direct effect of environment on X; and
 e_{mW} is the effect of the environment on the maternal
value of W.

Then the genotypic covariance between two related animals X and Y is given as

$$\begin{aligned} \text{Cov}(g_X, g_Y) = & \text{Cov}(g_{OX}, g_{OY}) + \text{Cov}(g_{OY}, g_{mW}) \\ & + \text{Cov}(g_{OX}, g_{mZ}) + \text{Cov}(g_{mW}, g_{mZ}) \end{aligned} \quad (2.5)$$

where Z is the dam of the individual Y. For additive genetic effects only, (2.5) reduces to

$$a_{xy}\sigma_{Ao}^2 + (a_{xz} + a_{yw})\sigma_{AoAm} + a_{wz}\sigma_{Am}^2 \quad (2.6)$$

Dickerson (1947) and Koch and Clark (1955) used the same result as in (2.6) to obtain covariances between specific relationships when maternal effects were considered. Eisen (1967) proposed three mating designs that generate different types of relatives. He used these designs to estimate direct and maternal additive and dominance variances, direct-maternal additive and dominance covariances, maternal environmental variance and random environmental variance.

Ahlschwede and Robison (1971a), Hohenboken and Brinks (1971a), Robison (1972) and Koch (1972) estimated variance components for direct and maternal effects and the correlation between direct and maternal effects by equating observed covariances between relatives to their expected compositions. The theoretical compositions of covariances between different types of relationships are given in Willham (1963,1972), Eisen (1967), Koch (1972), Thompson (1976a), and Foulley and Lefort (1978). Willham (1972) included the grand maternal effect in the path diagram showing the biometrical relationships of the phenotypic expression of a trait.

Falconer (1964) attributes some of the inconsistencies observed in predicted heritabilities and realized heritabilities to the influence of maternal effects. He used daughter-dam covariance and response to selection to estimate the variance components. Falconer expressed the phenotypic value, P , of an individual, measured as a deviation from the population mean, as

$$P = A + M + D + C + E$$

where

A is the individual's breeding value;

M is the maternal effect;

D is the dominance deviation;

C represents the environmental factors common to full-sibs that are not included in the maternal effect; and

E represents the environmental factors particular to the individual.

The maternal effect, M , was defined as a linear function of the dam's phenotypic value, P' , measured as a deviation from the population mean. That is,

$$M = mP'$$

where the coefficient m is the partial regression coefficient relating the phenotypic values of dams to their daughters in the absence of genetic variation amongst mothers. He derived the equations for the daughter-dam covariance and the expected value of the response to selection which can be expressed as

$$\text{Cov}_{PP'} = V_{A'} / (2-m) + mV_P,$$

and

$$R = (V_{AW} / V_{PW})S + mQ,$$

respectively, where V_P and $V_{A'}$ are the phenotypic and additive variances of the dams, V_{AW} and V_{PW} are the additive and phenotypic variances within families, R is the total response to selection, Q is the mean deviation from the control during the period from

which R is estimated and S is the cumulated selection differential. Falconer expressed V_{AW} in terms of V_A , using the proportion of the phenotypic variance of the dams to that of daughters. Then the two equations with two unknowns were solved to find V_A , and m. The variance attributed to the maternal effect was then estimated as

$$V_M = m^2 V_P.$$

The expression for Cov_{AM} , which is given by

$$Cov_{AM} = mV_A/(2-m),$$

was used to find the covariance between the individual's breeding value and the maternal effect. Finally, the expressions for phenotypic variance and the full-sib covariance were used to estimate the variances attributed to the dominance deviations, environmental factors common to full-sibs other than those included in the maternal effect, and environmental factors particular to the individual.

$$V_P = V_A + 2 Cov_{AM} + V_M + V_D + V_C + V_E$$

$$Cov(FS) = (V_{A's} + V_{A'd})/4 + 2mV_{A'd}/(2-m) + V_M + V_D/4 + V_C$$

In the above expressions, the subscripts s and d refer to the sire and dam, respectively. These two expressions do not give estimates for V_D , V_C and V_E . However estimates for $3V_D/4 + V_E$ and $V_D/4 + V_C$ can be obtained.

2.2.2. Method of least squares

Van Vleck and Hart (1966) used the method of least squares to estimate the genetic variances and covariances attributed to direct and maternal effects in their analysis of first lactation milk records of Holstein cows. Eisen (1967) used this method to obtain the variance components as partial regression coefficients.

He considered the model

$$\underline{y} = \underline{X}\underline{\beta} + \underline{e}$$

where the i th element of vector \underline{y} is the covariance of the i th relationship generated by his mating designs; \underline{X} is the matrix of expected coefficients; and $\underline{\beta}$ is the vector of causal components of the observed variances and covariances. It was also assumed that the mean and the variance of the vector of errors, \underline{e} , are given by

$$E(\underline{e}) = \underline{0} \text{ and } \text{Var}(\underline{e}) = \underline{V}.$$

The least squares estimate for $\underline{\beta}$, is then given by

$$\hat{\underline{\beta}} = (\underline{X}'\underline{X})^{-1}\underline{X}'\underline{y}.$$

This is an unbiased estimate of $\underline{\beta}$, and the variance-covariance matrix of $\hat{\underline{\beta}}$ is given by

$$\text{Var}(\hat{\underline{\beta}}) = (\underline{X}'\underline{X})^{-1}\underline{X}'\underline{V}\underline{X}(\underline{X}'\underline{X})^{-1}.$$

Noting that some of the elements of \underline{y} are estimated with greater precision than others, leading to unequal weighting, and that there may also be cases of heterogeneous variances, Eisen (1967) suggested the weighted least squares procedure as an alternative. The weighted least squares estimate of $\underline{\beta}$ is

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

with variance-covariance matrix

$$\text{Var}(\hat{\underline{\beta}}_w) = (\underline{X}'\underline{V}_w^{-1}\underline{X})^{-1}.$$

The diagonal elements of \underline{V}_w are the variances of the estimates of the elements in \underline{y} and the off-diagonal elements represent the variances of the estimates of pairwise covariances of the elements

in y . Van Vleck and Hart (1966) used the number of pairs of records included in the estimation of the covariances, for standardizing the covariances where a multiple regression was performed on the standardized covariances. They report that this procedure is similar to the weighting according to the inverse of the variances of the regressions or covariances.

2.2.3. Restricted maximum likelihood approach

Thompson (1976a) states that the least squares procedure is not very efficient if the variances and covariances between relatives are not homogeneous. The weighted least squares procedure which is suggested by Eisen (1967) in the case of heterogeneous variances, requires the calculation of the variance-covariance matrix of the covariances between relatives which is computationally difficult.

Thompson (1976a) demonstrated how the restricted maximum likelihood method suggested by Patterson and Thompson (1971) can be used to estimate maternal genetic and environmental variances. In this approach, he formed symmetric sums of squares and product matrices representing variation in a number of variates by subdividing the data into independent parts according to different sources of variation. Then the likelihood of the symmetric sums of squares and products matrices were maximized in order to obtain estimates of variance components. As an example, he suggested the hierarchical design considered by Hill and Nicholas (1974) and Thompson (1976b), where each of a set of sires is mated to several dams and number of offspring raised from each mating. Thompson (1976a) formed the sums of squares and products matrices using,

- (1) separate sums of squares within dams, between dams within sires and between sires from offspring data;
- (2) a 2x2 matrix that represents the variation between dams within sires with two variates corresponding to offspring and dams;
- (3) a 3x3 matrix representing variation between sires with

three variates corresponding to offspring, dams and sires.

Examples of elements of such matrices are given in Thompson (1976b) where he estimated the heritability when observations were available on parents and offspring.

He assumed that the observations are multivariate normal with means μ_1 , μ_2 and μ_3 for the sires, dams and offspring, respectively, and common variance σ_p^2 . Let the k th sums of squares and product matrix, S_k , which is assumed to be independent with S_j ($j \neq k$), be associated with d_k degrees of freedom. Then the mean squares and product matrix, M_k , is given by

$$M_k = S_k/d_k.$$

Thompson (1976a) expressed the expected value of M_k as

$$V_k = E(M_k) = \sum_{i=1}^p F_{ki} \theta_i$$

where θ_i ($i=1,2,\dots,p$) are the variance components of interest and F_{ki} are known symmetric matrices. The log likelihood, L , is then written as,

$$L = \text{constant} - \frac{1}{2} \left[\sum_{k=1}^s d_k (\ln |V_k| + \text{tr}(M_k V_k^{-1})) \right]$$

where s is the number of symmetric sums of squares and products matrices, $|V_k|$ is the determinant of V_k . Following Anderson (1973), Thompson showed that the restricted maximum likelihood estimates of θ_i satisfy the equations

$$\sum_{k=1}^s d_k [\text{tr}(V_k^{-1} M_k V_k^{-1} F_{ki}) - \text{tr}(V_k^{-1} F_{ki})] = 0$$

for $i=1,2,\dots,p$. This is equivalent to solving the equations

$$\underline{\underline{A}}\underline{\underline{\theta}} = \underline{\underline{b}}$$

where $\underline{\underline{A}}$ is a $p \times p$ matrix with (i, j) th element as

$$a_{ij} = \sum_{k=1}^S d_k \operatorname{tr}(\underline{\underline{V}}_k^{-1} \underline{\underline{F}}_{ki} \underline{\underline{V}}_k^{-1} \underline{\underline{F}}_{kj}) ;$$

$\underline{\underline{b}}$ is a $p \times 1$ vector with i th element as

$$b_i = \sum_{k=1}^S d_k \operatorname{tr}(\underline{\underline{V}}_k^{-1} \underline{\underline{M}}_k \underline{\underline{V}}_k^{-1} \underline{\underline{F}}_{ki}) ;$$

and $\underline{\underline{\theta}}$ is a $p \times 1$ vector with θ_i as the i th element. The asymptotic variance-covariance matrix of $\underline{\underline{\theta}}$ is given by $2\underline{\underline{A}}^{-1}$.

Thompson reports that the difference between this particular multivariate analysis and the usual multivariate analysis is that the number of variates associated with the different sources of variation need not be equal. He illustrated the method by using some data on pupae weight of *Tribolium*. He also demonstrated how this approach can be applied to Eisen's (1967) designs.

2.2.4. Analysis of reciprocal crosses

Cockerham and Weir (1977) used analysis of reciprocal crosses to estimate maternal and paternal variances. They discussed the estimation of variance components for two types of mating designs. The first involves a factorial mating design between two distinct sets of parental lines and the other is a diallel of all crosses from a single set of parental lines.

Earlier diallels have been used to measure additive and dominance variation and to describe the properties of parental lines. Jinks (1954) applied diallel crosses on inbred lines of *Nicotiana Rustica*. Hayman (1954) developed the theory of diallel crosses and investigated complex genetical systems. Kempthorne (1956) and Griffin (1956) described the situation in general, including arbitrary epistacy.

Cockerham and Weir represented a cross as

$$y_{ijk} = \mu + g_{ij} + e_{ijk} \quad (2.7)$$

where

y_{ijk} is an observation on an offspring of maternal parent i (parental line i) mated to paternal parent j (parental line j) ($j \neq i$);
 μ is the general mean;
 g_{ij} is the total of effects attributed to the parents; and
 e_{ijk} is the total of other effects.

The reciprocal of the above cross is given by y_{jik} .

They considered several models for g_{ij} in (2.7), and first of these takes the factorial nature of the pairwise matings into consideration. That is,

$$g_{ij} = m_i + p_j + (mp)_{ij} \quad (2.8)$$

where

m_i is the total maternal effect;
 p_j is the total paternal effect; and
 $(mp)_{ij}$ is the interaction between the maternal and paternal effects.

These effects are assumed to be random with variances σ_m^2 , σ_p^2 and σ_{mp}^2 , respectively. Further, they defined the two covariances C_{mp} and C_{mzp} , where C_{mp} represents the covariance between m_i and p_i and C_{mzp} is the covariance between $(mp)_{ij}$ and $(mp)_{ji}$.

Another model for reciprocals can be generated by transforming the effects of the model given in (2.8). This is the diallel model and is expressed as

$$g_{ij} = g_i^* + g_j^* + s_{ij} + d_i - d_j + r_{ij} \quad (2.9)$$

where the transformations are defined as follows:

$$\begin{aligned} g_i^* &= (m_i + p_i)/2, \quad (g_j^* \text{ defined similarly}); \\ d_i &= (m_i - p_i)/2, \quad (d_j \text{ defined similarly}); \\ s_{ij} &= [(mp)_{ij} + (mp)_{ji}]/2; \\ r_{ij} &= [(mp)_{ij} - (mp)_{ji}]/2; \end{aligned}$$

with

$$s_{ij} = s_{ji};$$

and

$$r_{ij} = -r_{ji}.$$

The variances of the effects in (2.9) can be obtained directly by using the transformations. That is,

$$\sigma_g^2 = (\sigma_m^2 + \sigma_p^2 + 2C_{mp})/4;$$

$$\sigma_d^2 = (\sigma_m^2 + \sigma_p^2 - 2C_{mp})/4;$$

$$\sigma_s^2 = (\sigma_{mp}^2 + C_{m \times p})/2;$$

and

$$\sigma_r^2 = (\sigma_{mp}^2 - C_{m \times p})/2.$$

In the factorial mating design mentioned earlier, a set of maternal parents ($i=1,2,\dots,N$) is mated to a set of paternal parents ($j=N+1,N+2,\dots,2N$). This, with the reciprocal, leads to two factorial mating designs ij and ji . Cockerham and Weir suggested separate analysis for the two factorials and the pooling of the corresponding sums of squares, for estimating the variance components for the effects in model (2.8). The mean squares are computed for the marginals and the interactions between the two factorials. The estimates of the variance components are then obtained by equating mean squares or products to their expectations.

2.3. Prediction techniques

The most common aim of animal breeding is to improve the genetic merit of the population by selecting the genetically superior animals as the parents for succeeding generations. For this, the animal breeder may have a vector of observations on some random variables from which to predict values of some non-observable random variables. Generally, the problem can be stated as follows:

"If \underline{y} and \underline{w} are two jointly distributed vectors of random variables with elements of \underline{y} and \underline{w} being observable and non-observable, respectively, then the problem is to predict \underline{w} from the observed values of \underline{y} ".

Predicting future records is a special case of the above problem where \underline{w} is a function of future records. Predicting the genetic merit of a dairy bull from the milk yield of his female relatives is another example. The predictor of the i th element of \underline{w} , which is denoted as \hat{w}_i , is a function of the observable random variables. That is,

$$\hat{w}_i = f(\underline{y}).$$

Detailed accounts of prediction techniques in animal breeding are given in Henderson (1973b, 1977).

2.3.1. Best prediction

In the method called best prediction (BP), the predictor \hat{w}_i is found such that $E(\hat{w}_i - w_i)^2$ is minimized, the \hat{w}_i obtained being known as the best predictor (BP). The BP of w_i is given by

$$\hat{w}_i = E(w_i | \underline{y}),$$

that is, the conditional mean of w_i given \underline{y} . A proof of this appears in Rao (1965). Searle (1973) provided proofs for the following properties of best predictors.

(1) \hat{w}_i is an unbiased predictor of w_i . That is,

$$E(\hat{w}_i) = w_i$$

(2) The variance-covariance matrix of the prediction errors is the average conditional variance of $w|\underline{y}$

$$\text{Var}[(\hat{w}-w)(\hat{w}-w)'] = E_y[\text{Var}(w|\underline{y})]$$

(3) Of all functions of \underline{y} , \hat{w}_i maximizes the correlation between \hat{w}_i and w_i .

(4) $\text{Var}(\hat{w}) = \text{Cov}(\hat{w}, w')$

(5) $\text{Cov}(w, \underline{y}') = \text{Cov}(\hat{w}, \underline{y}')$

The form of the joint distribution of records and the genetic values to be predicted, together with the numerical values of the parameters of the distribution should be known in order to find best predictors. In addition, the conditional mean of w_i given \underline{y} should be computed. These requirements have made prediction by this method difficult and hence best predictors are not generally used in practice.

2.3.2. Best linear prediction (Selection index)

Hazel (1943) was the first to apply the selection index to animal breeding. In best linear prediction (BLP), the predictor which is also known as the selection index (denoted as I) is calculated as a linear function of the observations. That is

$$I_i = w_i = a + \underline{b}_i' y$$

where "a" is a scalar and \underline{b}_i is a vector of weights chosen so that $E(\hat{w}_i - w_i)^2$ is minimized. The vector of predictors found as such is given by

$$\hat{\underline{w}} = E(\underline{w}) + \underline{C}\underline{V}^{-1}[\underline{y} - E(\underline{y})]$$

where

$$\underline{C} = \text{Cov}(\underline{w}, \underline{y}')$$

and

$$\underline{V} = \text{Var}(\underline{y}).$$

Some properties of BLP are outlined below [see Henderson (1973b, 1977)].

(1) $\hat{\underline{w}}$ is unbiased. That is,

$$E(\hat{\underline{w}}) = E(\underline{w})$$

(2) $\text{Var}(\hat{\underline{w}}) = \text{Cov}(\hat{\underline{w}}, \underline{w}') = \underline{C}\underline{V}^{-1}\underline{C}'$

(3) $\text{Var}(\hat{\underline{w}} - \underline{w}) = \underline{G} - \underline{C}\underline{V}^{-1}\underline{C}'$ where $\underline{G} = \text{Var}(\underline{w})$

(4) Of all linear functions of \underline{y} , BLP of w_i maximizes the correlation between w_i and \hat{w}_i .

(5) The BLP of a linear function of \underline{w} is the linear function of the BLP of \underline{w} . That is, BLP of $\underline{l}'\underline{w}$ is $\underline{l}'\hat{\underline{w}}$.

In best linear prediction the form of the joint distribution of the records and of the genetic values to be predicted need not be known, but the first and the second moments of the distributions must be known. Animal breeders substitute estimates of the variance parameters as if they were the true values and proceed with BLP. However, the expected value of \underline{y} creates a problem since this is usually unknown. In such cases, it is assumed that this has the form $\underline{X}\underline{\beta}$ where \underline{X} is a known matrix and $\underline{\beta}$ is an unknown vector of fixed effects. Estimates of some or all

of the $\underline{\beta}$'s are available from prior data and can be used. In the case of the normal distribution, BLP is the same as BP.

2.3.3. Best linear unbiased prediction

Henderson (1963) developed the theory of best linear unbiased prediction (BLUP) which overcomes the problem of estimating $\underline{X}\underline{\beta}$. In this method, he minimized $E(\hat{w}_i - w_i)^2$ subject to $E(\hat{w}_i) = E(w_i)$. The resultant predictor is given by

$$\hat{\underline{w}} = \underline{C}\underline{V}^{-1}[\underline{y} - \underline{X}\hat{\underline{\beta}}]$$

where \underline{C} and \underline{V} are defined as in the selection index method and $\hat{\underline{\beta}}$ is a solution to the generalized least squares equations

$$\underline{X}'\underline{V}^{-1}\underline{X}\hat{\underline{\beta}} = \underline{X}'\underline{V}^{-1}\underline{y}. \quad (2.10)$$

When $E(\underline{y})$ in the selection index is replaced by $\underline{X}\hat{\underline{\beta}}$ the best linear unbiased predictor is obtained. Best linear unbiased predictors have the following properties [see Henderson (1973b, 1977)].

- (1) $E(\hat{\underline{w}}) = E(\underline{w})$ (This was a requirement for the derivation).
- (2) $\text{Var}(\hat{\underline{w}} - \underline{w}) = \text{Var}(\underline{w}) - \underline{C}\underline{V}^{-1}\underline{C}' + \underline{C}\underline{V}^{-1}\underline{X}(\underline{X}'\underline{V}^{-1}\underline{X})^{-1}\underline{X}'\underline{V}^{-1}\underline{C}'$ where $(\underline{X}'\underline{V}^{-1}\underline{X})^{-1}$ is a generalized inverse of $\underline{X}'\underline{V}^{-1}\underline{X}$
- (3) $\text{Var}(\hat{\underline{w}}) = \text{Cov}(\hat{\underline{w}}, \underline{w}') = \underline{C}\underline{V}^{-1}\underline{C}' - \underline{C}\underline{V}^{-1}\underline{X}(\underline{X}'\underline{V}^{-1}\underline{X})^{-1}\underline{X}'\underline{V}^{-1}\underline{C}'$
- (4) Of all linear functions in \underline{y} that have zero means, \hat{w}_i maximizes the correlation between \hat{w}_i and w_i .
- (5) When the distribution is multivariate normal, $\hat{\underline{w}}$ is the best linear unbiased estimator and the maximum likelihood estimator of the conditional mean of \underline{w} given \underline{y} .

(6) BLUP of $\underline{1}'\underline{w}$ is $\underline{1}'\hat{\underline{w}}$ where $\hat{\underline{w}}$ is the BLUP of \underline{w} .

So far it has been assumed that the animals to be evaluated for selection are from the same population. Consequently the means of all animals have been considered to be equal, since it would not affect the ranking of the predictors. However, animal breeders are usually confronted with animals that come from different populations or from herds that have undergone selection. Henderson (1963,1975b) presented methods to deal with such data. Here he considers w_i 's of the form $k_i'\beta + m_i'u$ where u is assumed to have zero mean. As shown by Henderson (1963), the best linear unbiased predictor of $k'\beta + m'u$ for the general mixed model is given by

$$k'\hat{\beta} + m'GZ'V^{-1}(y - X\hat{\beta})$$

where G is the variance-covariance matrix of w and $\hat{\beta}$ is any solution to the generalized least squares equations given in (2.10).

The selection index method and the best linear unbiased prediction technique involve the inversion of the matrix V which is computationally difficult when the number of records is large as in the case of animal breeding. Henderson (1975b) shows that the use of mixed model equations suggested by Henderson (1950) is an easier method for certain prediction problems. He considered the mixed linear model of the form

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

where

- β is a vector of fixed effects;
- u and e are non-observable random vectors with mean zero and variance σ^2G and σ^2R , respectively, where G and R are known non-singular matrices; and
- X and Z are the matrices of coefficients associated with β and u respectively.

It was also assumed that $\text{Cov}(u, e')$ is a null matrix.

Henderson et al (1959) proved that $\hat{\beta}$ in the following set of equations is a generalized least squares solution for β and Henderson (1963) proved that \hat{u} in (2.11) is the best linear unbiased predictor of u .

$$\begin{bmatrix} \underline{X}'\underline{R}^{-1}\underline{X} & \underline{X}'\underline{R}^{-1}\underline{Z} \\ \underline{Z}'\underline{R}^{-1}\underline{X} & \underline{Z}'\underline{R}^{-1}\underline{Z} + \underline{G}^{-1} \end{bmatrix} \begin{bmatrix} \hat{\beta} \\ \hat{u} \end{bmatrix} = \begin{bmatrix} \underline{X}'\underline{R}^{-1}\underline{y} \\ \underline{Z}'\underline{R}^{-1}\underline{y} \end{bmatrix} \quad (2.11)$$

In addition, if β is known, \hat{u} is the solution to the equation

$$(\underline{Z}'\underline{R}^{-1}\underline{Z} + \underline{G}^{-1})\hat{u} = \underline{Z}'\underline{R}^{-1}(\underline{y} - \underline{X}\beta)$$

which is the same as the selection index. Henderson (1977) reports that this method has the further advantage that the sampling variances can be derived from the generalized inverse of the coefficient matrix in (2.11). When u is a vector of breeding values, the variance-covariance matrix of u is given by

$$\underline{G} = \sigma_a^2 \underline{A}$$

where \underline{A} is the numerator relationship matrix and σ_a^2 is the additive genetic variance. This implies that,

$$\underline{G}^{-1} = \frac{1}{\sigma_a^2} \underline{A}^{-1}.$$

In the past, the BLUP technique has not been routinely applied because of the computing difficulties and costs incurred when a large set of data is involved. However, with the increase in computing power this technique is becoming more applicable. In fact, the BLUP technique is routinely applied to dairy cattle and beef cattle data in North America. Another major impact is the introduction of computing shortcuts. For example, Henderson (1976) showed that the inverse of the numerator relationship matrix can be computed without generating the relationship matrix itself.

2.4. Prediction Techniques: Maternal effects models

2.4.1. Selection index for direct and maternal genetic components

Van Vleck (1970) extended the selection index procedure to multiple trait selection when the traits may have both direct and maternal effects. For selection involving q traits, each with direct and maternal genetic components, the total economic value, H , was defined to be

$$H = \underline{p}'\underline{g}$$

where \underline{g} and \underline{p} are $2q \times 1$ vectors of genetic values and economic values, respectively. These vectors can be partitioned as

$$\underline{g}' = (g'_1, g'_2, \dots, g'_q) \text{ with } g'_j = (g_{dj}, g_{mj})$$

and

$$\underline{p}' = (p'_1, p'_2, \dots, p'_q) \text{ with } p'_j = (p_{dj}, p_{mj})$$

where q is the number of traits involved. The g_d 's and g_m 's in vector g'_j correspond to g_{Ox} and g_{mw} in Willham's model [model given in (2.4)].

The selection index for each animal is based on records on the q traits of n relatives. Therefore the data vector can be partitioned as

$$\underline{y}' = (y'_1, y'_2, \dots, y'_n)$$

where

$$y'_i = (y_{i1}, y_{i2}, \dots, y_{iq}).$$

The latter is the observation vector of the q traits on the i th relative. It was assumed that

$$E(\underline{y}) = \underline{0} \text{ and } \text{Var}(\underline{y}) = \underline{V}$$

and also that

$$E(\underline{g}) = \underline{0} \text{ and } \text{Var}(\underline{g}) = \underline{G}.$$

The weights for the elements of \underline{y} which maximize the correlation between the index criterion and H satisfy the equation

$$\underline{V}\underline{b} = \underline{A}'\underline{G}\underline{p}$$

where \underline{A} is the $2q$ by qn matrix of additive relationships between the animals being evaluated with its relatives and the dams of the relatives. This can be partitioned as

$$\underline{A} = (\underline{A}_1, \underline{A}_2, \dots, \underline{A}_n)$$

where each \underline{A}_i is given as

$$\underline{A}_i = \underline{a}_i * \underline{I}_q$$

with

$$\underline{a}_i = (a_{i\alpha}, a_{id\alpha}).$$

In above, $a_{i\alpha}$ is the additive relationship between the i th relative and the animal being evaluated, $a_{id\alpha}$ is the additive relationship between the dam of the i th relative and the animal being evaluated and "*" refers to the Kronecker product of matrices. It follows that the index criterion for selection is given by

$$I = \underline{b}'\underline{y} = \underline{p}'\underline{G}\underline{A}\underline{V}^{-1}\underline{y}.$$

Van Vleck (1976) extended this procedure to include an effect of the maternal grand dam. In this case, additional effects were included in the vectors \underline{g}_j and \underline{p}_j . That is,

$$\underline{g}'_j = (g_{dj}, g_{mj}, g_{m'j})$$

and

$$\underline{p}'_j = (p_{dj}, p_{mj}, p_{m'j})$$

where $g_{m'j}$ and $p_{m'j}$ are the grand maternal genetic effect for trait j and the economic value for the grand maternal component of trait j , respectively. Also, the vector of additive relationships, \underline{a}_i , is extended so that

$$\underline{a}'_i = (a_{i\alpha}, a_{id\alpha}, a_{id'\alpha})$$

where $a_{id'\alpha}$ is the additive relationship between the animal being evaluated and the maternal grand dam of the i th relative.

2.4.2. Best linear unbiased prediction

Quaas (1975) defined an equivalent model (a model that generates the same first and second moments) for

$$G_x = r_s + r_d,$$

where G_x , r_s and r_d represent the random variables for the breeding value of animal X , average effect of the genes that X received from its sire and average effect of the genes X received from its dam, respectively. The equivalent model is given by

$$G_x = \frac{1}{2} (G_s + G_d) + E_x \quad (2.12)$$

where G_s and G_d are the random variables representing breeding values of the sire and the dam, respectively, and E_x is an independent variable representing Mendelian sampling.

Slanger (1977) extended (2.12) to two related traits where he introduced a constant coefficient to each of G_s and G_d in addition to the constant 0.5 that already exists. Let the breeding values

of the offspring for the two traits i and j be given by g_{oi} and g_{oj} , respectively. Then Slanger's model is given by

$$\begin{aligned} g_{oi} &= \frac{1}{2} (c_{di}g_{dp} + c_{si}g_{sq}) + e_{oi} \\ g_{oj} &= \frac{1}{2} (c_{dj}g_{dm} + c_{sj}g_{sn}) + e_{oj} \end{aligned} \quad (2.13)$$

where

g_{dp} and g_{sq} are the genetic values of the dam and the sire contributing to the genetic value for trait i of offspring; g_{dm} and g_{sn} are the genetic values of the dams and the sire contributing to the genetic value for trait j of offspring; and e_{oi} and e_{oj} are the Mendelian sampling random variables which are uncorrelated with any of the parents genetic values.

The possible values for the coefficients c_{di} , c_{si} , c_{dj} and c_{sj} are 1, σ_{ij}/σ_i^2 , σ_{ij}/σ_j^2 and 0 where σ_i^2 , σ_j^2 and σ_{ij} are the genetic variance for trait i , the genetic variance for trait j and the genetic covariance between traits i and j , respectively. For example, if $i=p$ (that is, contribution from the dam to the i th trait of the offspring is the genetic value of the i th trait of the dam), then c_{di} is equal to 1. If $i \neq k$, the value for c_{di} is given by σ_{ij}/σ_j^2 . When neither genetic value of the parent is included in the pedigree this coefficient is zero. Using (2.13), Mendelian sampling variables can be expressed as

$$e_{oi} = g_{oi} - \frac{1}{2}(c_{di}g_{dp} + c_{si}g_{sq}).$$

When it is assumed that the mates are unrelated, the variance of e_{oi} can be obtained as

$$\text{Var}(e_{oi}) = \sigma_i^2 + \frac{1}{4}(c_{di}^2\sigma_p^2 + c_{si}^2\sigma_q^2) - \frac{1}{2}(c_{di}\sigma_{ip} + c_{si}\sigma_{iq}).$$

For example, consider the following possibilities.

- (1) both parent coefficients are zero; $\text{Var}(e_{oi}) = \sigma_i^2$
- (2) both parents are included and $i=p=q$; $\text{Var}(e_{oi}) = \sigma_i^2/2$
- (3) both parents are included, $i=p$ and $j=q$; $\text{Var}(e_{oi}) = \sigma_i^2(3-\rho^2)/4$
where ρ is the genetic correlation between traits i and j

Similarly, assuming that the mates are unrelated, the covariance between the Mendelian sampling variables of trait i and trait j of the same individual is found to be as follows:

$$\begin{aligned} \text{Cov}(e_{oi}, e_{oj}) = & \sigma_{ij} + (c_{di}c_{dj}\sigma_{pm} + c_{si}c_{sj}\sigma_{qn})/4 \\ & - (c_{di}\sigma_{jp} + c_{si}\sigma_{jq} + c_{dj}\sigma_{im} + c_{sj}\sigma_{in})/4 \end{aligned}$$

In matrix notation (2.13) is given as

$$\underline{g} = \frac{1}{2}\underline{C}\underline{g} + \underline{e} \quad (2.14)$$

where \underline{g} is the vector of additive genetic values, \underline{C} is the matrix of coefficients of the parent genetic values and \underline{e} is the vector of Mendelian sampling variables. From (2.14),

$$\underline{g} = (\underline{I} - \frac{1}{2}\underline{C})^{-1}\underline{e}$$

which implies that

$$\underline{G}^{-1} = \underline{B}\underline{H}^{-1}\underline{B}'$$

where

$$\underline{G} = \text{Var}(\underline{g});$$

$$\underline{B} = \underline{I} - \frac{1}{2}\underline{C}';$$

and

$$\underline{H} = \text{Var}(\underline{e}).$$

If the covariance between the Mendelian sampling variables of two individuals is assumed to be zero, computing H^{-1} involves inverting scalars or 2x2 matrices only. Then diagonal elements and off-diagonal elements of G^{-1} are given by

$$g_{ij} = \begin{cases} \sum_{p=i}^n b_{ip}^2 h_{pp} + 2 \sum_{p=1}^{n-1} \sum_{q=p+1}^n b_{ip} b_{iq} h_{pq} & j=i \\ \sum_{p=i}^n b_{ip} \sum_{q=p}^n b_{jq} h_{pq} & j>i \end{cases}$$

Slanger (1979) used this procedure to compute G^{-1} , in the genetic evaluation of beef cattle for weaning weights, by BLUP. He specified the weaning weight of livestock as

$$y_{ijk} = h_i + d_j + m_k + e_{ijk} \quad (2.15)$$

where h_i is the mean for herd-year i ; d_j is the direct additive genetic value of individual j ; and m_k is the maternal additive genetic value for individual k influencing her offspring j 's weaning weight, y_{ijk} . The sum of the maternal and direct environmental errors is given by e_{ijk} . It was assumed that,

$$E \begin{bmatrix} h_i \\ d_j \\ m_k \\ e_{ijk} \end{bmatrix} = \begin{bmatrix} h_i \\ 0 \\ 0 \\ 0 \end{bmatrix}$$

and

$$\text{Var} \begin{bmatrix} d_j \\ m_k \\ e_{ijk} \end{bmatrix} = \begin{bmatrix} \sigma_d^2 & \sigma_{dm} & 0 \\ \sigma_{dm} & \sigma_m^2 & 0 \\ 0 & 0 & \sigma_e^2 \end{bmatrix}.$$

The number of equations to be solved were reduced by predicting the direct or the maternal genetic value for some animals. He imposed the restriction that at least one of the genetic values

would be predicted for each animal. Slanger provided an example using 13 identified individuals. He made predictions on 15 genetic values whereas if all direct and maternal breeding values were included in the pedigree this number would be at least 26. He excluded the direct genetic values of the unidentified dams, the direct genetic values of the identified dams with no individual records and the maternal genetic values of the animals with individual records, but have no offspring. However, except under special circumstances, this procedure does not yield the exact \hat{G}^{-1} . Slanger reported that the exact \hat{G}^{-1} can be generated by this approach if the direct genetic values of the identified dams with no records but having more than one progeny are included. For his particular example, this meant, the addition of two more genetic effects.

Slanger (1980) applied model (2.15) to actual beef cattle weaning weight data by three different approaches which are outlined below:

- (1) predicting both direct and maternal genetic values for each animal in the pedigree ($2n$ genetic values if the number of animals in the pedigree is n);
- (2) the $2n$ genetic values except the direct genetic values of unidentified dams, the direct genetic values of identified dams with no individual records and only one progeny each, and maternal genetic values of animals with individual records but no progeny;
- (3) the direct genetic values of dams with no records and two or more progeny were excluded in addition to the effects mentioned in (2).

Since approach (3) does not generate the correct \hat{G}^{-1} , the predictors obtained are not BLUP [Slanger (1979)]. For his example, the time required for computing was reduced by 37 percent and 43 percent for obtaining solution sets for (2) and (3), respectively. He compared the three sets of solutions by calculating the correlations between the predictors obtained by

the three methods and the average differences in rank. Very high values of correlations and small average differences in rank showed that the solution sets from the three methods are similar. Similar genetic, environmental and phenotypic trends were shown by the three sets of evaluations. This confirmed that genetic progress made from selection decisions based on the 3 sets of solutions would be similar.

Quaas and Pollak (1980) demonstrated how equivalent models can be used to simplify computations involved in mixed model methodology. They applied the equivalent model concept to predict direct and maternal breeding values for weaning weight and direct breeding values for yearling weight of beef cattle. The model

$$\begin{bmatrix} \underline{y}_w \\ \underline{y}_g \end{bmatrix} = \begin{bmatrix} \underline{X}_w & 0 \\ 0 & \underline{X}_g \end{bmatrix} \begin{bmatrix} \underline{\beta}_w \\ \underline{\beta}_g \end{bmatrix} + \begin{bmatrix} \underline{Z}_w & 0 & \underline{Z}_m & \underline{Z}_p \\ 0 & \underline{Z}_g & 0 & 0 \end{bmatrix} \begin{bmatrix} \underline{u}_w \\ \underline{u}_g \\ \underline{u}_m \\ \underline{u}_p \end{bmatrix} + \begin{bmatrix} \underline{e}_w \\ \underline{e}_g \end{bmatrix} \quad (2.16)$$

was assumed for beef cattle performance data, where

- $\underline{y}_w(\underline{y}_g)$ is the vector of weaning weight(gain) records;
- $\underline{\beta}_w(\underline{\beta}_g)$ is the vector of fixed effects affecting $\underline{y}_w(\underline{y}_g)$;
- $\underline{X}_w(\underline{X}_g)$ is the known matrix associated with $\underline{\beta}_w(\underline{\beta}_g)$;
- $\underline{u}_w(\underline{u}_g)$ is the random vector of direct breeding values for weaning weight(gain);
- \underline{u}_m is the random vector of maternal breeding values for weaning weight;
- \underline{u}_p is the random vector of permanent environmental effects on weaning weight;
- $\underline{Z}_w, \underline{Z}_g, \underline{Z}_m$ and \underline{Z}_p are the known matrices associated with $\underline{u}_w, \underline{u}_g, \underline{u}_m$ and \underline{u}_p , respectively; and
- $\underline{e}_w(\underline{e}_g)$ is the vector of random environmental effects peculiar to each weaning weight(gain) record.

If an animal with no record is represented in the \underline{u} vectors, then the corresponding column in the \underline{Z} matrix is considered to be null. This was also the case if a random effect which is not in (2.16) is included in \underline{u} , such as a maternal effect of a sire.

It was assumed that the vectors of random effects of (2.16) have zero means and that the \underline{u} vectors are uncorrelated with \underline{e} . Letting $\underline{u}'_1 = (\underline{u}'_w, \underline{u}'_g, \underline{u}'_m)$ and $\underline{u}_2 = \underline{u}_p$, the variance covariance matrix of $\underline{u}' = (\underline{u}'_1, \underline{u}'_2)$ was assumed to be

$$\text{Var}(\underline{u}) = \begin{bmatrix} \underline{G} & \underline{0} \\ \underline{0} & r_{33}\underline{I} \end{bmatrix}$$

where

$$\underline{G} = \underline{G}_0 * \underline{A}.$$

In above \underline{A} is the numerator relationship matrix, \underline{G}_0 is the 3x3 matrix of genetic variances and covariances. Further, assuming that records on both traits are available on each animal,

$$\text{Var}(\underline{e}) = \underline{R} = \underline{R}_0 * \underline{I}$$

where $\underline{e}' = (\underline{e}'_w, \underline{e}'_g)$ and \underline{R}_0 is the variance-covariance matrix of temporary environmental effects influencing weaning weights and gains. Appropriate rows and columns were deleted from \underline{R} , in the absence of records on some traits of animals.

The mixed model equations that yield the BLUP of the random effects of (2.16) are given by

$$\begin{bmatrix} \underline{X}'\underline{R}^{-1}\underline{X} & \underline{X}'\underline{R}^{-1}\underline{Z}_1 & \underline{X}'\underline{R}^{-1}\underline{Z}_2 \\ \underline{Z}'_1\underline{R}^{-1}\underline{X} & \underline{Z}'_1\underline{R}^{-1}\underline{Z}_1 + \underline{G}^{-1} & \underline{Z}'_1\underline{R}^{-1}\underline{Z}_2 \\ \underline{Z}'_2\underline{R}^{-1}\underline{X} & \underline{Z}'_2\underline{R}^{-1}\underline{Z}_1 & \underline{Z}'_2\underline{R}^{-1}\underline{Z}_2 + r_{33}\underline{I} \end{bmatrix} \begin{bmatrix} \hat{\underline{\beta}} \\ \hat{\underline{u}}_1 \\ \hat{\underline{u}}_2 \end{bmatrix} = \begin{bmatrix} \underline{X}'\underline{R}^{-1}\underline{y} \\ \underline{Z}'_1\underline{R}^{-1}\underline{y} \\ \underline{Z}'_2\underline{R}^{-1}\underline{y} \end{bmatrix} \quad (2.17)$$

where

$$\hat{\underline{\beta}}' = (\hat{\underline{\beta}}'_w , \hat{\underline{\beta}}'_g) ;$$

$$\underline{x} = \begin{bmatrix} \underline{x}_w & \underline{0} \\ \underline{0} & \underline{x}_g \end{bmatrix} ;$$

$$\underline{z}_1 = \begin{bmatrix} \underline{z}_w & \underline{0} & \underline{z}_m \\ \underline{0} & \underline{z}_g & \underline{0} \end{bmatrix} ;$$

$$\underline{z}_2 = \begin{bmatrix} \underline{z}_p \\ \underline{0} \end{bmatrix} ;$$

and

$$r_{33} = 1/r_{33}.$$

The \underline{u} 's, \underline{G} , r_{33} and \underline{R} were defined earlier. The set of equations given in (2.17) is a modification of the equations presented by Henderson and Quaas (1976).

Quaas and Pollak (1980) suggested several approaches for simplifying the computations involved in solving (2.17). The number of nonzero elements in the coefficient matrix were reduced by assuming that certain off-diagonal elements of \underline{G}_0 and \underline{R}_0 are zero. Elimination of some equations by absorption was suggested as a second approach. They noted that absorption of $\hat{\underline{u}}_p$ equations if the data are sorted by the dam reduces the problem by a factor equal to the number of dams. The structure of \underline{A}^{-1} , when the animals are ordered so that parents preceded progeny was also exploited greatly in order to reduce the equations. This particular structure is given by

$$\underline{A}^{-1} = \begin{bmatrix} \underline{A}_{sd}^{-1} + .25\underline{M}'\underline{D}\underline{M} & -.5\underline{M}'\underline{D} \\ -.5\underline{D}\underline{M} & \underline{D} \end{bmatrix}$$

where \underline{A}_{sd}^{-1} is the inverse of the relationship matrix of the sires and the dams, \underline{M} is the matrix relating parents to progeny and \underline{D} is a diagonal matrix. This structure makes it possible to eliminate the equations in (2.17) pertaining to animals with no progeny. Quaas and Pollak reported that solutions for a non-parent can be obtained by solving three equations since they depend only on its own records, the fixed solutions and the solutions of its parents. Quaas and Pollak (1980) presented rules for forming the reduced equations directly, by using the concept of equivalent models.

Consider the models

$$\underline{y} = \underline{X}\underline{\beta} + \underline{Z}_1\underline{u}_1 + \underline{Z}_2\underline{u}_2 + \underline{e}_1 \quad (2.18)$$

with

$$\text{Var} \begin{bmatrix} \underline{u}_1 \\ \underline{u}_2 \\ \underline{e}_1 \end{bmatrix} = \begin{bmatrix} \underline{V}_1 & \underline{0} & \underline{0} \\ \underline{0} & \underline{V}_2 & \underline{0} \\ \underline{0} & \underline{0} & \underline{R}_1 \end{bmatrix}$$

and

$$\underline{y} = \underline{X}\underline{\beta} + \underline{Z}_1\underline{u}_1 + \underline{e}_2 \quad (2.19)$$

with

$$\text{Var} \begin{bmatrix} \underline{u}_1 \\ \underline{e}_2 \end{bmatrix} = \begin{bmatrix} \underline{V}_1 & \underline{0} \\ \underline{0} & \underline{R}_2 \end{bmatrix}$$

where

$$\underline{R}_2 = \underline{Z}_2\underline{V}_2\underline{Z}_2' + \underline{R}_1.$$

The two models are equivalent since the mean vector and the variance-covariance matrix of the observations are given by

$$E(\underline{y}) = \underline{X}\underline{\beta}$$

and

$$\text{Var}(\underline{y}) = \underline{Z}_1\underline{V}_1\underline{Z}_1' + \underline{Z}_2\underline{V}_2\underline{Z}_2' + \underline{R}_1$$

for y in (2.18) and (2.19). The difference between (2.18) and (2.19) is the effects included in the error term. Any random effect can be included in the error term as long as they are not correlated with other random effects of the model. The mixed model equations corresponding to (2.18) and (2.19) are given by

$$\begin{bmatrix} \underline{X}'\underline{R}_1^{-1}\underline{X} & \underline{X}'\underline{R}_1^{-1}\underline{Z}_1 & \underline{X}'\underline{R}_1^{-1}\underline{Z}_2 \\ \underline{Z}_1'\underline{R}_1^{-1}\underline{X} & \underline{Z}_1'\underline{R}_1^{-1}\underline{Z}_1 + \underline{V}_1^{-1} & \underline{Z}_1'\underline{R}_1^{-1}\underline{Z}_2 \\ \underline{Z}_2'\underline{R}_1^{-1}\underline{X} & \underline{Z}_2'\underline{R}_1^{-1}\underline{Z}_1 & \underline{Z}_2'\underline{R}_1^{-1}\underline{Z}_2 + \underline{V}_2^{-1} \end{bmatrix} \begin{bmatrix} \hat{\underline{\beta}} \\ \hat{\underline{u}}_1 \\ \hat{\underline{u}}_2 \end{bmatrix} = \begin{bmatrix} \underline{X}'\underline{R}_1^{-1}\underline{y} \\ \underline{Z}_1'\underline{R}_1^{-1}\underline{y} \\ \underline{Z}_2'\underline{R}_1^{-1}\underline{y} \end{bmatrix} \quad (2.20)$$

and

$$\begin{bmatrix} \underline{X}'\underline{R}_2^{-1}\underline{X} & \underline{X}'\underline{R}_2^{-1}\underline{Z}_1 \\ \underline{Z}_1'\underline{R}_2^{-1}\underline{X} & \underline{Z}_1'\underline{R}_2^{-1}\underline{Z}_1 + \underline{V}_1^{-1} \end{bmatrix} \begin{bmatrix} \tilde{\underline{\beta}} \\ \tilde{\underline{u}}_1 \end{bmatrix} = \begin{bmatrix} \underline{X}'\underline{R}_2^{-1}\underline{y} \\ \underline{Z}_1'\underline{R}_2^{-1}\underline{y} \end{bmatrix}, \quad (2.21)$$

respectively.

In the case of diagonal \underline{R}_1 and \underline{V}_2 , forming (2.20) is not very difficult. However, (2.21) has the advantage that it involves fewer number of equations. Also, noting that

$$\underline{R}_2^{-1} = \underline{R}_1^{-1} - \underline{R}_1^{-1} \underline{Z}_2 (\underline{Z}_2'\underline{R}_1^{-1}\underline{Z}_2 + \underline{V}_2^{-1})^{-1} \underline{Z}_2' \underline{R}_1^{-1},$$

it can be observed that $\hat{\underline{u}}_1$ in (2.20) is equivalent to $\tilde{\underline{u}}_1$ in (2.21) and that estimable functions of $\underline{\beta}$ obtained from (2.20) and (2.21) are equivalent. Therefore if one chooses to solve (2.21) for $\tilde{\underline{\beta}}$ and $\tilde{\underline{u}}_1$, then $\tilde{\underline{u}}_2$ can be obtained as

$$\tilde{\underline{u}}_2 = (\underline{Z}_2'\underline{R}_1^{-1}\underline{Z}_2 + \underline{V}_2^{-1})^{-1} \underline{Z}_2' \underline{R}_1^{-1} (\underline{y} - \underline{X}\tilde{\underline{\beta}} - \underline{Z}_1\tilde{\underline{u}}_1).$$

However, this depends on whether the inverse of $\underline{Z}_2'\underline{R}_1^{-1}\underline{Z}_2 + \underline{V}_2^{-1}$ is obtained easily.

This concept was applied to the performance data of beef cattle, where the weaning weight and the gain of the calf can be

expressed as (from (2.16))

$$y_w^c = \mu_w^c + u_w^c + u_m^d + u_p^d + e_w^c$$

and

$$y_g^c = \mu_g^c + u_g^c + e_g^c$$

where

μ_w^c and μ_g^c are the linear functions of fixed effects affecting y_w^c and y_g^c , respectively;
 u_w^c and u_g^c are the calf's direct breeding values;
 u_m^d and u_p^d are the maternal breeding value and the permanent environmental effect of the calf's dam; and
 e_w^c and e_g^c are the environmental effects associated with y_w^c and y_g^c , respectively.

An equivalent model for y_w^c and y_g^c which does not involve u_w^c and u_g^c was obtained by expressing the calf's breeding values in terms of its parents, with the assumption that there was no inbreeding. That is, u_w^c and u_g^c were expressed as

$$u_w^c = (u_w^s + u_w^d)/2 + \phi_w^c$$

and

$$u_g^c = (u_g^s + u_g^d)/2 + \phi_g^c$$

where ϕ_w^c and ϕ_g^c represent Mendelian sampling variables. This was referred to as a gametic model whereas the former was defined as a genotypic model.

By considering records of a dam and her offspring, Quaas and Pollak demonstrated that the gametic model is not always equivalent for records on different animals. Although the gametic model is not equivalent for ancestors and descendants, it is equivalent when records of collateral relatives are considered. Therefore Quaas and Pollak suggested the use of both models where genotypic model and gametic model are to be used on records of animals who become parents and with no progeny, respectively.

This reduces the lengths of \underline{u}_w , \underline{u}_g and \underline{u}_m and consequently the number of columns in the respective \underline{Z} matrices. The columns of \underline{Z}_w (\underline{Z}_g) contain either a single "1" or two "1/2"s depending on whether an animal corresponding to a particular record is a parent or not. The variance-covariance matrix of \underline{u} is of similar form as before except for the fact that the relationship matrix pertains only to parents. The within-animal error variance-covariance matrix depend upon whether the animal is a parent or not. For a parent, this is given by \underline{R}_0 (defined earlier), whereas for a nonparent the error structure becomes

$$\underline{P}_0 = 1/2 \begin{bmatrix} g_{11} & g_{12} \\ g_{12} & g_{22} \end{bmatrix} + \underline{R}_0.$$

Pollak and Quaas (1981) applied (2.16) on a within-herd multiple trait evaluation, based on information on relatives from simulated beef cattle. One of their objectives was to compare the accuracy of estimating breeding values using equivalent or approximate models discussed by Quaas and Pollak (1980). They examined four models where model 1 was a complete representation of the observations. Models 2,3 and 4 were approximate models which were defined in order to reduce computations.

Model 1 was the same as that given in (2.16), except for the fact that \underline{e}_w is replaced by \underline{e}_w^* where

$$\underline{e}_w^* = \underline{e}_w + \underline{e}_m.$$

The vector \underline{e}_m contains the error terms for maternal performance which represent the environmental variation directly affecting the dam's maternal performance. It was assumed that genetic covariance between maternal ability and weaning weight (g_{13}); genetic covariance between maternal ability and yearling gain (g_{23}); and environmental covariance between weaning weight and gain were zero. The mixed model equations have the form given as in (2.17). However this has fewer nonzero elements as a result of assuming that $g_{13}=g_{23}=r_{12}=0$. This means

$$\underline{\underline{X}}' \underline{\underline{R}}^{-1} \underline{\underline{X}} = \begin{bmatrix} r^{11} \underline{\underline{X}}_w' \underline{\underline{X}}_w & \underline{\underline{0}} \\ \underline{\underline{0}} & r^{22} \underline{\underline{X}}_g' \underline{\underline{X}}_g \end{bmatrix};$$

$$\underline{\underline{X}}' \underline{\underline{R}}^{-1} \underline{\underline{Z}}_1 = \begin{bmatrix} r^{11} \underline{\underline{X}}_w' \underline{\underline{Z}}_w & \underline{\underline{0}} & r^{11} \underline{\underline{X}}_w' \underline{\underline{Z}}_m \\ \underline{\underline{0}} & r^{22} \underline{\underline{X}}_g' \underline{\underline{Z}}_g & \underline{\underline{0}} \end{bmatrix};$$

$$\underline{\underline{X}}' \underline{\underline{R}}^{-1} \underline{\underline{Z}}_2 = \begin{bmatrix} r^{11} \underline{\underline{X}}_w' \underline{\underline{Z}}_p \\ \underline{\underline{0}} \end{bmatrix};$$

$$\underline{\underline{Z}}_1' \underline{\underline{R}}^{-1} \underline{\underline{Z}}_1 = \begin{bmatrix} r^{11} \underline{\underline{Z}}_w' \underline{\underline{Z}}_w + g^{11} \underline{\underline{A}}^{-1} & g^{12} \underline{\underline{A}}^{-1} & r^{11} \underline{\underline{Z}}_w' \underline{\underline{Z}}_m \\ g^{12} \underline{\underline{A}}^{-1} & r^{22} \underline{\underline{Z}}_g' \underline{\underline{Z}}_g + g^{22} \underline{\underline{A}}^{-1} & \underline{\underline{0}} \\ r^{11} \underline{\underline{Z}}_m' \underline{\underline{Z}}_w & \underline{\underline{0}} & r^{11} \underline{\underline{Z}}_m' \underline{\underline{Z}}_m + g^{33} \underline{\underline{A}}^{-1} \end{bmatrix};$$

$$\underline{\underline{Z}}_1' \underline{\underline{R}}^{-1} \underline{\underline{Z}}_2 = \begin{bmatrix} r^{11} \underline{\underline{Z}}_w' \underline{\underline{Z}}_p \\ \underline{\underline{0}} \\ r^{11} \underline{\underline{Z}}_m' \underline{\underline{Z}}_p \end{bmatrix};$$

and

$$\underline{\underline{Z}}_2' \underline{\underline{R}}^{-1} \underline{\underline{Z}}_2 = r^{11} \underline{\underline{Z}}_p' \underline{\underline{Z}}_p + \gamma^{-1} \underline{\underline{I}}$$

where γ is the permanent environmental variance.

Model 1 was simplified by approximating $g^{11} \underline{\underline{A}}^{-1}$ to be $g^{11} \underline{\underline{I}}$ as well as reducing the number of equations by predicting maternal breeding values for the dams only, which led to model 2. This makes $r^{11} \underline{\underline{Z}}_m' \underline{\underline{Z}}_m + g^{33} \underline{\underline{A}}^{-1}$, a diagonal matrix which implies that this can be absorbed with $r^{11} \underline{\underline{Z}}_p' \underline{\underline{Z}}_p + \gamma^{-1} \underline{\underline{I}}$, into the remaining equations. In model 3, $\underline{\underline{e}}_w^*$ contains $\underline{\underline{u}}_m$ and $\underline{\underline{u}}_p$ in addition to $\underline{\underline{e}}_m$ and $\underline{\underline{e}}_w$, as a result of assuming zero covariances among maternal half sibs due to common maternal environment. Model 4 deals with a single trait evaluation of Y_w where Y_w is the sum of weaning weight and

yearling gain.

For Pollak's and Quaas's study where 413 animals were evaluated, the number of equations for the four models were 1376, 1083, 842 and 421, respectively. They found that obtaining solutions to equations resulting in model 1, to be a formidable task. The iterative procedures resulted in slower convergence rates due to the fact that the diagonal elements are not large comparative to the off-diagonal elements as in the case of sire models. They reported that further study of equivalent forms and methods to increase the rates of convergence is necessary before applying the models usefully, in practice. Also, the effect of assuming zero covariances when in fact they exist have to be investigated.

Crow and Howell (1982) regard measuring maternal ability in beef cattle using calf weaning weight, as a complicated task since the expression of maternal ability in calf performance is confounded with the genes for growth, half of which were received from the dam. They estimated the approximate magnitudes of maternal effects from the variation in weaning weight contributed by the maternal grandsire (MGS). The model considered, included fixed herd-year effects and random MGS effects. The estimates of variance components for MGS and error were obtained by using Henderson's method 4 described in Searle (1968).

Crow and Howell (1983) evaluated the maternal ability of beef sires using BLUP technique. The sires were evaluated for their daughter's influence on offspring weaning weight. The maternal grandsire and error variance components were estimated as in Crow and Howell (1982).

2.4.3. Using linear functions of breed means

Dickerson (1973) demonstrated how linear functions of least squares breed means can be used to compute breed transmitted effects, breed maternal effects and heterosis. Gregory, Cundiff, Koch, Laster and Smith (1978), Gregory, Laster, Cundiff, Koch and Smith (1978), Gregory, Koch, Laster, Cundiff and Smith (1978), and Gregory, Crouse, Koch, Laster, Cundiff and Smith (1978) used this method to estimate heterosis and breed maternal and transmitted effects on economic traits of beef cattle (Red Poll, Brown Swiss, Hereford and Angus breeds). Cundiff (1980) reviewed the exploitation of breed differences with alternative breeding systems and experimental approaches to assess breed differences. Here he discussed the experimental evaluation of maternal and paternal performances using breed differences. He also reviewed the results from the Cattle Germ Plasm Evaluation Program at the Roman L.Hruska US Meat Animal Research Center.

Alenda, Martin, Lasley and Ellersieck (1980) developed methods, based on linear functions of breed means to estimate additive genetic effects of each breed, individual and maternal heterosis effects for each two breed combination, and total maternal effects decomposed into maternal and grand maternal effects. Heterosis was defined as the deviation of the two breed crosses from the mean of the parental breeds. It was assumed that

- (1) the population mean is equal to the mean of the purebreds, and deviation from this mean by any breed class is due to genetic or maternal effects;
- (2) the means of the additive, maternal and grand maternal effects are zero.

The data from a diallel structure were used to estimate the additive, total maternal (maternal and grand maternal) and heterosis effects. Additive effect and the total maternal effect of the i th breed are estimated as

$$g_i^I = \frac{1}{n} [(n-1)B_{iii} - \sum_{\substack{j=1 \\ j \neq i}}^n (B_{jjj} + B_{jii} - B_{ijj})]$$

and

$$M_i = g_i^M + g_i^{M'} = \left[\sum_{\substack{j=1 \\ j \neq i}}^n (B_{jii} - B_{ijj}) \right] / 2$$

where n is the number of breeds and B_{ijk} is the least squares mean of the breed class having breed i as the sire, breed j as the maternal grand sire and breed k as the maternal grand dam. The values of g_i^M and $g_i^{M'}$ correspond to maternal and grand maternal effects of the i th breed, respectively. They estimated the individual heterosis effect due to interaction between breed i and breed j as

$$h_{ij}^I = [(B_{ijj} + B_{jii}) - (B_{iii} + B_{jjj})] / 2.$$

The individual heterosis effect can be decomposed into

$$h_{ij}^I = d_{ij}^I + aa_{ij}^I / 2$$

where d_{ij}^I is the sum of dominance effects and aa_{ij}^I is the sum of additive by additive effects. However, additional information is required to obtain estimates of maternal heterosis effects and to decompose the total maternal effects into maternal and grand maternal effects. Allenda et al added information on backcrosses to the diallel in order to estimate maternal heterosis effects. This is given by,

$$h_{ij}^M = \left[(B_{iij} + B_{iji} + B_{jji} + B_{jij}) - (B_{ijj} + B_{jii} + B_{iii} + B_{jjj}) \right] / 4.$$

The backcross information can also be used to estimate the grand maternal effect which subtracted by the total maternal effect would lead to the maternal effect. That is,

$$g_i^{M'} = \left[\sum_{\substack{j=1 \\ j \neq i}}^n (B_{ij} + B_{jji} - B_{iij} - B_{jij}) \right] / 2n$$

and

$$g_i^M = M_i - g_i^{M'}$$

They also suggested alternative estimates for h_{ij}^M and $g_i^{M'}$ if the information from three breed-crosses are available.

2.5. Evidence for the existence of maternal effects

Litter size, which is determined by ovulation rate, fertilization rate and pre-natal survival, is one of the main factors mediating maternal performance. Bradford (1972) reports that ovulation rate and fertilization rate are characteristics of the dam while pre-natal survival which too can be subject to maternal effects is a characteristic of the offspring. He also reports that it is the genotype of the dam rather than that of offspring which is responsible for genetic variation in pre-natal survival.

Bradford (1972) claims that birth weight and post-natal survival are closely related. The environmental effects on birth weight are the effects provided by the environment in-utero from conception to birth. Koch and Clark (1955) report that all pre-natal environmental variation is variation in maternal environment. Maternal environment for gain from birth to weaning is more easily understood than that of birth weight [Koch and Clark (1955)]. The milk supplied by the cow and the differences in the milking ability are the most obvious features of the maternal environment, since milk is the major source of nutrients during the early months of growth in mammals. Characters such as the number of offspring born, the number of offspring reared and the age of dam also affect the weaning weight of offspring, mainly due to milk production of the dam. It is known that, in the case of cattle and some breeds of sheep, the milking ability of the dam

affects the producing ability of the dam, apart from affecting the ability to produce good offspring. The dam's maternal ability, of which a main factor is her milking performance, will also affect her female offspring's lactational ability.

The relationship between birth weight and subsequent growth depends on the primary cause of variation in birth weight. There is no evidence that lower birth weight, which on average results from having large litters, affects growth rate when adequate post-natal nutrition is available. Koch and Clark (1955) report that the yearling gain and the yearling score are not directly influenced by maternal environment, but may be influenced by the carry-over effects from the pre-weaning period which is directly influenced by the maternal environment.

Koch (1972) reports that evidence on the existence and the magnitude of maternal effects comes from experiments which

- (1) measure known components of maternal effects such as milk production, from cows rearing their young;
- (2) from reciprocal crosses or cross-fostering;
- (3) by comparing the observed correlations with theoretical expectations for various kinds of relatives.

Comparison of various kinds of relatives has been commonly used while less attention is given to cross-fostering studies. Cross-fostering is generally used to partition pre-natal maternal influences from post-natal maternal influences. While several studies have indicated the importance of maternal effects for most mammals, only a few studies have reported the relative magnitudes of the direct and maternal genetic effects. Also, limited attention is given to the role of cytoplasmic effects. Most of the experimental work has been involved with mice and other laboratory species. Swine have received more attention than sheep or cattle, due to their large litter size and relatively rapid reproduction rate.

2.5.1. Swine

Dickerson (1947) was the first to include maternal effects in his work on genetic association of hog carcass character traits. His results suggested that a genetic antagonism exists between the suckling ability and economical fattening ability. This was given as the explanation for the slow progress in swine improvement. Using data from crosses among inbred lines, Bradford, Chapman and Grummer (1958) showed the existence of a high negative correlation between direct and maternal genetic effects for weaning weight (-0.4) and 5-month weight (-0.8). The maternal effects were more important than the general combining ability at 56 days of age whereas the opposite was observed at 5 months.

Cox and Willham (1962) carried out cross-fostering experiments to study the feasibility of such experiments and also to examine maternal effects in swine. Pre-natal effects accounted for 6 to 13% of the variance. Post-natal effects were maximum at 42 days representing 26% of the variance, sharply reducing to 5% at 154 days. Garwood, Waltz and Heidenreich (1967) observed a percentage between 4 and 10 for pre-natal effects in 56, 112 and 154 day weights. The post-natal effects accounted for only 0 to 2% of the total variance. Neither pre-natal nor post-natal effects were significant for backfat thickness.

Bereskin, Shelby and Hazel (1971) compared the carcass character data of straightbred Duroc and Yorkshire pigs and the reciprocal crossbred litters. Breed of dam was significant for all carcass traits whereas the breed of sire was significant only for carcass length, suggesting the existence of maternal influence. Ahlschwede and Robison (1971b) used cross-fostering techniques to investigate the relative importance of pre-natal and post-natal effects on growth and development of swine. The pre-natal and post-natal effects were almost similar in magnitude for weekly weights between 2 to 8 weeks. However, for weekly weight changes during first 5 weeks, post-natal effects were considerably larger than pre-natal effects. Contributions from

pre-natal and post-natal effects were approximately 17% and 11% in post-weaning growth and backfat. An antagonism was observed between direct and maternal effects after 4 weeks whereas there was no such indication for the first 3 to 4 weeks.

Ahlschwede and Robison (1971a) estimated the genetic and environmental components of variance for maternal effects by equating observed covariances to their expected compositions in order to assess the importance of maternal influences in Duroc and Yorkshire breeds. Genetic variances for direct and maternal effects were large for birth weight and 140 day weight. However, they obtained negative variance components for maternal effects of 56 day weight of Yorkshire breed and backfat thickness of Duroc breed. The proportion of maternal genetic variance for 140 day weight was approximately 4 times larger than that for 56 day weight. The direct genetic variance was larger than the maternal genetic variance for weaning weight (56 days) whereas the opposite was observed for 140 days. The correlation between direct and maternal effects were negative and large for all traits, exceeding 0.95 in all cases and even 1 in some cases.

Robison (1972), in his review on maternal effects in swine concluded that there is substantial evidence that maternal effects account for a significant portion of variance for most traits including the traits that manifest relatively late in life such as 140 day weight, backfat and litter size.

2.5.2. Cattle

Most of the published work in cattle is on pre-weaning growth traits such as birth weight, daily gain from birth to weaning and weaning weight. Koch (1972) reports that evidence for the existence of maternal effects in cattle comes from cross-breeding experiments where differences among reciprocal crosses are used to estimate maternal effects.

Koch and Clark (1955) concluded that maternal environment from conception to birth and from birth to weaning has a large influence on birth weight, gain from birth to weaning and weaning score whereas the influence on yearling gain and yearling score is small. They also reported a negative genetic correlation between direct and maternal effects on pre-weaning growth traits in beef cattle. Similar results were observed by Deese and Koger (1967). Everett and Magee (1965) obtained small heritabilities for maternal ability of gestation length and birth weight compared to the heritabilities obtained for direct effects. Their results also suggested that the sire influences the birth weight to a greater extent than the dam which conflicts with other results.

Van Vleck and Bradford (1966) investigated the first three lactation milk records of Holstein cows in order to assess the importance of maternal influence. It was indicated that maternal genetic effects are significant and these become smaller in succeeding lactations until the third. The results are in conflict with the results of Van Vleck and Hart (1966), who observed that the additive direct genetic effects are more important for first lactation milk records.

Hohenboken and Brinks (1971a) investigated the genetic and environmental relationships between direct and maternal effects on weaning weights in Hereford cattle. The results indicated that the heritability of maternal effects is slightly higher than that of direct effects. A weak genetic antagonism between direct and maternal effects on weaning weight was detected, which was later confirmed by Hohenboken and Brinks (1971b). Mangus and Brinks (1971), in their study of relationships between direct and maternal effects on growth in Herefords, concluded that weaning weight is a poor indicator of subsequent cow productivity. Higher pre-weaning nutritional levels and high cow inbreeding levels have detrimental effects on beef cow productivity.

Koch (1972) in his review of maternal effects in cattle concluded that genetic and environmental components of direct and maternal effects and covariance between direct and maternal effects accounted for 15-20% of variation in birth weight and 35-45% of variation in daily gain from birth to weaning. He comments that although reciprocal crosses provide evidence that maternal effects exist, they are not helpful for obtaining the magnitudes of the relevant variance components.

Mavrogenis, Dillard and Robison (1978) observed an antagonism between direct and maternal effects, which was apparent at least up to yearling stage. ^{The} investigation of Allenda et al (1980) where they used linear functions of breed means to estimate direct and maternal effects on birth and weaning weights of Angus, Charolais and Hereford cattle, implied that the rearing environment of the mother influences her own maternal ability. Positive maternal and negative grand maternal effects or vice versa were obtained for each breed they studied. Dillard, Rodriguez and Robison (1980) estimated the direct and maternal effects from cross-breeding Angus, Charolais and Hereford cattle. Birth weight, daily gain, weaning weight and a type score were analyzed using two models. Additive direct and maternal genetic effects were shown to be significant sources of variation, with maternal ability of some breeds exceeding others.

Baker (1980) reviewed the role of maternal effects in beef cattle. He concluded that a negative environmental correlation exists between maternal effects in adjacent generations. High levels of feeding during pre-weaning or post-weaning reduce the milk production in daughters. Baker noted that the exclusion of dam-offspring relationships in the estimation of variance components, led to very different estimates of the genetic correlation between direct and maternal effects. An average estimate of -0.42 was obtained for the correlation whereas when the estimates that involved the dam-offspring relationships were excluded the average correlation approached a value towards zero.

2.5.3. Sheep

Bradford (1972) states that maternal effects may be expected to be more important in sheep than in cattle or in swine because of the greater variation in litter size in sheep and the fact that many lambs are partially dependent on their mother's milk supply until the time of marketing or at least until they have achieved a higher proportion of their slaughter weight than in the case of swine and cattle.

Fewer studies have been reported on sheep, although characters such as birth weight and post-natal growth are well documented. Burris and Baugus (1955) studied the effects of milk production of the ewe on post-natal growth of its lamb. More emphasis was given to fat-lamb production. Their studies indicated that early growth and milk production is highly correlated (0.9), the magnitude rapidly decreasing as the lambs grew older. Also the total milk production and growth up to 16 weeks were highly correlated (0.83). The study also implied that post-natal maternal effects on weights are due to variation in milk production. Owen (1957) investigated lactation, effects of lactation and factors affecting it in hill sheep on hill and on lowland. He observed close (but diminishing) relationships between milk yield and growth of young. The relationships between milk yield and fleece weight or milk yield and fleece type were not significant. There was a significant positive correlation between dam's milk production and daughter's fertility at 2 years. However, there is not much information available on the role of maternal effects on reproduction. Ch'ang and Rae (1972) observed that in the Romney breed, maternal environment is positively correlated with the number of hogget oestruses but negatively correlated with the fertility of the ewe.

Gjedrem (1967) investigated the relative importance of pre-natal and post-natal maternal influence on lamb weights from birth to 160 days. The component of variance for pre-natal environment decreased from 100% at birth to 22% at weaning which

also implies that post-natal environmental component increased from 0 to 78%. His results also indicated that the maternal contribution is greater for weights at 2-6 weeks than at birth or 160 days, which is consistent with the studies of Burris and Baugus (1955). Ch'ang and Rae (1972) conducted a series of experiments to study growth and reproductive characters of New Zealand Romney ewes. Their studies indicated that the maternal effect is essentially a reflection of the variation in milk supply during lamb's growth from birth to weaning. A carry-over maternal effect was assumed in the study of post-weaning characters.

Holtmann and Bernard (1969) investigated the growth from birth to weaning, to assess the relative performance of pure-bred and cross-bred ewes. Their study involved Oxford, Suffolk and North Country Cheviot breeds. They obtained evidence for breed differences in maternal performance as well as evidence for the existence of maternal effects. Mothering ability of Suffolk breed was superior than that of the other breeds.

Schinckel and Short (1961) studied the effects of high and low feed intake during pregnancy in ewes and from birth to 4 months of age in lambs on adult body weight and wool production. Lambs of ewes that had a low intake were 34% smaller at birth and 9% smaller at maturity. Wool production too, was affected where the number of follicles per sheep was 15% less, and as adults, the wool production was 8.5% less. Shelton (1964) observed that birth weight has a positive correlation with fibre diameter and clean fleece weight. The study also indicated that an adverse pre-natal or early post-natal environment could permanently damage the potential for wool production. Wiener and Slee (1965) investigated the effect of maternal environment on follicle and fleece development of lamb, using egg transfer from Lincoln to Welsh Mountain breed and vice versa. The study indicated a strong maternal influence and also that the difference in maternal environment due to egg transfer affected follicle density, primary/secondary follicle ratio, fibre medulation, fibre diameter and fibre length. They report that wool production is not

influenced by maternal effects.

2.5.4. Laboratory species

Chapman (1946) used a cross-nursing experiment to study the importance of the variation in the weight response of immature rat ovary to a standard dose of gonadotrophin. The post-natal maternal effects accounted for 6% of the variation whereas the pre-natal effects were negligible. Bateman (1954) in his partitioning of the variance in 12 day weight of mice observed that pre-natal and post-natal factors accounted for 41% and 32% of the total variance. However, the set of data was too small to show that the results were statistically reliable. The results of Cox, Legates and Cockerham (1959) were in contrast to Bateman's (1954) results. The pre-natal and post-natal effects accounted for 9.7% and 71.5% of the total variance of 12 day weight of mice, which implied that post-natal maternal influence is the most important single factor determining the weight through weaning. Young, Legates and Farthing (1965) observed a large post-natal effect from 12-21 days and a decline in pre-natal component from birth to 12 days. The post-natal maternal influences on litter size and 12 day litter weight were negligible. Harvey, Casady, Suitor and Mize (1961) in their assessment of the importance of pre-natal and post-natal effects in rabbits observed that post-natal influences were less than those for mice. A similar study on rats [Blunn (1969)] indicated that post-natal influences were smaller than those for mice. The magnitude was comparable to that of rabbits.

Brumby (1960) carried out an ova transplantation to investigate the importance and nature of maternal influence on growth of large and small strains of mice. They noticed that neither transplantation nor fostering influenced the growth potential of the embryo. There was a marked difference between the maternal environments of large and small strains. Also an interaction between the pre-natal maternal environment of the female and the genotype of the implanted embryo was apparent.

Study of Carman (1963) indicated the existence of maternal effects for weights in mice. He concluded that there is no interaction between maternal effects and mating systems. Kidwell, Weeth, Harvey, Haverland, Shelby and Clark (1960) observed highly significant maternal effects in rats by using a diallel mating of four inbred lines. Legates (1972) in his review of maternal effects on laboratory species concluded that a low positive genetic correlation exists between post-natal maternal performance and direct effects for growth in mice. Legates recommends standardization of litter size commenting that maternal effects attributed to factors not related to size are difficult to detect in the absence of standardization.

Rutledge, Robison, Eisen and Legates (1972) used cross-fostering techniques to investigate the dynamics of direct and maternal genetic effects. The genetic correlation between the direct and maternal effects were small and positive for weights and gains in the absence of fostering effects. For tail length and gain the maternal component was greater than the direct component.

CHAPTER 3. MATHEMATICAL AND STATISTICAL PRELIMINARIES

3.1. Maximum likelihood estimation under the assumption of a normal distribution

Consider the general mixed linear model of the form

$$\underline{y} = \underline{X}\underline{\beta} + \sum_{i=1}^k \underline{Z}_i \underline{u}_i \quad (3.1)$$

where

- \underline{y} is an $n \times 1$ vector of observations;
- $\underline{\beta}$ is a $t \times 1$ vector of unknown fixed effects;
- \underline{X} , of order $n \times t$, is a known matrix;
- \underline{u}_i , of order $c_i \times 1$ ($i=1, \dots, k$) are vectors of non-observable random variables; and
- \underline{Z}_i , of order $n \times c_i$ ($i=1, \dots, k$) are known matrices.

Assuming that,

- (i) $E(\underline{u}_i) = \underline{0}$ for $i=1, \dots, k$;
- (ii) elements of \underline{u}_i are independently distributed with variance θ_i for all i ; and
- (iii) elements of \underline{u}_i and \underline{u}_j are independent for $i \neq j$,

then, from (3.1), the mean and the variance of the vector of observations, \underline{y} , are

$$E(\underline{y}) = \underline{X}\underline{\beta} \quad \text{and} \quad \text{Var}(\underline{y}) = \underline{V} = \sum_{i=1}^k \theta_i \underline{U}_i \quad (3.2)$$

where $\underline{U}_i = \underline{Z}_i \underline{Z}_i'$.

An alternative representation of (3.1) is

$$\underline{y} = \underline{X}\underline{\beta} + \underline{Z}\underline{u}$$

where

$$\underline{u}' = (u_1', \dots, u_1', \dots, u_k')$$

and

$$\underline{Z} = [\underline{z}_1 \mid \underline{z}_2 \mid \dots \mid \underline{z}_k].$$

Hence, the variance-covariance matrix can also be represented as

$$\underline{V} = \underline{Z}\underline{D}\underline{Z}'$$

where

$$\underline{D} = \sum_{i=1}^{k+} \theta_i \underline{I}_i.$$

In the above expression \underline{I}_i is the identity matrix of order c_i and \sum^+ denotes the direct sum of matrices.

Let elements of \underline{y} in general mixed linear model (3.1) have a multivariate normal distribution with parameters specified as in (3.2). Then the likelihood function of \underline{y} can be expressed in terms of $\underline{\beta}$ and θ_i ($i=1, \dots, k$) as [see Hartley and Rao (1967)]

$$L = (2\pi)^{-n/2} |\underline{V}|^{-1/2} \exp\left\{-\frac{1}{2}(\underline{y} - \underline{X}\underline{\beta})' \underline{V}^{-1}(\underline{y} - \underline{X}\underline{\beta})\right\}$$

so that the log likelihood is

$$\lambda = \ln L = \text{const} - \frac{1}{2} \ln |\underline{V}| - \frac{1}{2} (\underline{y} - \underline{X}\underline{\beta})' \underline{V}^{-1} (\underline{y} - \underline{X}\underline{\beta}). \quad (3.3)$$

Solutions to maximum likelihood equations are obtained by maximizing (3.3) with respect to $\underline{\beta}$ and θ_i ($i=1, \dots, k$). The log likelihood function can be differentiated with respect to θ_i , using the Lemmas [see Searle (1979)]

$$\frac{\partial}{\partial \theta_i} [\ln |\underline{V}|] = \text{tr}[\underline{V}^{-1} \underline{v}_i]$$

and

$$\frac{\partial}{\partial \theta_i} [\underline{V}^{-1}] = -\underline{V}^{-1} \underline{v}_i \underline{V}^{-1}$$

where

$$\underline{V}_i = \partial \underline{V} / \partial \theta_i.$$

Partial differentials with respect to $\underline{\beta}$ and θ_i (that is $\partial \lambda / \partial \underline{\beta}$ and $\partial \lambda / \partial \theta_i$) are given by

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

and

$$-\frac{1}{2} \text{tr}(\underline{V}^{-1} \underline{V}_i) + \frac{1}{2} (\underline{y} - \underline{X} \underline{\beta})' \underline{V}^{-1} \underline{V}_i \underline{V}^{-1} (\underline{y} - \underline{X} \underline{\beta}),$$

respectively. Solutions to maximum likelihood equations are obtained by solving $\partial \lambda / \partial \underline{\beta} = 0$ and $\partial \lambda / \partial \theta_i = 0$ for $i=1, \dots, k$, which means solving the following equations simultaneously:

$$\underline{X}' \hat{\underline{V}}^{-1} \hat{\underline{X}} \hat{\underline{\beta}} = \underline{X}' \hat{\underline{V}}^{-1} \underline{y} \quad (3.4)$$

$$\text{tr}(\hat{\underline{V}}^{-1} \hat{\underline{V}}_i) = (\underline{y} - \hat{\underline{X}} \hat{\underline{\beta}})' \hat{\underline{V}}^{-1} \hat{\underline{V}}_i \hat{\underline{V}}^{-1} (\underline{y} - \hat{\underline{X}} \hat{\underline{\beta}}) \quad (3.5)$$

Solving (3.5) is equivalent to maximizing F or minimizing $-F$ with respect to θ_i ($i=1, \dots, k$), where F is given by

$$F = -\ln |\underline{V}| - (\underline{y} - \underline{X} \underline{\beta})' \underline{V}^{-1} (\underline{y} - \underline{X} \underline{\beta}). \quad (3.6)$$

Large-sample variance-covariance matrices of the maximum likelihood estimates of $\underline{\beta}$ and $\underline{\theta}$ are given by [see Searle (1971)]

$$(\underline{X}' \underline{V}^{-1} \underline{X})^{-1} \quad (3.7)$$

and

$$2\underline{A}^{-1}, \quad (3.8)$$

respectively, where the (i,j) th element of \underline{A} is given by

$$\text{tr}\{\underline{V}^{-1}\underline{V}_i\underline{V}^{-1}\underline{V}_j\}$$

and \underline{V}_i and \underline{V}_j are the partial derivatives of \underline{V} with respect to θ_i and θ_j , respectively.

3.2. Computing the inverse of a numerator relationship matrix

Henderson (1973b) demonstrated how to incorporate the relationships among all animals that are to be evaluated, when using best linear unbiased prediction (BLUP). The advantages of using all available information on relatives in BLUP evaluation programmes have been discussed by Henderson (1975c,1975d). Incorporation of all relationships necessitates the computation of the inverse of the numerator relationship matrix amongst the animals, which usually is a prohibitive task if the conventional routines are used. Henderson (1975b,1976) presented a method for computing the inverse of a numerator relationship matrix directly from pedigree information without computing the relationship matrix itself.

Henderson expressed the numerator relationship matrix \underline{A} as

$$\underline{A} = \underline{L}\underline{L}'$$

where \underline{L} is a lower triangular matrix, which can easily be computed recursively. He presented an algorithm to compute \underline{L} , where the upper txt submatrix of \underline{L} is \underline{I} and corresponds to the base population (the animals with unspecified parents define a "base" population and these animals are regarded as non-inbred and unrelated). Henderson (1976) gave another expression for \underline{A} as

$$\underline{A} = \underline{T}\underline{D}^2\underline{T}' \quad (3.9)$$

where \tilde{T} is a matrix computed by exactly the same method as \tilde{L} except that all diagonal elements of \tilde{T} are 1 and \tilde{D} is a diagonal matrix.

Quaas (1976) presented a modification to Henderson's (1975b, 1976) procedure for finding the diagonal elements of L or A without storing the elements of \tilde{L} or \tilde{A} in computer memory. Here, two vectors of length n , where n is the number of animals, are used to accumulate the sums of squares of the elements of each row of \tilde{L} and to store the diagonal elements of \tilde{A} as they are computed. Let the two vectors be \underline{u} and \underline{v} , respectively. The number of iterations required to evaluate \underline{u} and \underline{v} is n . As in the previous cases, the animals are ordered so that parents precede progeny. Let unknown parents be identified by zero.

Steps for the kth iteration

(1)

$$v_k = \ell_{kk} = \begin{cases} [1 - .25(u_p + u_q)]^{1/2} & \text{if } 0 < p < q \\ [1 - .25u_p]^{1/2} & \text{if } p = 0 < q \\ 0 & \text{if } p = q = 0 \end{cases}$$

(2) Compute $v_i = \ell_{ik}$ for $i=k+1, \dots, n$. That is,

$$v_i = \begin{cases} (v_p + v_q)/2 & \text{if } k \leq p < q \\ v_q/2 & \text{if } p < k \leq q \\ 0 & \text{if } p \leq q < k \end{cases}$$

(3) For $i=k, \dots, n$

$$u_i^{(k)} = u_i^{(k-1)} + v_i^2$$

where $u_i^{(k-1)}$ is the value of u_i after iteration $k-1$. The values of v_i and u_i for $i=1, \dots, k-1$ remain unchanged.

(4) To obtain A^{-1} , calculate

$$d = 1/V_k^2 = 1/\ell_{kk}^2$$

- (i) If both parents are known ($0 < p < q$);
store (k, k, d) ; $(p, k, -.5d)$; $(q, k, -.5d)$;
 $(p, p, .25d)$; $(p, q, .25d)$ and $(q, q, .25d)$
- (ii) If one parent is known ($p=0 < q$);
store (k, k, d) ; $(q, k, -.5d)$ and $(q, q, .25d)$
- (iii) If both parents are unknown ($p=q=0$);
store (k, k, d)

Quaas (1975, 1984) presented the theory underlying the calculations given in this section. The vector of breeding values to be predicted is expressed in terms of a matrix, \underline{P} , that relates parents to progeny. That is,

$$\underline{u} = \frac{1}{2} \underline{P} \underline{u} + \underline{\phi} \quad (3.10)$$

where elements of $\underline{\phi}$ are the Mendelian sampling random variables. From (3.10),

$$\underline{u} = (\underline{I} - \frac{1}{2} \underline{P})^{-1} \underline{\phi}$$

which implies that

$$\underline{G} = \text{Var}(\underline{u}) = \sigma_u^2 (\underline{I} - \frac{1}{2} \underline{P})^{-1} \underline{D} (\underline{I} - \frac{1}{2} \underline{P})^{-1}$$

where

$$\sigma_u^2 \underline{D} = \text{Var}(\underline{\phi})$$

Since,

$$\text{Var}(\underline{u}) = \sigma_u^2 \underline{A}$$

it follows that

$$\underline{A} = (\underline{I} - \frac{1}{2}\underline{P})^{-1} \underline{D} (\underline{I} - \frac{1}{2}\underline{P}')^{-1}. \quad (3.11)$$

By comparing (3.9) and (3.11), Quaas noted that \underline{I} in (3.9) is identical to $(\underline{I} - .5\underline{P})^{-1}$ in (3.11) and that \underline{D}^2 in Henderson's (1976) expression is the same as \underline{D} in his expression for \underline{A} . From (3.11), the inverse of the numerator relationship matrix can be obtained as

$$\underline{A}^{-1} = \underline{D}^{-1} - \frac{1}{2}\underline{P}'\underline{D}^{-1} - \frac{1}{2}\underline{D}^{-1}\underline{P}' + \frac{1}{4}\underline{P}'\underline{D}^{-1}\underline{P}.$$

Therefore, \underline{A}^{-1} can be computed by proceeding through a list of animals and adding contributions from each animal. For the i th animal with j and k as parents, the contributions are as follows:

$$d_i^{-1} \text{ to } a^{ii};$$

$$-.5d_i^{-1} \text{ to } a^{ij}, a^{ik}, a^{ji} \text{ and } a^{ki};$$

$$.25d_i^{-1} \text{ to } a^{jj}, a^{kk}, a^{jk} \text{ and } a^{kj}.$$

The d_i 's are the elements of the diagonal matrix \underline{D} and a^{ij} is the (i,j) th element of \underline{A}^{-1} .

The diagonal elements of \underline{A} are required to calculate the d_i 's, since

$$d_i = \begin{cases} 1 - (a_{jj} + a_{kk})/4 & \text{j and k are parents of i} \\ 1 - a_{jj}/4 & \text{j is the only known parent} \\ 0 & \text{both parents are unknown} \end{cases}$$

Quaas proved that, \underline{T} can be written as

$$\underline{T} = (\underline{I} - \frac{1}{2}\underline{P})^{-1} = \underline{I} + \frac{1}{2}\underline{P} + \frac{1}{4}\underline{P}^2 + \dots + (\frac{1}{2}\underline{P})^k$$

where k is the minimum number of segregations separating an ancestor-descendant pair. In the case where only the parent-offspring relationships are considered

$$\underline{T} = \underline{I} + \frac{1}{2}\underline{P}.$$

As a consequence, \underline{T} can be computed recursively and the elements of \underline{T} are obtained as

$$t_{ii} = 1$$

and

$$t_{im} = (t_{jm} + t_{km})/2 \quad \text{j and k are parents of i}$$

Also, since $\underline{A} = \underline{L}\underline{L}'$, the diagonal elements of \underline{A} can be written as

$$a_{ii} = \sum_{p=1}^i \ell_{ip}^2.$$

By using,

$$\underline{L} = \underline{T}\underline{D}^{1/2}$$

the matrix \underline{L} can be computed as

$$\ell_{im} = d_m^{1/2} (t_{jm} + t_{km})/2$$

$$= (e_{jm} + e_{km})/2$$

and

$$e_{ii} = d_i^{1/2}.$$

Therefore two vectors of length equal to the number of animals are sufficient to store the diagonal elements of \underline{L} and to accumulate the sums of squares of each row in \underline{L} which are required for the computation of \underline{A}^{-1} .

3.3. Vec operator and Kronecker product of matrices

The vec operator stacks the columns of a matrix one beneath the other (the (i+1)th beneath the ith) to form a single vector. For an $r \times c$ matrix \underline{X} with \underline{x}_i ($i=1, \dots, c$) being the columns of \underline{X} , $\text{vec}\underline{X}$ is a vector with rc elements, and is given by

$$\text{vec}\underline{X} = \begin{bmatrix} \underline{x}_1 \\ \vdots \\ \underline{x}_c \end{bmatrix}.$$

The Kronecker product of the two matrices, \underline{A} (order $p \times q$) and \underline{B} (order $r \times s$) is the $pr \times qs$ matrix

$$\underline{A} * \underline{B} = \{a_{ij}\underline{B}\}.$$

Henderson and Searle (1979a) in their review, traced the origins of the vec operator and the Kronecker product. More recently, these concepts have been exploited in several applications of statistics, especially in the area of multivariate statistics, by Aitken (1949), Neudecker (1969), Anderson, Quaas and Searle (1977), Anderson (1978), Searle (1978), Anderson (1979), Henderson and Searle (1979b), Anderson, Henderson, Pukelsheim and Searle (1984) and several others. Some useful properties of the vec operator and Kronecker product are given below. When required, the matrices \underline{A} , \underline{B} and \underline{C} are assumed to be conformable for

multiplication.

$$(1) (\underline{A} * \underline{B})(\underline{C} * \underline{D}) = \underline{AC} * \underline{BD}$$

$$(2) (\underline{A} * \underline{B})' = \underline{A}' * \underline{B}'$$

$$(3) (\underline{A} * \underline{B})^{-1} = \underline{A}^{-1} * \underline{B}^{-1}$$

$$(4) (\underline{A} + \underline{B}) * (\underline{C} + \underline{D}) = (\underline{A} * \underline{C}) + (\underline{B} * \underline{C}) + (\underline{A} * \underline{D}) + (\underline{B} * \underline{D})$$

$$(5) \text{tr}(\underline{A} * \underline{B}) = (\text{tr}\underline{A})(\text{tr}\underline{B})$$

(6) If \underline{A} and \underline{B} are square matrices of order a and b respectively,

$$|\underline{A} * \underline{B}| = |\underline{A}|^b |\underline{B}|^a$$

$$(7) \text{tr}(\underline{AB}) = (\text{vec}\underline{A}')' \text{vec}\underline{B}$$

$$(8) \text{vec}(\underline{ABC}) = (\underline{C}' * \underline{A}) \text{vec}\underline{B}$$

$$\text{vec}(\underline{AB}) = (\underline{I} * \underline{A}) \text{vec}\underline{B} \quad (\text{a special case})$$

Results (1) - (7) are given in Neudecker (1969). The result in (8) was first derived by Roth (1934) and rediscovered by Aitken (1949) and Neudecker (1969).

3.4. Inverse and determinant of a partitioned matrix

It is possible to express the inverse and the determinant of a partitioned matrix which is non-singular, in terms of its submatrices. Consider the matrix,

$$\underline{A} = \begin{bmatrix} \underline{A}_{11} & \underline{A}_{12} \\ \underline{A}_{21} & \underline{A}_{22} \end{bmatrix}$$

where A_{11} and A_{22} are both square and non-singular. Then the inverse of A is given as [see Morrison (1976)],

$$A^{-1} = \begin{bmatrix} B_{11} & B_{12} \\ B_{21} & B_{22} \end{bmatrix} \quad (3.12)$$

where

$$B_{11} = (A_{11} - A_{12}A_{22}^{-1}A_{21})^{-1}$$

$$B_{12} = -B_{11}A_{12}A_{22}^{-1}$$

$$B_{21} = -A_{22}^{-1}A_{21}B_{11}$$

and

$$B_{22} = A_{22}^{-1} + A_{22}^{-1}A_{21}B_{11}A_{12}A_{22}^{-1}.$$

An alternative expression can be obtained by reversing the positions of A_{11} and A_{22} in the original matrix.

The determinant of A can be computed as [see Morrison (1976)]

$$|A| = |A_{11}| |A_{22} - A_{21}A_{11}^{-1}A_{12}| \text{ if } A_{11} \text{ is non-singular}$$

or

$$|A| = |A_{22}| |A_{11} - A_{12}A_{22}^{-1}A_{21}| \text{ if } A_{22} \text{ is non-singular.} \quad (3.13)$$

Now consider the matrix, V , where V is partitioned into 3^2 submatrices. That is,

$$\underline{V} = \begin{bmatrix} \underline{V}_{11} & \underline{V}_{12} & \underline{V}_{13} \\ \underline{V}_{21} & \underline{V}_{22} & \underline{V}_{23} \\ \underline{V}_{31} & \underline{V}_{32} & \underline{V}_{33} \end{bmatrix}.$$

Suppose that the submatrices at position (2,3) and (3,2) are zero, which is the case in the variance-covariance matrix of the observations for the particular design used in this thesis for estimating fixed effects and variance components in maternal effects models. Then the above matrix is given by

$$\underline{V} = \begin{bmatrix} \underline{V}_{11} & \underline{V}_{12} & \underline{V}_{13} \\ \underline{V}_{21} & \underline{V}_{22} & \underline{0} \\ \underline{V}_{31} & \underline{0} & \underline{V}_{33} \end{bmatrix}. \quad (3.14)$$

Assume that \underline{V}_{11} , \underline{V}_{22} and \underline{V}_{33} are non-singular and let

$$\underline{V}_{11} = \underline{A}_{11}$$

$$[\underline{V}_{12} \quad \underline{V}_{13}] = \underline{A}_{12}$$

$$\begin{bmatrix} \underline{V}_{21} \\ \underline{V}_{31} \end{bmatrix} = \underline{A}_{21}$$

and

$$\begin{bmatrix} \underline{V}_{22} & \underline{0} \\ \underline{0} & \underline{V}_{33} \end{bmatrix} = \underline{A}_{22}.$$

Then, the inverse of the matrix \underline{V} in (3.14) can be easily obtained by using (3.12). This is given by

$$\underline{v}^{-1} = \begin{bmatrix} \underline{u}_{11} & \underline{u}_{12} & \underline{u}_{13} \\ \underline{u}_{21} & \underline{u}_{22} & \underline{u}_{23} \\ \underline{u}_{31} & \underline{u}_{32} & \underline{u}_{33} \end{bmatrix} \quad (3.15)$$

where

$$\underline{u}_{11} = (\underline{v}_{11} - \underline{v}_{12}\underline{v}_{22}^{-1}\underline{v}_{21} - \underline{v}_{13}\underline{v}_{33}^{-1}\underline{v}_{31})^{-1}$$

$$\underline{u}_{12} = -\underline{u}_{11}\underline{v}_{12}\underline{v}_{22}^{-1}$$

$$\underline{u}_{13} = -\underline{u}_{11}\underline{v}_{13}\underline{v}_{33}^{-1}$$

$$\underline{u}_{21} = -\underline{v}_{22}^{-1}\underline{v}_{21}\underline{u}_{11}$$

$$\underline{u}_{22} = \underline{v}_{22}^{-1} + \underline{v}_{22}^{-1}\underline{v}_{21}\underline{u}_{11}\underline{v}_{12}\underline{v}_{22}^{-1}$$

$$\underline{u}_{23} = \underline{v}_{22}^{-1}\underline{v}_{21}\underline{u}_{11}\underline{v}_{13}\underline{v}_{33}^{-1}$$

$$\underline{u}_{31} = -\underline{v}_{33}^{-1}\underline{v}_{31}\underline{u}_{11}$$

$$\underline{u}_{32} = \underline{v}_{33}^{-1}\underline{v}_{31}\underline{u}_{11}\underline{v}_{12}\underline{v}_{22}^{-1}$$

and

$$\underline{u}_{33} = \underline{v}_{33}^{-1} + \underline{v}_{33}^{-1}\underline{v}_{31}\underline{u}_{11}\underline{v}_{13}\underline{v}_{33}^{-1}.$$

Assuming \underline{v}_{22} and \underline{v}_{33} are non-singular and by using (3.13), the determinant of the matrix given in (3.14) can be obtained as

$$|\underline{v}| = |\underline{v}_{22}| |\underline{v}_{33}| |\underline{v}_{11} - \underline{v}_{12}\underline{v}_{22}^{-1}\underline{v}_{21} - \underline{v}_{13}\underline{v}_{33}^{-1}\underline{v}_{31}|. \quad (3.16)$$

CHAPTER 4. MAXIMUM LIKELIHOOD METHOD FOR ESTIMATING VARIANCE COMPONENTS WITH UNBALANCED DATA IN A MATERNAL EFFECTS MODEL

For the case of balanced data, Thompson (1976a) used a maximum likelihood approach based on the multivariate analysis of variance to estimate maternal genetic variances when observations are available on parents and offspring. Thompson (1977) modified this procedure to estimate heritability when data are unbalanced and suggested it could be applied to estimate variance parameters when maternal effects are included in the model. Following Patterson and Thompson (1971), he maximized the log likelihood function of certain symmetric sums of squares and product matrices, which led to the restricted maximum likelihood estimates of variance components. In this thesis, the log likelihood function of the observations is maximized over the entire sample space in order to obtain estimates of the variance components and the fixed effects in a maternal effects model, simultaneously.

4.1. A maternal effects model

Suppose that the measurement on a trait of individual i , which is influenced by the maternal effects of i 's dam, w , can be expressed as

$$y_i = f_i(\underline{\beta}) + g_{di} + g_{mw} + e_{mw} + e_{di} \quad (4.1)$$

where

$f_i(\underline{\beta})$ is a linear function of the unknown fixed effects;

g_{di} is the direct additively genetic effect of i ;

g_{mw} is the maternal additively genetic effect of w , influencing i 's phenotypic value;

e_{mw} represents the residual effect common to the offspring of w ; and

e_{di} represents the residual effect unique to the individual i .

Assuming that the genetic effects are independent of the residual effects and that the two residual effects are independent of each other, the covariance between phenotypic values of two related individuals i and i' , whose dams are w and w' , respectively, can be expressed as

$$a_{ii'}\sigma_{AO}^2 + (a_{iw'} + a_{i'w})\sigma_{AOAm} + a_{ww'}\sigma_{Am}^2 + b_{ww'}\sigma_{Em}^2 + b_{ii'}\sigma_{EO}^2 \quad (4.2)$$

where

σ_{AO}^2 is the direct additively genetic variance;
 σ_{Am}^2 is the maternal additively genetic variance;
 σ_{AOAm} is the covariance between direct additively genetic and maternal additively genetic effects;
 σ_{Em}^2 is the variance of the residual effects common to full-sibs and maternal half-sibs;
 σ_{EO}^2 is the variance of those residual effects which are unique to the individuals;
 $a_{ii'}$ is the coefficient of additive relationship between i and i' ; and

$$b_{ii'}, (b_{ww'}) = \begin{cases} 1 & \text{if } i=i' \text{ (} w=w') \\ 0 & \text{if } i \neq i' \text{ (} w \neq w'). \end{cases}$$

In matrix terminology, the model can be written as

$$\underline{y} = \underline{X}\underline{\beta} + \sum_{i=1}^4 \underline{Z}_i \underline{u}_i \quad (4.3)$$

where

$\underline{\beta}$ is the vector of unknown fixed effects;
 \underline{u}_1 is the vector of direct additively genetic effects;
 \underline{u}_2 is the vector of maternal additively genetic effects;
 \underline{u}_3 is the vector of residual effects common to full-sibs and maternal half-sibs;
 \underline{u}_4 is the vector of residual effects unique to the individuals; and
 \underline{X} and \underline{Z}_i ($i=1, \dots, 4$) are known matrices.

The mean vector and the variance-covariance matrix of \underline{y} are given by

$$E(\underline{y}) = \underline{X}\underline{\beta} \quad \text{and} \quad \underline{V} = \sum_{i=1}^5 \theta_i \underline{U}_i \quad (4.4)$$

respectively, where θ_i and \underline{U}_i for $i=1, \dots, 5$ are given in Table 4.1.

Table 4.1 - Expressions
for θ_i and \underline{U}_i in (4.4)

i	θ_i	\underline{U}_i
1	σ_{AO}^2	$\underline{Z}_1 \underline{Z}_1'$
2	σ_{Am}^2	$\underline{Z}_2 \underline{Z}_2'$
3	σ_{AOAm}	$\underline{Z}_1 \underline{Z}_2'$
4	σ_{Em}^2	$\underline{Z}_3 \underline{Z}_3'$
5	σ_{EO}^2	$\underline{Z}_4 \underline{Z}_4'$

4.2. Estimation of the parameters: A single-trait setting

The hierarchical mating design used by Hill and Nicholas (1974) and Thompson (1976a, 1976b, 1977) will be considered initially. In this design, each of a set of sires is mated to several dams and a number of offspring raised from each mating. Suppose s , n_i and n_{ij} are the number of sires, the number of dams mated to the i th sire and the number of offspring of the j th dam mated to the i th sire, respectively. Assume that

- (1) observations are available on all animals;
- (2) the phenotypic variance of an observation is σ_p^2 , irrespective of the generation;
- (3) the families are independent of each other, where the i th family consists of the i th sire, the dams mated to the i th sire and the progeny of the i th sire; and

(4) the sires and the dams within a family are unrelated.

This design generates four relationships, namely; full-sibs, paternal half-sibs, dam-offspring and sire-offspring. This means that the variance-covariance matrix of the observations consists of five distinct elements, namely; the phenotypic variance and the covariances arising amongst the above relationships. Let γ_h ($h=1, \dots, 5$) be the phenotypic variance, the covariance between full-sibs, the covariance between paternal half-sibs, the covariance between dam and offspring and the covariance between sire and offspring, respectively. Then from the expression given in (4.2), it is clear that γ_h ($h=1, \dots, 5$) can be written as

$$\gamma_h = \sum_{m=1}^5 f_{hm} \theta_m \quad (4.5)$$

where the values of f_{hm} are given in Table 4.2.

Table 4.2 - Coefficients (f_{hm}) associated with the variance parameters (θ_m) in the phenotypic variance and the full-sib, paternal half-sib, dam-offspring and sire-offspring covariances

$h \backslash m$	1	2	3	4	5
1	1	1	1	1	1
2	1/2	1	1	1	0
3	1/4	0	0	0	0
4	1/2	1/2	5/4	0	0
5	1/2	0	1/4	0	0

Therefore the expression (4.5) shows that the relationships generated by this mating plan provide sufficient information to estimate the variance components of the model.

4.2.1. The likelihood function under normality assumptions

Suppose that the observations are ordered within the sires, so that the vector of observations can be written as

$$\underline{y}' = (y_1', \dots, y_i', \dots, y_s')$$

where y_i is the vector of observations of the i th family. The coefficient matrix corresponding to the fixed effects can also be partitioned according to the families. That is

$$\underline{X}' = [\underline{X}_1' | \dots | \underline{X}_i' | \dots | \underline{X}_s']$$

where \underline{X}_i corresponds to the i th family.

Now assume that y in (4.3) is normally distributed with parameters specified as in (4.4). Then the log likelihood of y (say λ), can be written as

$$\lambda = \text{const} - \frac{1}{2} \ln |\underline{V}| - \frac{1}{2} (\underline{y} - \underline{X}\underline{\beta})' \underline{V}^{-1} (\underline{y} - \underline{X}\underline{\beta}).$$

Since the families are independent, $\text{Cov}(y_i, y_j)$ is null for $i \neq j$.
Therefore

$$\underline{V} = \sum_{i=1}^s \underline{V}_i$$

where \underline{V}_i is the variance-covariance matrix of the observations of the i th family and \sum^+ denotes the direct sum of matrices. Then \underline{V}^{-1} and $|\underline{V}|$ can be written as

$$\underline{V}^{-1} = \sum_{i=1}^s \underline{V}_i^{-1}$$

and

$$|\underline{V}| = \prod_{i=1}^s |\underline{V}_i|$$

which means that λ can be rewritten as

$$\lambda = -\frac{1}{2} \sum_{i=1}^s \ln |\underline{V}_i| - \frac{1}{2} \sum_{i=1}^s (\underline{y}_i - \underline{X}_i \underline{\beta})' \underline{V}_i^{-1} (\underline{y}_i - \underline{X}_i \underline{\beta}). \quad (4.6)$$

Equations for obtaining ML solutions for the fixed effects and ML estimators of variance components are generated by differentiating (4.6) with respect to $\underline{\beta}$ and $\underline{\theta}$. These equations are given by

$$\frac{\partial \lambda}{\partial \underline{\beta}} = \sum_{i=1}^s \underline{X}_i' \underline{V}_i^{-1} (\underline{y}_i - \underline{X}_i \underline{\beta})$$

and

$$\frac{\partial \lambda}{\partial \theta_m} = -\frac{1}{2} \sum_{i=1}^s \text{tr}(\underline{V}_i^{-1} \underline{V}_{im}) + \frac{1}{2} \sum_{i=1}^s (\underline{y}_i - \underline{X}_i \underline{\beta})' \underline{V}_i^{-1} \underline{V}_{im} \underline{V}_i^{-1} (\underline{y}_i - \underline{X}_i \underline{\beta})$$

where

$$\underline{V}_{im} = \frac{\partial \underline{V}_i}{\partial \theta_m}.$$

Then $\hat{\beta}$ and $\hat{\theta}_m$ ($m=1, \dots, 5$) can be obtained by solving, simultaneously, the equations

$$\sum_{i=1}^s \underline{x}_i' \hat{V}_i^{-1} (\underline{y}_i - \underline{x}_i \hat{\beta}) = \underline{0} \quad (4.7)$$

and

$$\sum_{i=1}^s \text{tr}(\hat{V}_i^{-1} \hat{V}_{im}) - \sum_{i=1}^s (\underline{y}_i - \underline{x}_i \hat{\beta})' \hat{V}_i^{-1} \hat{V}_{im} \hat{V}_i^{-1} (\underline{y}_i - \underline{x}_i \hat{\beta}) = 0, \quad (4.8)$$

for $m=1, \dots, 5$.

4.2.2. The structure of the variance-covariance matrix

Let the vector of observations of the i th family be written as

$$\underline{y}_i' = (\underline{y}_{oi}', \underline{y}_{di}', y_{si}) \quad (4.9)$$

where \underline{y}_{oi}' , \underline{y}_{di}' and y_{si} represent the vector of observations of the progeny of the i th sire, the vector of observations of the dams mated to the i th sire and the observation of the i th sire, respectively. Let

$$\underline{y}_{oi}' = (y_{oi1}', \dots, y_{oij}', \dots, y_{oin_i}') \quad (4.10)$$

and

$$\underline{y}_{di}' = (y_{di1}', \dots, y_{dij}', \dots, y_{din_i}') \quad (4.11)$$

where \underline{y}_{oij} is the $n_{ij} \times 1$ vector of observations of the offspring of the j th dam mated to the i th sire and y_{dij} is the observation of the j th dam mated to the i th sire. The vector \underline{y}_{oij} is given by

$$\underline{y}_{oij} = (y_{oij1}, \dots, y_{oijk}, \dots, y_{oijn_{ij}}) \quad (4.12)$$

where y_{oijk} is the observation of the k th offspring of the j th dam mated to the i th sire. From (4.9),

$$\underline{V}_i = \begin{bmatrix} \underline{V}_{i11} & \underline{V}_{i12} & \underline{V}_{i13} \\ \underline{V}'_{i12} & \underline{V}_{i22} & \underline{V}_{i23} \\ \underline{V}'_{i13} & \underline{V}'_{i23} & \underline{V}_{i33} \end{bmatrix}$$

where

$$\underline{V}_{i11} = \text{Var}(y_{oi})$$

$$\underline{V}_{i12} = \text{Cov}(y_{oi}, y'_{di})$$

$$\underline{V}_{i13} = \text{Cov}(y_{oi}, y_{si})$$

$$\underline{V}_{i22} = \text{Var}(y_{di})$$

$$\underline{V}_{i23} = \text{Cov}(y_{di}, y_{si})$$

and

$$\underline{V}_{i33} = \text{Var}(y_{si}).$$

From (4.10) it is clear that, \underline{V}_{i11} can be partitioned into n_i^2 block matrices. It can also be observed that the j th diagonal block and the (j,k) th off-diagonal block of \underline{V}_{i11} can be expressed as

$$\text{Var}(y_{oij}) = (\gamma_1 - \gamma_2) \underline{I}_{ijj} + \gamma_2 \underline{J}_{ijj}$$

and

$$\text{Cov}(y_{oij}, y'_{oik}) = \gamma_3 \underline{J}_{ijk}$$

where \underline{I}_{ijj} is the identity matrix of order n_{ij} and \underline{J}_{ijk} is the $n_{ij} \times n_{ik}$ matrix of "1"s. The γ 's were defined earlier. Hence \underline{V}_{i11} has the following form:

$$\begin{bmatrix} (\gamma_1 - \gamma_2) \underline{I}_{i11} + \gamma_2 \underline{J}_{i11} & \gamma_3 \underline{J}_{i12} & \gamma_3 \underline{J}_{in_1 1} \\ \gamma_3 \underline{J}_{i21} & (\gamma_1 - \gamma_2) \underline{I}_{i22} + \gamma_2 \underline{J}_{i22} & \gamma_3 \underline{J}_{in_1 2} \\ \vdots & \vdots & \vdots \\ \gamma_3 \underline{J}_{in_1 1} & \gamma_3 \underline{J}_{in_1 2} & (\gamma_1 - \gamma_2) \underline{I}_{in_1 n_1} + \gamma_2 \underline{J}_{in_1 n_1} \end{bmatrix} \quad (4.13)$$

From (4.10) and (4.11) note that

$$\underline{V}_{i12} = \begin{bmatrix} \text{Cov}(y_{oi1}, y'_{di}) \\ \text{Cov}(y_{oi2}, y'_{di}) \\ \vdots \\ \text{Cov}(y_{oin_i}, y'_{di}) \end{bmatrix}.$$

Now $\text{Cov}(y_{oij}, y'_{di})$ has γ_4 in the j th column with all other elements zero. Therefore,

$$\underline{V}_{i12} = \gamma_4 \sum_{j=1}^{n_i} \underline{1}_{ij} \quad (4.14)$$

where $\underline{1}_{ij}$ is the vector of n_{ij} "1"s. Since y_{oi} is the vector of observations of the offspring of the i th sire

$$\underline{V}_{i13} = \gamma_5 \underline{1}_{i0} \quad (4.15)$$

where $\underline{1}_{i0}$ is the $n_{i0} \times 1$ vector of "1"s and

$$n_{i0} = \sum_{j=1}^{n_i} n_{ij}.$$

It was assumed that the sires and the dams within a family are unrelated. Therefore,

$$\underline{V}_{i22} = \gamma_1 \underline{I}_i \quad (4.16)$$

and

$$\underline{V}_{i23} = \underline{0}_i \quad (4.17)$$

where \underline{I}_i is the identity matrix of order n_i and $\underline{0}_i$ is the $n_i \times 1$ null vector. Finally,

$$\underline{V}_{i33} = \gamma_1 \quad (4.18)$$

and

$$V_{ikj} = V_{ijk} \quad \text{for } j=1,2 \text{ and } k=2,3. \quad (4.19)$$

4.2.3. The inverse of the variance-covariance matrix

Estimating variance components using ML method with unbalanced data can be computationally difficult. Thompson (1976a) comments:

"The ML method is probably most useful when the data are balanced. When the data are unbalanced, full ML methods can be computationally unfeasible."

One of the main difficulties is obtaining the inverse of the variance-covariance matrix of the observations which is involved in the likelihood function and its derivatives. In the previous section, expressions for the variance-covariance matrices of the observations of the families were derived under the assumption that the sires and the dams are unrelated. Also, the observations within the families were arranged in such a way that the variance-covariance matrix became highly structured. In this section, this particular structure is exploited in order to obtain explicit expressions for the elements of the inverse of the variance-covariance matrix of the observations. This means that iterative routines are not required to generate the inverse of the variance-covariance matrix. This saves considerable computing time and cost.

The matrix V_i has similar form as that of (3.14). Therefore, from (3.15)

$$V_i^{-1} = \begin{bmatrix} A_{111} & A_{112} & A_{113} \\ A_{112} & A_{122} & A_{123} \\ A_{113} & A_{123} & A_{133} \end{bmatrix} \quad (4.20)$$

where

$$A_{i11} = (V_{i11} - V_{i12}V_{i22}^{-1}V_{i12} - V_{i13}V_{i33}^{-1}V_{i13})^{-1}$$

$$A_{i12} = -A_{i11}V_{i12}V_{i22}^{-1}$$

$$A_{i13} = -A_{i11}V_{i13}V_{i33}^{-1}$$

$$A_{i22} = V_{i22}^{-1} - V_{i22}^{-1}V_{i12}A_{i12}$$

$$A_{i23} = -V_{i22}^{-1}V_{i12}A_{i13}$$

and

$$A_{i33} = V_{i33}^{-1} - V_{i33}^{-1}V_{i13}A_{i13}$$

But

$$\begin{aligned} V_{i12}V_{i22}^{-1}V_{i12} &= [\gamma_4 \sum_{j=1}^{n_i+} 1_{ij}] [\gamma_1^{-1} I_i] [\gamma_4 \sum_{j=1}^{n_i+} 1_{ij}] \\ &= \gamma_6 \sum_{j=1}^{n_i+} J_{ijj} \end{aligned}$$

and

$$\begin{aligned} V_{i13}V_{i33}^{-1}V_{i13} &= \gamma_5 1_{i0} \gamma_1^{-1} \gamma_5 1_{i0} \\ &= \gamma_7 J_{i0} \end{aligned}$$

where

$$\gamma_6 = \gamma_4^2 / \gamma_1$$

and

$$\gamma_7 = \gamma_5^2 / \gamma_1.$$

Therefore $V_{i11} - V_{i12}V_{i22}^{-1}V_{i12} - V_{i13}V_{i33}^{-1}V_{i13}$ can be written in the form

$$\begin{bmatrix} a_{i11} + b_{i11} & c_{i12} & \dots & c_{i1n_i} \\ c_{i21} & a_{i22} + b_{i22} & \dots & c_{i2n_i} \\ \vdots & \vdots & \ddots & \vdots \\ c_{in_i1} & c_{in_i2} & \dots & a_{in_i n_i} + b_{in_i n_i} \end{bmatrix} \quad (4.21)$$

where

$$a = \gamma_1 - \gamma_2$$

$$b = \gamma_2 - \gamma_6 - \gamma_7$$

and

$$c = \gamma_3 - \gamma_7.$$

The only inverses required to obtain the submatrices of \underline{V}_i^{-1} (that is, \underline{A}_{ijk} for $j=1,2,3$ and $k=j,3$) are the inverses of \underline{V}_{i22} , \underline{V}_{i33} and $\underline{V}_{i11} - \underline{V}_{i12}\underline{V}_{i22}^{-1}\underline{V}_{i12} - \underline{V}_{i13}\underline{V}_{i33}^{-1}\underline{V}_{i13}$. However, \underline{V}_{i33} is a scalar and \underline{V}_{i22} is given by $\gamma_1 \underline{I}_i$. Therefore, obtaining the inverse of $\underline{V}_{i11} - \underline{V}_{i12}\underline{V}_{i22}^{-1}\underline{V}_{i12} - \underline{V}_{i13}\underline{V}_{i33}^{-1}\underline{V}_{i13}$ (that is \underline{A}_{i11}) is the only computational difficulty. As seen in (4.21), this matrix is highly structured. Therefore explicit expressions for the elements of \underline{A}_{i11} can be obtained by following the procedure given in Appendix 1.

As shown in Appendix 1, \underline{A}_{i11} has the form

$$\begin{bmatrix} \underline{B}_{i11} & \cdots & \underline{B}_{i1j} & \cdots & \underline{B}_{i1k} & \cdots & \underline{B}_{i1n_i} \\ & & \cdots & & & & \\ \underline{B}_{ij1} & \cdots & \underline{B}_{ijj} & \cdots & \underline{B}_{ijk} & \cdots & \underline{B}_{ijn_i} \\ & & \cdots & & & & \\ \underline{B}_{in_i 1} & \cdots & \underline{B}_{in_i j} & \cdots & \underline{B}_{in_i k} & \cdots & \underline{B}_{in_i n_i} \end{bmatrix} \quad (4.22)$$

where

$$\underline{B}_{ijk} = \begin{cases} q_{ikj} \underline{J}_{ijk} & \text{if } k < j \\ p \underline{I}_{ijj} + q_{ijj} \underline{J}_{ijj} & \text{if } k = j \\ q_{ijk} \underline{J}_{ijk} & \text{if } k > j. \end{cases}$$

The values of p and q_{ijk} ($i=1, \dots, s$; $j=1, \dots, n_i$; $k=j, \dots, n_i$) can be computed using the algorithm given in Appendix 1. Once \underline{A}_{i11} is generated, obtaining the other submatrices of \underline{V}_i^{-1} involves matrix multiplication only. Using (4.20) it can be shown that

- (1) A_{i12} is an $n_{i0} \times n_{i0}$ matrix which can be partitioned into n_i^2 block vectors and the (j,k) th vector is given by

$$(j,k)\text{th vector} = \begin{cases} -\gamma_8 n_{ik} q_{ikj} \underline{1}_{ij} & \text{if } k < j \\ -\gamma_8 (p + n_{ij} q_{ijj}) \underline{1}_{ij} & \text{if } k = j \\ -\gamma_8 n_{ik} q_{ijk} \underline{1}_{ij} & \text{if } k > j \end{cases}$$

where $\gamma_8 = \gamma_4 / \gamma_1$.

- (2) A_{i13} is an $n_{i0} \times 1$ vector which can be partitioned into n_i column vectors and the j th vector is given by

$$-\gamma_9 (p + r_{ij}) \underline{1}_{ij}$$

where

$$\gamma_9 = \gamma_5 / \gamma_1$$

and

$$r_{ij} = \sum_{k=1}^{j-1} n_{ik} q_{ikj} + \sum_{k=j}^{n_i} n_{ik} q_{ijk}.$$

- (3) A_{i22} is an $n_i \times n_i$ matrix and the (j,k) th element is given by

$$(j,k)\text{th element} = \begin{cases} \gamma_8^2 n_{ij} n_{ik} q_{ikj} & \text{if } k < j \\ \gamma_1^{-1} + \gamma_8^2 n_{ij} (p + n_{ij} q_{ijj}) & \text{if } k = j \\ \gamma_8^2 n_{ij} n_{ik} q_{ijk} & \text{if } k > j. \end{cases}$$

- (5) A_{i23} is an $n_i \times 1$ vector and the j th element is given by

$$\gamma_8 \gamma_9 n_{ij} (p + r_{ij}).$$

- (6) A_{i33} is a scalar and is given by

$$\gamma_1^{-1} + \gamma_9^2 [p n_{i0} + \sum_{j=1}^{n_i} n_{ij} r_{ij}].$$

4.2.4. The determinant of the variance-covariance matrix

The equations given in (4.7) and (4.8) can be solved alternately until the solutions converge to obtain ML solutions for fixed effects and ML estimates of variance components. This procedure does not guarantee non-negative variances nor a genetic correlation between -1 and $+1$, as no constraints were imposed on the solutions. Another procedure is to maximize the log likelihood function subject to constraints using a constrained optimization routine, substituting the solutions to (4.7) as the values for the fixed effects. That is, solving (4.7) and maximizing the log likelihood function subject to constraints is carried out alternately, until convergence occurs. The log likelihood function involves the determinant of the variance-covariance matrix, in addition to the inverse. Therefore, once again, the special structure of the variance-covariance matrix is exploited in order to find the determinant. The derivation of this determinant is outlined in Appendix 2.

As shown in Appendix 2, the determinant of $|V_i|$ is given by

$$|V_i| = \gamma_i^{g_i(n)} a^{f_i(n)} \prod_{j=1}^{n_i} (a + n_{ij} \zeta_{ij}) \quad (4.23)$$

where

$$g_i(n) = n_i + 1$$

and

$$f_i(n) = n_{i0} - n_i.$$

The values of ζ_{ij} for $i=1, \dots, s$ and $j=1, \dots, n_i$ are generated using the algorithm given in Appendix 2.

4.2.5. Generating the equations

The ML solutions for fixed effects and the ML estimates of variance components can be obtained by solving the two systems in (4.7) and (4.8) simultaneously. If estimates of the variance components are available, the system in (4.7) becomes linear. Therefore a convenient procedure would be to solve the two systems alternately until the solution converges. Since there are several routines available for solving linear and nonlinear systems of equations, all that needs to be done here is, to construct algorithms for generating (4.7) and (4.8).

4.2.5.1. Generating the linear equations (system (4.7))

An alternative representation for (4.7) is given by

$$\underline{\Omega} \underline{\beta} = \underline{\eta} \quad (4.24)$$

where $\underline{\Omega}$ is a $t \times t$ matrix (t is the number of levels of fixed effects in the model) and $\underline{\eta}$ is a $t \times 1$ vector such that .

$$\underline{\Omega} = \sum_{i=1}^S \underline{x}_i' \hat{V}_i^{-1} \underline{x}_i$$

and

$$\underline{\eta} = \sum_{i=1}^S \underline{x}_i' \hat{V}_i^{-1} \underline{y}_i,$$

respectively. The elements of $\underline{\Omega}$ and $\underline{\eta}$ are functions of $\underline{\theta}$. Suppose each \underline{x}_i is partitioned according to the partitioning of the \underline{y} vector. That is

$$\underline{x}_i = \begin{bmatrix} \underline{x}_{oi} \\ \underline{x}_{di} \\ \underline{x}_{si} \end{bmatrix}.$$

Then the (i,j,k) th row of \underline{x}_{oi} (x'_{oijk}), the (i,j) th row of \underline{x}_{di} (x'_{dij}) and the only row of \underline{x}_{si} (x'_{si}) represent the coefficients of the fixed effects pertaining to the k th offspring of the j th dam

mated to the i th sire, the j th dam mated to the i th sire and the i th sire, respectively. Therefore

$$\underline{x}'_{oijk} = (x_{oijk1}, \dots, x_{oijk r}, \dots, x_{oijk t})$$

$$\underline{x}'_{dij} = (x_{dij1}, \dots, x_{dij r}, \dots, x_{dij t})$$

and

$$\underline{x}'_{si} = (x_{si1}, \dots, x_{si r}, \dots, x_{sit})$$

where $x_{oijk r}$, $x_{dij r}$ and $x_{si r}$ are the coefficients associated with the r th fixed effect and these coefficients take the values one or zero.

Explicit expressions for the elements of \underline{V}_i^{-1} were given in Section 4.2.3. This means that the equations given in (4.7) can be generated by using the following algorithm:

An algorithm for generating the linear equations in (4.7)

Step 1

Assume initial values for θ_m ($m=1, \dots, 5$).

Step 2

Calculate γ_h ($h=1, \dots, 9$).

Step 3

Calculate p and q_{ijk} ($i=1, \dots, s; j=1, \dots, n_i; k=j, \dots, n_i$). An algorithm for computing these are given in Appendix 1.

Step 4

Calculate $x_{oij.r}$ and $y_{oij.}$, where

$$x_{oij.r} = \sum_{k=1}^{n_{ij}} x_{oijk r}$$

and

$$y_{oij.} = \sum_{k=1}^{n_{ij}} y_{oijk}.$$

Step 5

For $r=1, \dots, t$ and $r'=r, \dots, t$

(1) calculate $\alpha_{rr'}$, where

$$\alpha_{rr'} = N_1(rr')/a + [N_2(rr') + N_3(rr')]/\gamma_1.$$

In the above expression,

$$N_1(rr') = \sum_{i=1}^s \sum_{j=1}^{n_i} \sum_{k=1}^{n_{ij}} x_{oijk} x_{oijk}'$$

$$N_2(rr') = \sum_{i=1}^s \sum_{j=1}^{n_i} x_{dijr} x_{dijr}'$$

and

$$N_3(rr') = \sum_{i=1}^s x_{sir} x_{sir}'.$$

(2) Calculate $\sum_{i=1}^s \sum_{j=1}^{n_i} \alpha_{ijrr'}$, where

$$\begin{aligned} \alpha_{ijrr'} &= \phi_{11}(ij)N_{11}(ijrr') + \phi_{12}(ij)N_{12}(ijrr') \\ &+ \phi_{13}(ij)N_{13}(ijrr') + \phi_{22}(ij)N_{22}(ijrr') \\ &+ \phi_{23}(ij)N_{23}(ijrr') + \phi_{33}(ij)N_{33}(ijrr'). \end{aligned}$$

In the above expression

$$N_{11}(ijrr') = x_{oij.r} x_{oij.r}'$$

$$N_{12}(ijrr') = x_{oij.r} x_{dijr}' + x_{oij.r'} x_{dijr}$$

$$N_{13}(ijrr') = x_{oij.r} x_{sir}' + x_{oij.r'} x_{sir}$$

$$N_{22}(ijrr') = x_{dijr}x_{dijr'}$$

$$N_{23}(ijrr') = x_{dijr}x_{sir'} + x_{dijr'}x_{sir}$$

$$N_{33}(ijrr') = x_{sir}x_{sir'}$$

$$\phi_{11}(ij) = q_{ijj}$$

$$\phi_{12}(ij) = -\gamma_8(p + n_{ij}q_{ijj})$$

$$\phi_{13}(ij) = -\gamma_9(p + n_{ij}q_{ijj})$$

$$\phi_{22}(ij) = \gamma_8^2 n_{ij}(p + n_{ij}q_{ijj})$$

$$\phi_{23}(ij) = \gamma_8\gamma_9 n_{ij}(p + n_{ij}q_{ijj})$$

and

$$\phi_{33}(ij) = \gamma_9^2 n_{ij}(p + n_{ij}q_{ijj}).$$

(3) Calculate $\sum_{i=1}^s \sum_{j=1}^{n_1-1} \sum_{k=j+1}^{n_i} \alpha_{ijkrr'}$, where

$$\begin{aligned} \alpha_{ijkrr'} &= \phi_{11}(ijk)N_{11}(ijkrr') + \phi_{12}(ijk)N_{12}(ijkrr') \\ &+ \phi_{13}(ijk)N_{13}(ijkrr') + \phi_{22}(ijk)N_{22}(ijkrr') \\ &+ \phi_{23}(ijk)N_{23}(ijkrr') + \phi_{33}(ijk)N_{33}(ijkrr'). \end{aligned}$$

In the above expression

$$N_{11}(ijkrr') = x_{oij.r}x_{oik.r'} + x_{oij.r'}x_{oik.r}$$

$$\begin{aligned} N_{12}(ijkrr') &= n_{ik}(x_{oij.r}x_{dikr'} + x_{oij.r'}x_{dikr}) \\ &+ n_{ij}(x_{oik.r}x_{dijr'} + x_{oik.r'}x_{dijr}) \end{aligned}$$

$$N_{13}(ijkrr') = n_{ik}(x_{oij.r}x_{sir'} + x_{oij.r'}x_{sir}) \\ + n_{ij}(x_{oik.r}x_{sir'} + x_{oik.r'}x_{sir})$$

$$N_{22}(ijkrr') = n_{ij}n_{ik}(x_{dijr}x_{dikr'} + x_{dikr}x_{dijr'})$$

$$N_{23}(ijkrr') = n_{ij}n_{ik}x_{sir'}(x_{dijr} + x_{dikr}) \\ + n_{ij}n_{ik}x_{sir}(x_{dijr'} + x_{dikr'})$$

$$N_{33}(ijkrr') = 2n_{ij}n_{ik}x_{sir}x_{sir'}$$

$$\phi_{11}(ijk) = q_{ijk}$$

$$\phi_{12}(ijk) = -\gamma_8 q_{ijk}$$

$$\phi_{13}(ijk) = -\gamma_9 q_{ijk}$$

$$\phi_{22}(ijk) = \gamma_8^2 q_{ijk}$$

$$\phi_{23}(ijk) = \gamma_8 \gamma_9 q_{ijk}$$

and

$$\phi_{33}(ijk) = \gamma_9^2 q_{ijk}.$$

(4) Then obtain the (r, r') th element of $\underline{\Omega}$ as

$$\omega_{rr'} = \alpha_{rr'} + \sum_{i=1}^s \sum_{j=1}^{n_i} \alpha_{ijrr'} + \sum_{i=1}^s \sum_{j=1}^{n_i-1} \sum_{k=j+1}^{n_i} \alpha_{ijkrr'}.$$

Note that $\omega_{rr'}$ can be obtained without storing N's, ϕ 's or the α 's in computer memory.

Step 6

For $r=1, \dots, t$

(1) Calculate σ_r , where

$$\sigma_r = W_1(r)/a + [W_2(r) + W_3(r)]/\gamma_1.$$

In the above expression

$$W_1(r) = \sum_{i=1}^s \sum_{j=1}^{n_i} \sum_{k=1}^{n_{ij}} y_{oijk} x_{oijk} r$$

$$W_2(r) = \sum_{i=1}^s \sum_{j=1}^{n_i} y_{dij} x_{dij} r$$

and

$$W_3(r) = \sum_{i=1}^s y_{si} x_{sir}.$$

(2) Calculate $\sum_{i=1}^s \sum_{j=1}^{n_i} \sigma_{ijr}$, where

$$\begin{aligned} \sigma_{ijr} &= \phi_{11}(ij)W_{11}(ijr) + \phi_{12}(ij)W_{12}(ijr) \\ &+ \phi_{13}(ij)W_{13}(ijr) + \phi_{22}(ij)W_{22}(ijr) \\ &+ \phi_{23}(ij)W_{23}(ijr) + \phi_{33}(ij)W_{33}(ijr). \end{aligned}$$

In the above expression

$$W_{11}(ijr) = y_{oij} x_{oij} r$$

$$W_{12}(ijr) = y_{dij} x_{oij} r + y_{oij} x_{dij} r$$

$$W_{13}(ijr) = y_{si} x_{oij} r + y_{oij} x_{sir} r$$

$$W_{22}(ijr) = y_{dij} x_{dij} r$$

$$W_{23}(ijr) = y_{dij} x_{sir} r + y_{si} x_{dij} r$$

and

$$W_{33}(ijr) = y_{si} x_{sir} r.$$

The values of ϕ 's are as for step 5.

(3) Calculate $\sum_{i=1}^s \sum_{j=1}^{n_i-1} \sum_{k=j+1}^{n_i} \sigma_{ijk}$, where

$$\begin{aligned}\sigma_{ijk r} &= \phi_{11}(ijk)W_{11}(ijk r) + \phi_{12}(ijk)W_{12}(ijk r) \\ &+ \phi_{13}(ijk)W_{13}(ijk r) + \phi_{22}(ijk)W_{22}(ijk r) \\ &+ \phi_{23}(ijk)W_{23}(ijk r) + \phi_{33}(ijk)W_{33}(ijk r).\end{aligned}$$

In the above expression

$$W_{11}(ijk r) = y_{oik}.x_{oij.r} + y_{oij}.x_{oik.r}$$

$$\begin{aligned}W_{12}(ijk r) &= n_{ij}(y_{dij}x_{oik.r} + y_{oik}.x_{dijr}) \\ &+ n_{ik}(y_{dik}x_{oij.r} + y_{oij}.x_{dikr})\end{aligned}$$

$$\begin{aligned}W_{13}(ijk r) &= n_{ij}(y_{si}x_{oik.r} + y_{oik}.x_{sir}) \\ &+ n_{ik}(y_{si}x_{oij.r} + y_{oij}.x_{sir})\end{aligned}$$

$$W_{22}(ijk r) = n_{ij}n_{ik}(y_{dij}x_{dikr} + y_{dik}x_{dijr})$$

$$\begin{aligned}W_{23}(ijk r) &= n_{ij}n_{ik}y_{si}(x_{dijr} + x_{dikr}) \\ &+ n_{ij}n_{ik}x_{sir}(y_{dij} + y_{dik})\end{aligned}$$

and

$$W_{33}(ijk r) = 2n_{ij}n_{ik}y_{si}x_{sir}.$$

The values of ϕ 's are as for step 5.

(4) Then obtain the r th element of $\tilde{\eta}$ as

$$\eta_r = \sigma_r + \sum_{i=1}^s \sum_{j=1}^{n_i} \sigma_{ijr} + \sum_{i=1}^s \sum_{j=1}^{n_i-1} \sum_{k=j+1}^{n_i} \sigma_{ijk r}.$$

Note that η_r can be obtained without storing ϕ 's, W 's or σ 's in computer memory.

Step 7

Then the r th equation in (4.7) is given by

$$\sum_{i=1}^{r-1} \omega_{ir} \hat{\beta}_i + \sum_{i=r}^t \omega_{ri} \hat{\beta}_i = \eta_r.$$

4.2.5.2. Generating the nonlinear equations (system (4.8))

Since \underline{V}_i is a partitioned matrix, $\text{tr}(\underline{V}_i^{-1} \underline{V}_{im})$ in (4.8) can be written as

$$\begin{aligned} & \text{tr}(\underline{A}_{i11} \underline{V}_{i11m}) + \text{tr}(\underline{A}_{i12} \underline{V}'_{i12m}) + \text{tr}(\underline{A}_{i13} \underline{V}'_{i13m}) \\ & + \text{tr}(\underline{A}'_{i12} \underline{V}_{i12m}) + \text{tr}(\underline{A}_{i22} \underline{V}_{i22m}) + \text{tr}(\underline{A}_{i23} \underline{V}'_{i23m}) \\ & + \text{tr}(\underline{A}'_{i13} \underline{V}_{i13m}) + \text{tr}(\underline{A}'_{i23} \underline{V}_{i23m}) + \text{tr}(\underline{A}_{i33} \underline{V}_{i33m}) \end{aligned}$$

where \underline{A}_{ijk} 's were defined earlier (in section 4.2.3.) and

$$\underline{V}_{ijkm} = \frac{\partial}{\partial \theta_m} \underline{V}_{ijk}.$$

Expressions for \underline{V}_{ijkm} can be obtained by replacing γ_h in (4.13) to (4.18) by f_{hm} . Also let,

$$\underline{u}_i = \underline{V}_i^{-1} (\underline{y}_i - \underline{X}_i \beta)$$

where \underline{u}_i can also be partitioned according to the sire, the dams and the offspring. That is

$$\underline{u}_i = (\underline{u}_{oi}, \underline{u}_{di}, \underline{u}_{si})$$

where

$$\underline{u}_{oi} = \underline{A}_{i11} \underline{y}_{oi}^* + \underline{A}_{i12} \underline{y}_{di}^* + \underline{A}_{i13} \underline{y}_{si}^*$$

$$\underline{u}_{di} = \underline{A}'_{i12} \underline{y}_{oi}^* + \underline{A}_{i22} \underline{y}_{di}^* + \underline{A}_{i23} \underline{y}_{si}^*$$

and

$$u_{si} = A_{i13}^* y_{oi}^* + A_{i23}^* y_{di}^* + A_{i33}^* y_{si}^*$$

The (i,j,k) th element of y_{oi}^* (y_{oijk}^*), the (i,j) th element of y_{di}^* (y_{dij}^*) and y_{si}^* are given by

$$y_{oijk}^* = y_{oijk} - x'_{oijk} \beta$$

$$y_{dij}^* = y_{dij} - x'_{dij} \beta$$

and

$$y_{si}^* = y_{si} - x'_{si} \beta,$$

respectively. These are known if estimates of the fixed effects are available. This means that $(y_i - X_i \beta)' V_i^{-1} V_{im} V_i^{-1} (y_i - X_i \beta)$ in (4.8) can be written as

$$\begin{aligned} & u'_{oi} V_{i11m} u_{oi} + 2u'_{oi} V_{i12m} u_{di} + 2u'_{oi} V_{i13m} u_{si} \\ & + u'_{di} V_{i22m} u_{di} + 2u'_{di} V_{i23m} u_{si} + u'_{si} V_{i33m} u_{si}. \end{aligned}$$

By arranging elements of u_{oi} and u_{di} corresponding to the y vectors, it can be shown that:

(1) The k th element of u_{oij} , where

$$u'_{oi} = (u'_{oi1}, \dots, u'_{oij}, \dots, u'_{oin_i})$$

can be expressed as

$$u_{oijk} = u_{oijk}^* + u_{oij}^*$$

In above

$$u_{oijk}^* = p(y_{oijk}^* - \gamma_8 y_{dij}^* - \gamma_9 y_{si}^*)$$

and

$$u_{oij}^* = \sum_{\ell=1}^{j-1} \epsilon_{i\ell} q_{i\ell j} + \sum_{\ell=j}^{n_i} \epsilon_{i\ell} q_{i\ell j}$$

where

$$\epsilon_{i\ell} = -\gamma_8 n_{i\ell} y_{di}^* - \gamma_9 n_{i\ell} y_{si}^* + \sum_{k=1}^{n_{i\ell}} y_{oi\ell k}^*$$

(2) The j th element of \underline{u}_{di} is given by

$$u_{dij} = \gamma_1^{-1} y_{dij}^* - p\gamma_8 \epsilon_{ij} - \gamma_8 n_{ij} u_{oij}^*$$

(3) u_{si} is given by

$$u_{si} = \gamma_1^{-1} y_{si}^* - p\gamma_9 \sum_{j=1}^{n_i} \epsilon_{ij} - \gamma_9 \sum_{j=1}^{n_i} n_{ij} u_{oij}^*$$

Therefore the following algorithm can be proposed for obtaining the nonlinear equations in (4.8):

An algorithm to generate the nonlinear equations in system (4.8)

Step 1

Assuming some values for θ_m ($m=1, \dots, 5$), calculate γ_h ($h=1, \dots, 5$).

Step 2

Calculate p and q_{ijk} ($i=1, \dots, s; j=1, \dots, n_i; k=j, \dots, n_i$).

Step 3

Calculate $\pi_{\ell m}$ for $\ell=0, \dots, 4$ and $m=1, \dots, 5$, where

$$\pi_{0m} = 1$$

$$\pi_{1m} = f_{1m} - 2\gamma_8 f_{4m} - 2\gamma_9 f_{5m}$$

$$\pi_{2m} = f_{1m} - f_{2m}$$

$$\pi_{3m} = f_{2m} - 2\gamma_8 f_{4m} - 2\gamma_9 f_{5m}$$

and

$$\pi_{4m} = f_{3m} - 2\gamma_9 f_{5m}.$$

The values of f_{hm} were given in Table 4.2.

Step 4

Calculate S_ℓ for $\ell=0, \dots, 4$, where

$$S_1 = pn_{00}$$

$$S_2 = \sum_{i=1}^s \sum_{j=1}^{n_i} n_{ij} q_{ijj}$$

$$S_3 = \sum_{i=1}^s \sum_{j=1}^{n_i} n_{ij}^2 q_{ijj}$$

$$S_4 = 2 \sum_{i=1}^s \sum_{j=1}^{n_i-1} \sum_{k=j+1}^{n_i} n_{ij} n_{ik} q_{ijk}$$

and

$$S_0 = \gamma_1^{-1}(s+n_0) + (\gamma_8^2 + \gamma_9^2)(S_1 + S_3) + \gamma_9^2 S_4.$$

In the above expressions

$$n_0 = \sum_{i=1}^s n_i$$

and

$$n_{00} = \sum_{i=1}^s \sum_{j=1}^{n_i} n_{ij}.$$

Step 5

Then obtain Λ_{1m} for $m=1, \dots, 5$, where

$$\Lambda_{1m} = \sum_{\ell=0}^4 \pi_{\ell m} S_\ell.$$

Step 6

Using an estimate for β , calculate y_{oijk}^* , y_{dij}^* and y_{si}^* for $i=1, \dots, s$; $j=1, \dots, n_i$ and $k=1, \dots, n_{ij}$.

Step 7

Calculate ϵ_{ij} and then u_{oij}^* for $i=1, \dots, s$ and $j=1, \dots, n_i$.

Step 8

Calculate u_{si} , u_{dij} and u_{oijk} for $i=1, \dots, s$; $j=1, \dots, n_i$ and $k=1, \dots, n_{ij}$.

Step 9

Calculate $\tau_{\ell m}$ for $\ell=0, \dots, 5$ and $m=1, \dots, 5$, where

$$\begin{aligned}\tau_{0m} &= 1 \\ \tau_{1m} &= f_{1m} - f_{2m} \\ \tau_{2m} &= f_{2m} \\ \tau_{\ell m} &= 2f_{\ell m} \text{ for } \ell = 3, 4, 5.\end{aligned}$$

Step 10

Calculate T_{ℓ} for $\ell=0, \dots, 5$, where

$$\begin{aligned}T_1 &= \sum_{i=1}^s \sum_{j=1}^{n_i} \sum_{k=1}^{n_{ij}} (u_{oijk})^2 \\ T_2 &= \sum_{i=1}^s \sum_{j=1}^{n_i} (u_{oij.})^2 \text{ where } u_{oij.} = \sum_{k=1}^{n_{ij}} u_{oijk} \\ T_3 &= \sum_{i=1}^s \sum_{j=1}^{n_i-1} \sum_{k=j+1}^{n_i} u_{oij.} u_{oik.} \\ T_4 &= \sum_{i=1}^s \sum_{j=1}^{n_i} u_{oij.} u_{dij} \\ T_5 &= \sum_{i=1}^s \sum_{j=1}^{n_i} u_{oij.} u_{si} \\ \text{and} \\ T_0 &= \sum_{i=1}^s (u_{si})^2 + \sum_{i=1}^s \sum_{j=1}^{n_i} (u_{dij})^2.\end{aligned}$$

Step 11

Obtain Λ_{2m} for $m=1, \dots, 5$, where

$$\Lambda_{2m} = \sum_{\ell=0}^5 \tau_{\ell m} T_{\ell}.$$

Step 12

Then the left hand side of the m th equation in system (4.8) is given by

$$\Lambda_{1m} - \Lambda_{2m}.$$

Obtaining the ML solutions for the fixed effects and the ML estimates of variance components

Maximum likelihood solutions for β and ML estimates of θ are obtained by solving (4.7) and (4.8) simultaneously. Therefore a convenient procedure would be as follows:

- (1) Assume initial values for the variance components.
- (2) Using these estimates, solve the linear system in (4.7) in order to find solutions for the fixed effects.
- (3) Using these solutions obtain a new set of estimates for the variance components.
- (4) Follow (2) and (3) alternately until the solution converges.

However, this procedure does not avoid negative estimates of the variance components. Also, it is possible that the estimate of the genetic correlation between direct and maternal effects may be outside the range -1 and $+1$. In such situations an obvious procedure is to minimize $(\Lambda_{1m} - \Lambda_{2m})^2$ subject to the constraints that the estimates of the variances are greater than or equal to zero and the genetic correlation between the direct and maternal effects is between -1 and $+1$.

4.2.6. Constrained maximization of the likelihood function

Negative estimates of variance components and the correlation between direct and maternal genetic effects outside the range -1 and $+1$ can also be avoided by maximizing F or minimizing $-F$, instead of solving the system (4.8), subject to

$$\theta_1, \theta_2, \theta_4, \theta_5 \geq 0$$

and

$$\theta_1 \theta_2 - \theta_3^2 \geq 0$$

where F is given by

$$F = - \sum_{i=1}^s \ln |V_i| - \sum_{i=1}^s (y_i - X_i \beta)' V_i^{-1} (y_i - X_i \beta).$$

From (4.23),

$$\ln |V_i| = (n_i + 1) \ln \gamma_1 + (n_{i0} - n_i) \ln a + \sum_{j=1}^{n_i} \ln (a + n_{ij} \zeta_{ij})$$

which gives

$$\sum_{i=1}^s \ln |V_i| = (n_0 + s) \ln \gamma_1 + (n_{00} - n_0) \ln a + \sum_{i=1}^s \sum_{j=1}^{n_i} \ln (a + n_{ij} \zeta_{ij}).$$

Generating the above expression is not difficult, since an explicit expression for $|V_i|$ is derived in Appendix 2. Since explicit expressions for the elements of V_i^{-1} have been derived, it is also possible to generate

$$\sum_{i=1}^s (y_i - X_i \beta)' V_i^{-1} (y_i - X_i \beta)$$

easily. Therefore, the following algorithm can be proposed to generate $-F$.

An algorithm for generating $-F$

Step 1

Assume initial values for θ_m ($m=1, \dots, 5$).

Step 2

Calculate p and q_{ijk} for $i=1, \dots, s$; $j=1, \dots, n_i$ and $k=j, \dots, n_i$.

Step 3

Calculate ζ_{ij} for $i=1, \dots, s$ and $j=1, \dots, n_i$. The formulae for calculating ζ_{ij} are given in Appendix 2.

Step 4

Calculate Δ , where

$$\Delta = (n_o + s) \ln \gamma_1 + (n_{oo} - n_o) \ln a + \sum_{i=1}^s \sum_{j=1}^{n_i} \ln(a + n_{ij} \zeta_{ij}).$$

Step 5

Calculate ρ , where

$$\rho = M_1/a + (M_2 + M_3)/\gamma_1.$$

In the above expression

$$M_1 = \sum_{i=1}^s \sum_{j=1}^{n_i} \sum_{k=1}^{n_{ij}} (y_{oijk}^*)^2$$

$$M_2 = \sum_{i=1}^s \sum_{j=1}^{n_i} (y_{dij}^*)^2$$

and

$$M_3 = \sum_{i=1}^s (y_{si}^*)^2.$$

Step 6

Calculate $\sum_{i=1}^s \sum_{j=1}^{n_i} \rho_{ij}$, where

$$\rho_{ij} = \sum_{\ell=1}^3 \sum_{\ell'=\ell}^3 \phi_{\ell\ell'}(ij) M_{\ell\ell'}(ij).$$

In the above expression

$$M_{11}(ij) = (y_{oij}^*)^2$$

$$M_{12}(ij) = 2y_{oij}^* y_{dij}^*$$

$$M_{13}(ij) = 2y_{oij}^* y_{si}^*$$

$$M_{22}(ij) = (y_{dij}^*)^2$$

$$M_{23}(ij) = 2y_{dij}^* y_{si}^*$$

and

$$M_{33}(ij) = (y_{si}^*)^2.$$

Step 7

Calculate $\sum_{i=1}^s \sum_{j=1}^{n_i-1} \sum_{k=j+1}^{n_i} \rho_{ijk}$, where

$$\rho_{ijk} = \sum_{\ell=1}^3 \sum_{\ell'=1}^3 \phi_{\ell\ell'}(ijk) M_{\ell\ell'}(ijk).$$

In the above expression

$$M_{11}(ijk) = 2y_{oij}^* y_{oik}^*.$$

$$M_{12}(ijk) = 2(n_{ik} y_{dik}^* y_{oij}^* + n_{ij} y_{dij}^* y_{oik}^*.)$$

$$M_{13}(ijk) = 2(n_{ik} y_{oij}^* + n_{ij} y_{oik}^*.) y_{si}^*$$

$$M_{22}(ijk) = 2n_{ij} n_{ik} y_{dij}^* y_{dik}^*$$

$$M_{23}(ijk) = 2n_{ij} n_{ik} y_{si}^* (y_{dij}^* + y_{dik}^*)$$

and

$$M_{33}(ijk) = 2n_{ij} n_{ik} (y_{si}^*)^2.$$

Step 8

Calculate Ψ , where

$$\Psi = \rho + \sum_{i=1}^s \sum_{j=1}^{n_i} \rho_{ij} + \sum_{i=1}^s \sum_{j=1}^{n_i-1} \sum_{k=j+1}^{n_i} \rho_{ijk}.$$

Step 9

Then obtain $-F$, where

$$-F = \Delta + \Psi.$$

The expressions for ϕ 's in step 7 and step 8 are the same as those for section 4.2.5.1. As before the ϕ 's, M 's or the ρ 's do not

have to be stored in computer memory when calculating ψ .

4.2.7. Large-sample variances for the estimates of fixed effects and variance components

The large-sample variance-covariance matrices of the vectors of the estimates of fixed effects and the variance components are given by [see section 3.1.]

$$\left[\sum_{i=1}^S (X_i' V_i^{-1} X_i) \right]^{-1}$$

and

$$2\underline{H}^{-1},$$

respectively, where the (m, m') th element of \underline{H} is given by

$$\sum_{i=1}^S \text{tr} \{ \underline{V}_i^{-1} \underline{v}_{im} \underline{V}_i^{-1} \underline{v}_{im'} \}.$$

In the above expression

$$\underline{v}_{im} = \frac{\partial \underline{v}_i}{\partial \theta_m}.$$

The (r, r') th element of

$$\left[\sum_{i=1}^S (X_i' V_i^{-1} X_i) \right]^{-1}$$

is the covariance between $\hat{\beta}_r$ and $\hat{\beta}_{r'}$. This is not difficult to compute, as an explicit expression for the (r, r') th element of

$$\sum_{i=1}^S (X_i' V_i^{-1} X_i)$$

was given in section 4.2.5.

The covariance between the estimates of the m th variance component and the m' th variance component is given by the (m, m') th element of $2\underline{H}^{-1}$, where \underline{H} was defined earlier. The matrix \underline{H} can

alternatively be represented as

$$\text{tr} \sum_{i=1}^s \sum_{j=1}^3 \sum_{k=1}^3 B_{ijkm} B_{ikjm},$$

where

$$B_{i11m} = A_{i11} V_{i11m} + A_{i12} V_{i12m} + A_{i13} V_{i13m}$$

$$B_{i12m} = A_{i11} V_{i12m} + A_{i12}$$

$$B_{i13m} = A_{i11} V_{i13m} + A_{i13}$$

$$B_{i21m} = A_{i12} V_{i11m} + A_{i22} V_{i12m} + A_{i23} V_{i13m}$$

$$B_{i22m} = A_{i12} V_{i12m} + A_{i22}$$

$$B_{i23m} = A_{i12} V_{i13m} + A_{i23}$$

$$B_{i31m} = A_{i13} V_{i11m} + A_{i23} V_{i12m} + A_{i33} V_{i13m}$$

$$B_{i32m} = A_{i13} V_{i12m} + A_{i23}$$

and

$$B_{i33m} = A_{i13} V_{i13m} + A_{i33}.$$

Since explicit expressions for the elements of the matrices A_{ijk} are available, obtaining the large-sample variance-covariance matrix of the estimates of the variance components, is not difficult.

4.3. Estimation of the parameters: A multiple-trait setting

Sheep, swine and beef cattle breeders are often concerned with multiple-trait selection. This also applies for maternally affected traits. An example is the weaning weight and

post-weaning gain records of beef cattle [see Quaas and Pollak (1980)]. The direct and maternal genetic covariances amongst these multiple traits are required in order to predict the genetic values of the animals in a multiple-trait selection programme. The method of estimating variance components for a single trait with unbalanced data, by analogy, suggests a method which can be applied in a multiple-trait setting. The ML estimators of variance components for a multiple-trait setting will be derived in this section.

Suppose y_{i1} and $y_{i'2}$ are the measurements on trait 1 of individual i , whose dam is w , and trait 2 of individual i' , whose dam is w' , respectively. Then by extending (4.1) we can express y_{i1} and $y_{i'2}$ as

$$y_{i1} = f_i(\beta_1) + g_{di1} + g_{mw1} + e_{mw1} + e_{di1}$$

and

$$y_{i'2} = f_{i'}(\beta_2) + g_{di'2} + g_{mw'2} + e_{mw'2} + e_{di'2} \quad (4.25)$$

where

$f_i(\beta_1)$ ($f_{i'}(\beta_2)$) is a linear function of the unknown fixed effects of trait 1 of individual i (trait 2 of individual i');

g_{di1} ($g_{di'2}$) is the direct additively genetic effect of trait 1 of i (trait 2 of i');

g_{mw1} ($g_{mw'2}$) is the maternal additively genetic effect of trait 1 of w (trait 2 of w') influencing y_{i1} ($y_{i'2}$);

e_{mw1} ($e_{mw'2}$) is the residual effect common to trait 1 (trait 2) of offspring of w (w'); and

e_{di1} ($e_{di'2}$) is the residual effect unique to trait 1 (trait 2) of individual i (i').

Assume that all genetic effects are independent of all residual effects. Also assume that the residual effects common to full-sibs and maternal half-sibs are independent of the residual effects unique to the individuals. Then the covariance between y_{i1} and $y_{i'2}$ can be written as

$$a_{ii'}g_{oo}^{12} + a_{ww'}g_{mm}^{12} + a_{iw'}g_{om}^{12} + a_{i'w}g_{mo}^{12} + b_{ww'}r_{mm}^{12} + b_{ii'}r_{oo}^{12} \quad (4.26)$$

where

- g_{oo}^{12} is the covariance between the direct additively genetic effects of traits 1 and 2;
- g_{mm}^{12} is the covariance between the maternal additively genetic effects of traits 1 and 2;
- g_{om}^{12} is the covariance between the direct additively genetic effect of trait 1 and maternal additively genetic effect of trait 2;
- g_{mo}^{12} is the covariance between the maternal additively genetic effect of trait 1 and direct additively genetic effect of trait 2;
- r_{mm}^{12} is the covariance between the residual effects common to full-sibs and maternal half-sibs of trait 1 and the residual effects common to full-sibs and maternal half-sibs of trait 2;
- r_{oo}^{12} is the covariance between the residual effects unique to trait 1 of an individual and the residual effects unique to trait 2 of an individual;
- $a_{ii'}$ is the coefficient of additive relationship between i and i' ; and

$$b_{ii'}, (b_{ww'}) = \begin{cases} 1 & \text{if } i = i' (w = w') \\ 0 & \text{if } i \neq i' (w \neq w'). \end{cases}$$

For two correlated traits, the total number of variance components involved are 16. In general, for q correlated traits this number is given by

$$5q + 3q(q-1).$$

For estimating these components, consider the previous mating plan with the additional assumption that measurements on all traits are available on all animals. This makes the use of this method restrictive as measurements on all traits of all animals are usually not available. Then, if the vector of observations is normally distributed with parameters specified as in (4.4), the log likelihood function of the observations has the form given in (4.6).

4.3.1. The structure of the variance-covariance matrix

As before, let y_i , the vector of observations of the i th family be partitioned as

$$y_i' = (y_{oi}', y_{di}', y_{si}')$$

with

$$y_{oi}' = (y_{oi1}', \dots, y_{oij}', \dots, y_{oin_i}')^{\prime}$$

and

$$y_{di}' = (y_{di1}', \dots, y_{dij}', \dots, y_{din_i}')^{\prime}.$$

The vector y_{oij}' can be written as

$$y_{oij}' = (y_{oij1}', \dots, y_{oijk}', \dots, y_{oijn_{ij}}')^{\prime}$$

where y_{oijk} is the vector of observations on q traits of the k th offspring of the j th dam mated to the i th sire. Similarly, y_{dij} and y_{si} represent the vectors of observations on q traits of the j th dam mated to the i th sire and the i th sire, respectively. Suppose that the qxq variance-covariance matrices of y_{oijk} , y_{dij} and y_{si} are denoted as Σ_1 . Then the (p, p') th element of Σ_1 is given by

$$\sigma_{1pp'} = g_{oo}^{pp'} + g_{mm}^{pp'} + \frac{1}{2} (g_{om}^{pp'} + g_{mo}^{pp'}) + r_{mm}^{pp'} + r_{oo}^{pp'}.$$

Define

$$\Sigma_2 = \text{Cov}(y_{oijk}, y'_{oijk'}) \quad \text{for } k \neq k'$$

where the (p, p') th element of Σ_2 is the covariance between trait p of X and trait p' of Y when X and Y are full-sibs which means that this element is given by

$$\sigma_{2pp'} = \frac{1}{2} g_{oo}^{pp'} + g_{mm}^{pp'} + \frac{1}{2} (g_{om}^{pp'} + g_{mo}^{pp'}) + r_{mm}^{pp'}$$

Also define

$$\Sigma_3 = \text{Cov}(y_{oijk}, y'_{oij'k'}) \quad \text{for } j \neq j'$$

where $\sigma_{3pp'}$, which is equal to $g_{oo}^{pp'}/4$ is the covariance between the observations on trait p of X and trait p' of Y when X and Y are paternal half-sibs. From above, it is clear that Σ_1 , Σ_2 and Σ_3 are symmetric matrices. Then the variance-covariance matrix of y_{oi} can be written in the form

$$V_{i11} = \begin{bmatrix} B_{i11} & \dots & B_{i1j} & \dots & B_{i1n_i} \\ \vdots & & \vdots & & \vdots \\ B_{ij1} & \dots & B_{ijj} & \dots & B_{ijn_i} \\ \vdots & & \vdots & & \vdots \\ B_{in_i1} & \dots & B_{in_ij} & \dots & B_{in_in_i} \end{bmatrix}$$

where

$$B_{ijk} = \begin{cases} I_{ijj} * (\Sigma_1 - \Sigma_2) + J_{ijj} * \Sigma_2 & \text{for } j=k \\ J_{ijk} * \Sigma_3 & \text{for } j \neq k. \end{cases}$$

In the above expressions I_{ijj} is the identity matrix of order n_{ij} , J_{ijk} is the $n_{ij} \times n_{ik}$ matrix of "1"s. Suppose

$$\Sigma_4 = \text{Cov}(y_{oijk}, y'_{dij})$$

The (p, p') th element of Σ_4 gives the covariance between trait p of the offspring and trait p' of the dam. This is equal to

$$\sigma_{4pp'} = \frac{1}{2}g_{oo}^{pp'} + \frac{1}{2}g_{mm}^{pp'} + \frac{1}{4}g_{om}^{pp'} + g_{mo}^{pp'}.$$

Then the covariance between y_{oi} and y_{di} can be written as

$$V_{i12} = \sum_{j=1}^{n_i+} (1_{ij} * \Sigma_4).$$

Similarly, define the variance-covariance matrix of the q traits between a sire and its offspring as Σ_5 . Then the (p,p') th element of Σ_5 is given by

$$\sigma_{5pp'} = \frac{1}{2}g_{oo}^{pp'} + \frac{1}{4}g_{om}^{pp'}.$$

Then it follows that

$$V_{i13} = 1_{io} * \Sigma_5.$$

Note that Σ_4 and Σ_5 are not symmetric. Since the sires and the dams within a family are assumed to be unrelated

$$V_{i22} = I_i * \Sigma_1 \text{ and } V_{i23} = 0.$$

4.3.2. The inverse of the variance-covariance matrix

As for the single-trait case, an explicit expression for the inverse of the variance-covariance matrix of the observations is derived in this section.

The inverse of this matrix has the form given in (4.20). Using properties (1) - (4) of section 3.3., it can be found that

$$V_{i12} V_{i22}^{-1} V_{i12}' = \sum_{j=1}^{n_i+} (J_{ijj} * \Sigma_6)$$

and

$$V_{i13} V_{i33}^{-1} V_{i13}' = J_{io} * \Sigma_7$$

where

$$\underline{\Sigma}_6 = \underline{\Sigma}_4 \underline{\Sigma}_1^{-1} \underline{\Sigma}_4$$

and

$$\underline{\Sigma}_7 = \underline{\Sigma}_5 \underline{\Sigma}_1^{-1} \underline{\Sigma}_5'$$

In the above expressions \underline{J}_{i0} is the $n_{i0} \times n_{i0}$ matrix of "1"s. Since $\underline{\Sigma}_1$ is symmetric, $\underline{\Sigma}_6$ and $\underline{\Sigma}_7$ are also symmetric. Therefore the j th diagonal block matrix and the (j,k) th off-diagonal block matrix of $\underline{V}_{i11} = \underline{V}_{i12} \underline{V}_{i22}^{-1} \underline{V}_{i12}' - \underline{V}_{i13} \underline{V}_{i33}^{-1} \underline{V}_{i13}'$ can be written as

$$\underline{I}_{ijj} * \underline{A} + \underline{J}_{ijj} * \underline{B}$$

and

$$\underline{J}_{ijk} * \underline{C},$$

respectively, where \underline{A} , \underline{B} and \underline{C} are symmetric matrices which are given by

$$\underline{A} = \underline{\Sigma}_1 - \underline{\Sigma}_2$$

$$\underline{B} = \underline{\Sigma}_2 - \underline{\Sigma}_6 - \underline{\Sigma}_7$$

and

$$\underline{C} = \underline{\Sigma}_3 - \underline{\Sigma}_7.$$

The matrix \underline{A}_{i11} has to be computed in order to obtain the inverse of the variance-covariance matrix. \underline{A}_{i11} can be computed by proceeding in a similar manner as to that for the single-trait situation. This matrix is found to be

$$\underline{A}_{i11} = \begin{bmatrix} \underline{B}_{i11} & \cdots & \underline{B}_{i1j} & \cdots & \underline{B}_{i1n_i} \\ \vdots & & \vdots & & \vdots \\ \underline{B}_{ij1} & \cdots & \underline{B}_{ijj} & \cdots & \underline{B}_{ijn_i} \\ \vdots & & \vdots & & \vdots \\ \underline{B}_{in_i1} & \cdots & \underline{B}_{in_ij} & \cdots & \underline{B}_{in_in_i} \end{bmatrix}$$

where

$$\underline{B}_{ijk} = \begin{cases} \underline{J}_{ijk} * \underline{Q}_{ikj} & \text{for } k < j \\ \underline{I}_{ijj} * \underline{P} + \underline{J}_{ijj} * \underline{Q}_{ijj} & \text{for } k = j \\ \underline{J}_{ijk} * \underline{Q}_{ijk} & \text{for } k > j. \end{cases}$$

An algorithm to compute the matrices \underline{P} , \underline{Q}_{ijk} (for $i=1, \dots, s$; $j=1, \dots, n_i$; $k=j, \dots, n_i$), and then \underline{A}_{i11} for a multiple-trait setting is given in Appendix 3.

Then by simple matrix multiplication, it can be shown that

- (1) \underline{A}_{i12} can be partitioned into n_i^2 block matrices and the (j,k) th block is given by

$$(j,k)\text{th block} = \begin{cases} -\underline{1}_{ij} * n_{ik} \underline{Q}_{ikj} \underline{\Sigma}_8 & \text{for } k < j \\ -\underline{1}_{ij} * (\underline{P} + n_{ij} \underline{Q}_{ijj}) \underline{\Sigma}_8 & \text{for } k = j \\ -\underline{1}_{ij} * n_{ik} \underline{Q}_{ijk} \underline{\Sigma}_8 & \text{for } k > j \end{cases}$$

where

$$\underline{\Sigma}_8 = \underline{\Sigma}_4 \underline{\Sigma}_1^{-1}.$$

- (2) \underline{A}_{i13} can be partitioned into a column of block matrices and the j th block is given by

$$-\underline{1}_{ij} * (\underline{P} + \underline{R}_{ij}) \underline{\Sigma}_9$$

where

$$\underline{R}_{ij} = \sum_{k=1}^{j-1} n_{ik} \underline{Q}_{ikj} + \sum_{k=j}^{n_i} n_{ik} \underline{Q}_{ijk}$$

and

$$\underline{\Sigma}_9 = \underline{\Sigma}_5 \underline{\Sigma}_1^{-1}.$$

- (3) \underline{A}_{i22} can be partitioned into n_i^2 block matrices and the (j,k) th block is a $q \times q$ matrix which is given by

$$(j,k)\text{th block} = \begin{cases} n_{ij}n_{ik}\Sigma_8 Q_{ikj}\Sigma_8 & \text{if } k < j \\ \Sigma_1^{-1} + n_{ij}\Sigma_8(P + n_{ij}Q_{ijj})\Sigma_8 & \text{if } k = j \\ n_{ij}n_{ik}\Sigma_8 Q_{ijk}\Sigma_8 & \text{if } k > j. \end{cases}$$

(4) A_{i23} can be partitioned into a column of n_i block matrices and the j th block is given by

$$n_{ij}\Sigma_8(P + R_{ij})\Sigma_9.$$

(5) A_{i33} is given by

$$A_{i33} = \Sigma_1^{-1} + \sum_{j=1}^{n_i} n_{ij}\Sigma_8(P + R_{ij})\Sigma_9.$$

4.3.3. Generating the equations

Denote g_{oo}^{pp} , g_{mm}^{pp} , r_{oo}^{pp} , r_{mm}^{pp} and g_{om}^{pp} by θ_{mp} ($m=1, \dots, 5$), respectively. Also denote $g_{oo}^{pp'}$, $g_{mm}^{pp'}$, $r_{oo}^{pp'}$, $r_{mm}^{pp'}$, $g_{om}^{pp'}$ and $g_{mo}^{pp'}$ by $\theta_{mpp'}$ ($m=1, \dots, 6$), respectively. Then $\sigma_{hpp'}$ ($h=1, \dots, 5; p=1, \dots, q; p'=1, \dots, q$) can be written as

$$\sigma_{hpp'} = \begin{cases} \sum_{m=1}^4 f_{hm}\theta_{mp} + (f_{h5} + f_{h6})\theta_{5p} & \text{for } p=p' \\ \sum_{m=1}^6 f_{hm}\theta_{mpp'} & \text{for } p \neq p' \end{cases}$$

where f_{hm} ($h=1, \dots, 5; m=1, \dots, 6$) are given in Table 4.3.

Table 4.3 - Values of f_{hm}

$\begin{matrix} m \\ h \end{matrix}$	1	2	3	4	5	6
1	1	1	1	1	1/2	1/2
2	1/2	1	0	1	1/2	1/2
3	1/4	0	0	0	0	0
4	1/2	1/2	0	0	1/4	1
5	1/2	0	0	0	1/4	0

By differentiating the log likelihood function of y with respect to θ_{mp} ($m=1, \dots, 5; p=1, \dots, q$) and $\theta_{mpp'}$ ($m=1, \dots, 5; p=1, \dots, q; p'=1, \dots, q$) and equating to zero, we obtain $3q^2 + 2q$ (that is $5q + 3q(q-1)$) equations. It can be observed that

where

$$\frac{\partial \Sigma_h}{\partial \theta_{mp}} = g_{hm} \underline{e}_p \underline{e}_p'$$

$$g_{hm} = \begin{cases} f_{hm} & m \leq 4 \\ f_{h5} + f_{h6} & m = 5 \end{cases}$$

and \underline{e}_p is a $q \times 1$ vector with "1" as the p th element. All other elements of \underline{e}_p are zero. Also

$$\frac{\partial \Sigma_h}{\partial \theta_{mpp'}} = g_{1hm} \underline{e}_p \underline{e}_{p'}' + g_{2hm} \underline{e}_{p'} \underline{e}_p'$$

where

$$g_{1hm} = f_{hm} \text{ for } m = 1, \dots, 6$$

and

$$g_{2hm} = \begin{cases} f_{hm} & \text{for } m \leq 4 \\ f_{h6} & \text{for } m = 5 \\ f_{h5} & \text{for } m = 6 \end{cases}$$

The vector β (with t^* elements), for the multi-trait case can be defined as

$$\beta' = (\beta_1', \dots, \beta_p', \dots, \beta_q')$$

where β_p is the vector of fixed effects associated with the p th trait, and

$$t^* = \sum_{p=1}^q t_p.$$

In the above expression t_p is the number of fixed effects associated with trait p . By proceeding as for the uni-trait case, the following algorithms can be proposed for generating the maximum likelihood equations:

4.3.3.1. An algorithm to compute the system of equations used for obtaining solutions for the fixed effects

Step 1

Assume initial values for θ_{mp} and θ_{mpp} .

Step 2

Calculate the qxq matrices Σ_h ($h=1, \dots, 9$).

Step 3

Calculate the qxq matrices P and Q_{ijk} . An algorithm for computing these are given in Appendix 3.

Step 4

Suppose \tilde{x}'_{oijkp} , \tilde{x}'_{dijp} and \tilde{x}'_{sip} are the vectors of

coefficients associated with the fixed effects of trait p of the k th offspring of j th dam mated to the i th sire, the j th dam mated to the i th sire and the i th sire, respectively.

Define

$$\underline{X}_{oijk} = \sum_{p=1}^{q+} x'_{oijkp}$$

$$\underline{X}_{dij} = \sum_{p=1}^{q+} x'_{dijp}$$

and

$$\underline{X}_{si} = \sum_{p=1}^{q+} x'_{sip}$$

Further define

$$\underline{X}_{ij1} = \underline{X}_{oij} \quad \text{where} \quad \underline{X}_{oij} = \sum_{k=1}^{n_{ij}} \underline{X}_{oijk}$$

$$\underline{X}_{ij2} = \underline{X}_{dij}$$

and

$$\underline{X}_{ij3} = \underline{X}_{si}$$

(1) Calculate $\underline{\Phi}$, where

$$\begin{aligned} \underline{\Phi} = & \sum_{i=1}^s \underline{X}'_{si} \underline{\Sigma}_1^{-1} \underline{X}_{si} + \sum_{i=1}^s \sum_{j=1}^{n_i} \underline{X}'_{dij} \underline{\Sigma}_1^{-1} \underline{X}_{dij} \\ & + \sum_{i=1}^s \sum_{j=1}^{n_i} \sum_{k=1}^{n_{ij}} \underline{X}'_{oijk} \underline{P} \underline{X}_{oijk} \end{aligned}$$

(2) Calculate $\sum_{i=1}^s \sum_{j=1}^{n_i} \underline{\Phi}_{ij}$, where

$$\underline{\Phi}_{ij} = \sum_{\ell=1}^3 \sum_{\ell'=1}^3 \underline{X}_{ij\ell} \underline{\Lambda}_{ij\ell\ell'} \underline{X}_{ij\ell'}$$

Expressions for $\underline{\Lambda}_{ij\ell\ell'}$, are as follows:

$\ell \backslash \ell'$	1	2	3
1	Q_{ijj}	$-(P+n_{ij}Q_{ijj})\Sigma_8$	$-(P+n_{ij}Q_{ijj})\Sigma_9$
2	$-\Sigma_8(P+n_{ij}Q_{ijj})$	$n_{ij}\Sigma_8(P+n_{ij}Q_{ijj})\Sigma_8$	$n_{ij}\Sigma_8(P+n_{ij}Q_{ijj})\Sigma_9$
3	$-\Sigma_9(P+n_{ij}Q_{ijj})$	$n_{ij}\Sigma_9(P+n_{ij}Q_{ijj})\Sigma_8$	$n_{ij}\Sigma_9(P+n_{ij}Q_{ijj})\Sigma_9$

(2) Calculate $\sum_{i=1}^s \sum_{j=1}^{n_i} \sum_{\substack{k=1 \\ k \neq j}}^{n_{ij}} \phi_{ijk}$, where

$$\phi_{ijk} = \sum_{\ell=1}^3 \sum_{\ell'=1}^3 x_{ij\ell} \Gamma_{ijk\ell\ell'} x_{ik\ell'}$$

Expressions for $\Gamma_{ijk\ell\ell'}$ are as follows:

$\ell \backslash \ell'$	1	2	3	
$k < j$	1	Q'_{ikj}	$-n_{ik}Q'_{ikj}\Sigma_8$	$-n_{ik}Q'_{ikj}\Sigma_9$
	2	$-n_{ij}\Sigma_8 Q'_{ikj}$	$n_{ij}n_{ik}\Sigma_8 Q'_{ikj}\Sigma_8$	$n_{ij}n_{ik}\Sigma_8 Q'_{ikj}\Sigma_9$
	3	$-n_{ij}\Sigma_9 Q'_{ikj}$	$n_{ij}n_{ik}\Sigma_9 Q'_{ikj}\Sigma_8$	$n_{ij}n_{ik}\Sigma_9 Q'_{ikj}\Sigma_9$
$k > j$	1	Q_{ijk}	$-n_{ik}Q_{ijk}\Sigma_8$	$-n_{ik}Q_{ijk}\Sigma_9$
	2	$-n_{ij}\Sigma_8 Q_{ijk}$	$n_{ij}n_{ik}\Sigma_8 Q_{ijk}\Sigma_8$	$n_{ij}n_{ik}\Sigma_8 Q_{ijk}\Sigma_9$
	3	$-n_{ij}\Sigma_9 Q_{ijk}$	$n_{ij}n_{ik}\Sigma_9 Q_{ijk}\Sigma_8$	$n_{ij}n_{ik}\Sigma_9 Q_{ijk}\Sigma_9$

Step 5

Then calculate the t^*xt^* matrix

$$\sum_{i=1}^s x_i' V^{-1} x_i = \phi + \sum_{i=1}^s \sum_{j=1}^{n_i} \phi_{ij} + \sum_{i=1}^s \sum_{j=1}^{n_i} \sum_{\substack{k=1 \\ k \neq j}}^{n_{ij}} \phi_{ijk}$$

Step 6

(1) Calculate ω , where

$$\begin{aligned} \bar{y} = & \sum_{i=1}^s X'_{si} \Sigma^{-1} y_{si} + \sum_{i=1}^s \sum_{j=1}^{n_i} X'_{dij} \Sigma^{-1} y_{dij} \\ & + \sum_{i=1}^s \sum_{j=1}^{n_i} \sum_{k=1}^{n_{ij}} X'_{oijk} P y_{oijk}. \end{aligned}$$

(2) Calculate $\sum_{i=1}^s \sum_{j=1}^{n_i} \omega_{ij}$, where

$$\omega_{ij} = \sum_{\ell=1}^3 \sum_{\ell'=1}^3 X'_{ij\ell} \Gamma_{ij\ell\ell'} d_{ij\ell'}.$$

(3) calculate $\sum_{i=1}^s \sum_{j=1}^{n_i} \sum_{\substack{k=1 \\ k \neq j}}^{n_i} \omega_{ijk}$, where

$$\omega_{ijk} = \sum_{\ell=1}^3 \sum_{\ell'=1}^3 X'_{ij\ell} \Gamma_{ijk\ell\ell'} d_{ik\ell'}.$$

In the above expressions

$$d_{ij1} = y_{oij}.$$

$$d_{ij2} = y_{dij}$$

and

$$d_{ij3} = y_{si}.$$

Step 7

Then the $t^* \times 1$ right hand side vector is given by

$$\bar{w} + \sum_{i=1}^s \sum_{j=1}^{n_i} \omega_{ij} + \sum_{i=1}^s \sum_{j=1}^{n_i} \sum_{\substack{k=1 \\ k \neq j}}^{n_i} \omega_{ijk}.$$

4.3.3.2. An algorithm to compute the equations used to obtain the ML estimates of variance components

Step 1

Assuming initial values for θ_{mp} and θ_{mpp} , calculate Σ_h ($h=1, \dots, 9$).

Step 2

Calculate \tilde{P} and \tilde{Q}_{ijk} .

Step 3

Calculate (1) Δ_{0hm} for $h=1, \dots, 4$ and $m=1, \dots, 5$

(2) $\Delta_{\ell hm}$ for $\ell=1, 2$; $h=1, \dots, 4$ and $m=1, \dots, 6$

where

$$\Delta_{01m} = g_{1m} \tilde{I} - 2g_{4m} \tilde{I}_8 - 2g_{5m} \tilde{I}_9$$

$$\Delta_{02m} = (g_{1m} - g_{2m}) \tilde{I}$$

$$\Delta_{03m} = g_{2m} \tilde{I} - 2g_{4m} \tilde{I}_8 - 2g_{5m} \tilde{I}_9$$

$$\Delta_{04m} = g_{3m} \tilde{I} - 2g_{5m} \tilde{I}_9$$

$$\Delta_{11m} = g_{11m} \tilde{I} - 2g_{24m} \tilde{I}_8 - 2g_{25m} \tilde{I}_9$$

$$\Delta_{12m} = (g_{11m} - g_{12m}) \tilde{I}$$

$$\Delta_{13m} = g_{12m} \tilde{I} - 2g_{24m} \tilde{I}_8 - 2g_{25m} \tilde{I}_9$$

$$\Delta_{14m} = g_{13m} \tilde{I} - 2g_{25m} \tilde{I}_9$$

$$\Delta_{21m} = g_{21m} \tilde{I} - 2g_{14m} \tilde{I}_8 - 2g_{15m} \tilde{I}_9$$

$$\Delta_{22m} = (g_{21m} - g_{22m}) \tilde{I}$$

$$\Delta_{23m} = g_{22m} \tilde{I} - 2g_{14m} \tilde{I}_8 - 2g_{15m} \tilde{I}_9$$

and

$$\Delta_{24m} = g_{23m} \tilde{I} - 2g_{15m} \tilde{I}_9.$$

Step 4

Calculate \tilde{T}_h for $h=1, \dots, 4$, where

$$\tilde{T}_1 = n_{00} \tilde{P}$$

$$\tilde{T}_2 = \sum_{i=1}^s \sum_{j=1}^{n_i} n_{ij} Q_{ijj}$$

$$\tilde{T}_3 = \sum_{i=1}^s \sum_{j=1}^{n_i} n_{ij}^2 Q_{ijj}$$

and

$$\underline{T}_4 = \sum_{i=1}^s \sum_{j=1}^{n_i} n_{ij} \underline{R}_{ij}^* \quad \text{where} \quad \underline{R}_{ij}^* = \underline{R}_{ij} - n_{ij} \underline{Q}_{ijj}.$$

Step 5

(1) Calculate \underline{D} where

$$\underline{D} = (n_0 + s) \underline{\Sigma}_1^{-1} + \underline{\Sigma}_8 (\underline{T}_1 + \underline{T}_3) \underline{\Sigma}_8 + \underline{\Sigma}_9 (\underline{T}_1 + \underline{T}_3 + \underline{T}_4) \underline{\Sigma}_9.$$

(2) $\underline{D}_{\ell m}$ for $\ell=1, 2$ and $m=1, \dots, 6$, where

$$\underline{D}_{\ell m} = \sum_{h=1}^4 \underline{T}_h \Delta_{\ell h m}.$$

(3) \underline{D}_{0m} for $m=1, \dots, 5$, where

$$\underline{D}_{0m} = \sum_{h=1}^4 \underline{T}_h \Delta_{0h m}.$$

Step 6

Then calculate \underline{T}_{1mp} and $\underline{T}_{1mpp'}$ for $p=1, \dots, q$ and $p' = p+1, \dots, q$, where

$$\underline{T}_{1mp} = \underline{e}'_p (\underline{D} + \underline{D}_{0m}) \underline{e}_p$$

and

$$\begin{aligned} \underline{T}_{1mpp'} &= \underline{g}_{11m} \underline{e}'_{p'} \underline{D} \underline{e}_p + \underline{g}_{21m} \underline{e}'_{p'} \underline{D} \underline{e}_{p'} \\ &+ \underline{e}'_{p'} \underline{D}_{1m} \underline{e}_p + \underline{e}'_{p'} \underline{D}_{2m} \underline{e}_{p'}. \end{aligned}$$

Step 7

Using an estimate for $\underline{\beta}$, calculate \underline{y}_{oijk}^* , \underline{y}_{dij}^* and \underline{y}_{si}^* where

$$\underline{y}_{oijk}^* = \underline{y}_{oijk} - \underline{X}_{oijk} \underline{\beta}$$

$$\underline{y}_{dij}^* = \underline{y}_{dij} - \underline{X}_{dij} \underline{\beta}$$

and

$$y_{si}^* = y_{si} - x_{si}\beta.$$

Step 8

Calculate ε_{ij} and u_{oij}^* for $i=1, \dots, s$ and $j=1, \dots, n_i$, where

$$\varepsilon_{ij} = y_{oij}^* - n_{ij}\Sigma_8 y_{dij}^* - n_{ij}\Sigma_9 x_{si}^*$$

and

$$u_{oij}^* = \sum_{k=1}^{j-1} Q_{ikj} \varepsilon_{ik} + \sum_{k=j}^{n_i} Q_{ijk} \varepsilon_{ik}.$$

In the above expression

$$y_{oij}^* = \sum_{k=1}^{n_{ij}} y_{oijk}^*.$$

Step 9

Calculate u_{oijk} , u_{dij} and u_{si}

where

$$u_{oijk} = P(y_{oijk}^* - \Sigma_8 y_{dij}^* - \Sigma_9 y_{si}^*) + u_{oij}^*$$

$$u_{dij} = \Sigma_1^{-1} y_{dij}^* - \Sigma_8 P \varepsilon_{ij} - n_{ij} \Sigma_8 u_{oij}^*$$

and

$$u_{si} = \Sigma_1^{-1} y_{si}^* - \Sigma_9 P \sum_{j=1}^{n_i} \varepsilon_{ij} - \Sigma_9 \sum_{j=1}^{n_i} n_{ij} u_{oij}^*.$$

Step 10

Calculate (1) δ_{0hm} for $h=1, \dots, 5$ and $m=1, \dots, 5$

(2) $\delta_{\ell hm}$ for $\ell=1, 2$; $h=1, \dots, 5$ and $m=1, \dots, 6$

where

$$\delta_{0hm} = \begin{cases} g_{1m} - g_{2m} & \text{for } h=1 \\ g_{hm} & \text{for } h=2, 3 \\ 2g_{hm} & \text{for } h=4, 5 \end{cases}$$

$$\delta \ell_{hm} = \begin{cases} g_{hm} - g_{hm} & \text{for } h=1 \\ g_{hm} & \text{for } h=2,3 \\ 2g_{hm} & \text{for } h=4,5 \end{cases}$$

Step 11

Calculate S_h , where

$$S_1 = \sum_{i=1}^s \sum_{j=1}^{n_i} \sum_{k=1}^{n_{ij}} u_{oijk} u'_{oijk}$$

$$S_2 = \sum_{i=1}^s \sum_{j=1}^{n_i} u_{oij} u'_{oij}$$

$$S_3 = \sum_{i=1}^s \sum_{j=1}^{n_i} \sum_{\substack{k=1 \\ k \neq j}}^{n_i} u_{oij} u'_{oik}$$

$$S_4 = \sum_{i=1}^s \sum_{j=1}^{n_i} u_{dij} u'_{oij}$$

and

$$S_5 = \sum_{i=1}^s \sum_{j=1}^{n_i} u_{si} u'_{oij}$$

Step 12

Calculate G and $G_{\ell m}$ for $\ell=0,1,2$, where

$$G = \sum_{i=1}^s u_{si} u'_{si} + \sum_{i=1}^s \sum_{j=1}^{n_i} u_{dij} u'_{dij}$$

$$G_{0m} = \sum_{h=1}^5 \delta_{0hm} S_h \quad \text{for } m=1, \dots, 5$$

and

$$G_{\ell m} = \sum_{h=1}^5 \delta_{\ell hm} S_h \quad \text{for } m=1, \dots, 6 \text{ and } \ell=1,2.$$

Step 13

Calculate T_{2mp} and $T_{2mpp'}$ for $m=1, \dots, 5$;
 $p=1, \dots, q$ and $p'=1, \dots, q$, where

$$T_{2mp} = e_p'(G + G_{0m})e_p$$

and

$$T_{2mpp'} = g_{11m}e_p'Ge_p + g_{21m}e_p'Ge_{p'} \\ + e_p'G_{1m}e_p + e_p'G_{2m}e_{p'}$$

Step 14

Then the left hand sides of the equations corresponding to θ_{mp} and $\theta_{mpp'}$ are given by

$$T_{1mp} - T_{2mp}$$

and

$$T_{1mpp'} - T_{2mpp'}$$

respectively.

In the case where constraints are imposed on the variance parameters, an obvious procedure is to minimize

$$(T_{1mp} - T_{2mp})^2$$

and

$$(T_{1mpp'} - T_{2mpp'})^2$$

subject to

$$\theta_{1p}, \theta_{2p}, \theta_{3p}, \theta_{4p} \geq 0;$$

$$\theta_{1p}\theta_{2p} - \theta_{5p} \geq 0;$$

$$\theta_{1p}\theta_{2p'} - \theta_{5pp'} \geq 0;$$

and

$$\theta_{1p'}\theta_{2p} - \theta_{6pp'} \geq 0.$$

The method of estimating variance components and fixed effects developed in this chapter for a single-trait case was applied to weaning weight data of Romney sheep and 8-week weights of Yorkshire or Large White pigs. The results of these analyses are given in Chapter 6.

CHAPTER 5. BEST LINEAR UNBIASED PREDICTION
OF DIRECT AND MATERNAL GENETIC EFFECTS

Henderson's (1963) best linear unbiased prediction procedure (BLUP) can be used for predicting direct and maternal additively genetic values. However, practical applications of BLUP technique to animal breeding data require efficient computing strategies. One of the main difficulties is obtaining the inverse of the variance-covariance matrix of direct and maternal genetic effects which is essential in forming the BLUP equations. When predictions are made of the direct and the maternal genetic values of all animals, inversion of the variance-covariance matrix is not difficult since predicting direct and maternal genetic values of all animals is a special case of multiple-trait evaluation [see Henderson and Quaas (1976)]. Then the variance-covariance matrix has order $2n \times 2n$, where n is the number of animals, the general form being

$$\underline{G} = \underline{\Sigma} * \underline{A}$$

where \underline{A} is the numerator relationship matrix of the n animals and

$$\underline{\Sigma} = \begin{bmatrix} \sigma_{AO}^2 & \sigma_{AOAm} \\ \sigma_{AOAm} & \sigma_{Am}^2 \end{bmatrix},$$

for σ_{AO}^2 , σ_{Am}^2 and σ_{AOAm} being as defined in (4.2). The inverse of this matrix is

$$\underline{G}^{-1} = \underline{\Sigma}^{-1} * \underline{A}^{-1}.$$

Since $\underline{\Sigma}$ is a 2×2 matrix and simple methods of inverting the numerator relationship matrix exist, it is not difficult to obtain \underline{G}^{-1} .

The use of BLUP for predicting direct and maternal genetic values for weaning weights of beef cattle is considered in detail by Slinger (1979, 1980). Three general approaches for applying a maternal effects model to actual data were discussed. In the first instance, direct and maternal genetic values of all animals were predicted. In the second and third cases the number of genetic predictions were reduced by excluding certain genetic values. For example, in the second approach, the direct genetic values of unidentified dams, the direct genetic values of identified dams with records but having just one progeny and the maternal genetic values of animals with records but no progeny, were excluded.

If the objective is to predict the genetic merit of each individual free of the maternal genetic effects of their dams, predictors are required for the direct genetic values of the animals of interest together with the maternal genetic values of just their dams. Such situations arise in the case of meat breeds, where maternal genetic ability for offspring growth is of no importance commercially. Then the animals are selected on their individual genetic merit. However, since the genetic effect of an individual is a combination of the direct genetic value of the individual and the maternal genetic value of its dam, it is important to distinguish the individual's genetic ability from the maternal ability of the dam. In such circumstances predicting direct and maternal genetic values of all animals would make the number of BLUP equations unnecessarily large.

Although no analysis was carried out using actual data, BLUP equations for predicting direct genetic values of all animals and the maternal genetic values of their dams are derived in this thesis. In the process, Quaas's (1975, 1984) method of inverting the relationship matrix is modified to derive rules for obtaining the inverse of the variance-covariance matrix of the direct genetic values of all animals and the maternal genetic values of their dams. If required, it is also possible to predict the

maternal genetic values of sires or the maternal genetic values of animals with no progeny. An expression for \underline{R}^{-1} where \underline{R} is the variance-covariance matrix of the combined residual effects (combined residual effect is the sum of the residual effect common to full-sibs and maternal half-sibs and the residual effect unique to the individual) is also derived.

5.1. BLUP equations for predicting direct genetic values of all animals and the maternal genetic values of their corresponding dams

The expression given in (4.1), that is, for a phenotypic observation on an individual which is influenced by the maternal effects of it's dam, can also be written as

$$y_i = f_i(\underline{\beta}) + g_{di} + g_{mw} + e_i \quad (5.1)$$

where e_i is a combined residual effect, that is

$$e_i = e_{mw} + e_{di} \quad (5.2)$$

for e_{mw} and e_{di} defined in (4.1). In matrix terminology, (5.1) can be expressed as

$$\underline{y} = \underline{X}\underline{\beta} + \underline{Z}\underline{u} + \underline{e} \quad (5.3)$$

where

\underline{y} is the vector of records adjusted, if possible, for known fixed effects estimated from prior data;

$\underline{\beta}$ is the vector of remaining unknown fixed effects;

\underline{u} is the unknown vector of direct genetic and maternal genetic effects;

\underline{e} is the vector of combined residual effects; and

\underline{X} and \underline{Z} are known matrices.

Assume that

$$E \begin{bmatrix} \underline{u} \\ \underline{e} \end{bmatrix} = \begin{bmatrix} \underline{0} \\ \underline{0} \end{bmatrix}$$

and

$$\text{Var} \begin{bmatrix} \underline{u} \\ \underline{e} \end{bmatrix} = \begin{bmatrix} \underline{G} & \underline{0} \\ \underline{0} & \underline{R} \end{bmatrix}$$

where \underline{G} and \underline{R} are known non-singular matrices. Then, the best linear unbiased estimator of $\underline{\beta}$ and the best linear unbiased predictor of \underline{u} are obtained by solving the following set of equations:

$$\begin{bmatrix} \underline{X}'\underline{R}^{-1}\underline{X} & \underline{X}'\underline{R}^{-1}\underline{Z} \\ \underline{Z}'\underline{R}^{-1}\underline{X} & \underline{Z}'\underline{R}^{-1}\underline{Z} + \underline{G}^{-1} \end{bmatrix} \begin{bmatrix} \hat{\underline{\beta}} \\ \hat{\underline{u}} \end{bmatrix} = \begin{bmatrix} \underline{X}'\underline{R}^{-1}\underline{y} \\ \underline{Z}'\underline{R}^{-1}\underline{y} \end{bmatrix} \quad (5.4)$$

Suppose there are n animals whose direct additively genetic values and the maternal additively genetic values of their dams are to be predicted. Let the vector of genetic values be written as

$$\underline{u}' = (\underline{u}'_d, \underline{u}'_m)$$

where \underline{u}'_d is the $n \times 1$ vector of direct genetic values of the n animals and \underline{u}'_m is the $n_0 \times 1$ vector of maternal genetic values of the dams of the n animals (n_0 is the number of dams). Then the variance-covariance matrix of \underline{u} is the $(n+n_0)^2$ matrix

$$\underline{G} = \begin{bmatrix} \sigma_{A_0 A_{dd}}^2 & \sigma_{A_0 A_{dm}} \\ \sigma_{A_0 A_{dm}} & \sigma_{A_m A_{mm}}^2 \end{bmatrix}$$

where \underline{A}_{dd} is the numerator relationship matrix of the n animals, \underline{A}_{dm} is the matrix of additive relationships amongst all n animals and the dams thereof and \underline{A}_{mm} is the numerator relationship matrix amongst the dams of the n animals. Then

$$\underline{G}^{-1} = \begin{bmatrix} \underline{H}_{dd} & \underline{H}_{dm} \\ \underline{H}'_{dm} & \underline{H}_{mm} \end{bmatrix}$$

where \underline{H}_{dd} , \underline{H}_{dm} and \underline{H}_{mm} are matrices of order $n \times n$, $n \times n_0$ and $n_0 \times n_0$, respectively. Also let,

$$\underline{Z} = [\underline{Z}_d \quad \underline{Z}_m],$$

where the two matrices \underline{Z}_d and \underline{Z}_m correspond to \underline{u}_d and \underline{u}_m , respectively. Then from (5.4), the best linear unbiased estimator of $\underline{\beta}$ and the best linear unbiased predictors of \underline{u}_d and \underline{u}_m can be obtained by solving

$$\begin{bmatrix} \underline{X}'\underline{R}^{-1}\underline{X} & \underline{X}'\underline{R}^{-1}\underline{Z}_d & \underline{X}'\underline{R}^{-1}\underline{Z}_m \\ \underline{Z}'_d\underline{R}^{-1}\underline{X} & \underline{Z}'_d\underline{R}^{-1}\underline{Z}_d + \underline{H}_{dd} & \underline{Z}'_d\underline{R}^{-1}\underline{Z}_m + \underline{H}_{dm} \\ \underline{Z}'_m\underline{R}^{-1}\underline{X} & \underline{Z}'_m\underline{R}^{-1}\underline{Z}_d + \underline{H}'_{dm} & \underline{Z}'_m\underline{R}^{-1}\underline{Z}_m + \underline{H}_{mm} \end{bmatrix} \begin{bmatrix} \hat{\underline{\beta}} \\ \hat{\underline{u}}_d \\ \hat{\underline{u}}_m \end{bmatrix} = \begin{bmatrix} \underline{X}'\underline{R}^{-1}\underline{y} \\ \underline{Z}'_d\underline{R}^{-1}\underline{y} \\ \underline{Z}'_m\underline{R}^{-1}\underline{y} \end{bmatrix}.$$

Direct inversion of \underline{G} (using (3.10)) for obtaining \underline{H}_{dd} , \underline{H}_{dm} and \underline{H}_{mm} involves inverting either

$$\underline{A}_{mm} - r^{-2}\underline{A}'_{dm}\underline{A}^{-1}_{dd}\underline{A}_{dm}$$

or

$$\underline{A}_{dd} - r^{-2}\underline{A}_{dm}\underline{A}^{-1}_{mm}\underline{A}'_{dm},$$

where r is the correlation between direct and maternal genetic effects. Although the method of computing the inverse of a relationship matrix [Henderson (1975b,1976), Quaas (1975,1976)] can be used to invert \underline{A}_{dd} and \underline{A}_{mm} , inverting the above matrices is

a formidable task. However, if the elements of u are rearranged, the methods used in Quaas (1975,1984) can be modified to enable inversion of the matrix G .

5.2. The inverse of the variance-covariance matrix of direct and maternal genetic values

In this section, Quaas's (1975,1984) method for obtaining the inverse of the numerator relationship matrix is modified to enable inversion of the variance-covariance matrix of direct and maternal genetic effects defined in (5.3).

Without loss of generality, denote the vector of genetic values of the i th individual by \underline{u}_i . If both direct and maternal genetic values of i are to be predicted, \underline{u}_i is a vector with two elements, otherwise it is a scalar. That is

$$\underline{u}_i' = (u_{di}, u_{mi})$$

or

$$\underline{u}_i = u_{di},$$

respectively, where u_{di} and u_{mi} are the direct and maternal genetic values of the i th individual. In above, u_{mi} is only expressed in the phenotype of the offspring of individual i .

Following Quaas (1975,1984), define u_{di} and u_{mi} as

$$u_{di} = \frac{1}{2}u_{dj} + \frac{1}{2}u_{dk} + \phi_{di}$$

and

$$u_{mi} = \frac{1}{2}u_{mj} + \frac{1}{2}u_{mk} + \phi_{mi}$$

where

u_{dj} and u_{mj} are the direct and maternal genetic values of i 's dam (j);

u_{dk} and u_{mk} are the direct and maternal genetic values of i 's sire (k); and ϕ_{di} and ϕ_{mi} represent Mendelian sampling effects.

In Slanger's (1979) expressions for u_{di} and u_{mi} , the coefficients associated with the parents genetic values were not taken to be $1/2$.

Let the n vectors of the n individuals be arranged in such a way that the vectors of parents precede the vectors of progeny. That is

$$\underline{u}' = (\underline{u}'_1, \dots, \underline{u}'_i, \dots, \underline{u}'_n)$$

where vectors of i 's parents (\underline{u}'_j and \underline{u}'_k) precede \underline{u}'_i . The vector \underline{u} can be expressed as (see Chapter 3)

$$\underline{u} = (\underline{I} - \frac{1}{2}\underline{P})^{-1}\underline{\phi} \quad (5.5)$$

where \underline{P} , in contrast to its definition in Slanger's (1979) paper, is a matrix of zeroes and ones and

$$\underline{\phi}' = (\underline{\phi}'_1, \dots, \underline{\phi}'_i, \dots, \underline{\phi}'_n).$$

In the expression above, $\underline{\phi}'_i$ corresponds to \underline{u}'_i and therefore is a vector with two elements, or alternatively a scalar. Then it follows that

$$\text{Var}(\underline{u}) = \underline{G} = (\underline{I} - \frac{1}{2}\underline{P})^{-1}\underline{D}(\underline{I} - \frac{1}{2}\underline{P}')^{-1} \quad (5.6)$$

where

$$\underline{D} = \text{Var}(\underline{\phi}).$$

Assuming that

$$\text{Cov}(\phi_i, \phi_j') = \underline{0} \quad \text{for } i \neq j,$$

it can be observed that

$$\underline{D} = \sum_{i=1}^{n+} \underline{D}_i$$

where

$$\underline{D}_i = \text{Var}(\phi_i).$$

Each \underline{D}_i is a scalar or a 2x2 matrix depending on whether \underline{u}_i contains just u_{di} or both u_{di} and u_{mi} . From (5.6)

$$\underline{G}^{-1} = \underline{D}^{-1} - \frac{1}{2} \underline{P}' \underline{D}^{-1} - \frac{1}{2} \underline{D}^{-1} \underline{P} + \frac{1}{4} \underline{P}' \underline{D}^{-1} \underline{P}. \quad (5.7)$$

Inverting \underline{D} is not difficult, since

$$\underline{D}^{-1} = \sum_{i=1}^{n+} \underline{D}_i^{-1}.$$

Therefore simple modifications of Quaas's (1975, 1984) rapid method of inverting the relationship matrix can be utilized in inverting \underline{G} .

5.2.1. Expressions for \underline{D}_i

The Mendelian sampling random variables ϕ_{di} and ϕ_{mi} can be written as

$$\phi_{di} = u_{di} - \frac{1}{2} u_{dj} - \frac{1}{2} u_{dk}$$

and

$$\phi_{mi} = u_{mi} - \frac{1}{2} u_{mj} - \frac{1}{2} u_{mk}.$$

Then

$$\underline{D}_i = \begin{bmatrix} a_{dd}^* \sigma_{Ao}^2 & a_{dm}^* \sigma_{AoAm} \\ a_{dm}^* \sigma_{AoAm} & a_{mm}^* \sigma_{Am}^2 \end{bmatrix} \quad (5.8)$$

where

$$a_{dd}^* = a_{dm}^* = a_{mm}^* = 1 - \frac{1}{4}a_{jj} - \frac{1}{4}a_{kk}.$$

However, certain genetic values are not included in the vector of genetic values to be predicted. For example, maternal genetic values of some animals (sires and animals with no progeny) are not considered in (5.3). For such cases, \underline{D}_i is a scalar and is given by $a_{dd}^* \sigma_{Ao}^2$. If the genetic values of one or both parents are not included, a_{jj} and/or a_{kk} are assumed to be zero. The possible expressions for \underline{D}_i are outlined below:

- (1) $\underline{u}_i = u_{di}$; both parents of i are unknown

$$D_i = \sigma_{Ao}^2$$

- (2) $\underline{u}_i = (u_{di}, u_{mi})$; both parents of i are unknown

\underline{D}_i has the form given in (5.8) with

$$a_{dd}^* = a_{dm}^* = a_{mm}^* = 1$$

- (3) $\underline{u}_i = u_{di}$; direct genetic value of one parent (u_{dj}) is included

$$a_{dd}^* = 1 - \frac{1}{4}a_{jj}$$

- (4) $\underline{u}_i = (u_{di}, u_{mi})$; dam's direct and maternal genetic values are included

$$a_{dd}^* = a_{dm}^* = a_{mm}^* = 1 - \frac{1}{4}a_{jj}$$

- (5) $\underline{u}_i = u_{di}$; direct genetic values of both parents are included

$$D_i = (1 - \frac{1}{4}a_{jj} - \frac{1}{4}a_{kk})\sigma_{Ao}^2$$

- (6) $\underline{u}_i' = (u_{di}, u_{mi})$; direct genetic values of both parents and the maternal genetic value of the dam are included

$$a_{dd}^* = a_{dm}^* = 1 - \frac{1}{4}a_{jj} - \frac{1}{4}a_{kk}$$

$$a_{mm}^* = 1 - \frac{1}{4}a_{jj}$$

- (7) $\underline{u}_i' = (u_{di}, u_{mi})$; direct and maternal genetic values of both parents are included

$$a_{dd}^* = a_{dm}^* = a_{mm}^* = 1 - \frac{1}{4}a_{jj} - \frac{1}{4}a_{kk}$$

The above expressions for D_i involve the diagonal values of the relationship matrix. Quaas (1975,1984) demonstrated how these can be computed using only two vectors of length n . This method which is outlined in Chapter 3 can be used to obtain the diagonal elements of the relationship matrix.

Denote \underline{D}_i^{-1} as

$$\underline{D}_i^{-1} = \begin{cases} d_{oo}^{ii} & \text{if } \underline{u}_i = u_{di} \\ \begin{bmatrix} d_{oo}^{ii} & d_{om}^{ii} \\ d_{mo}^{ii} & d_{mm}^{ii} \end{bmatrix} & \text{if } \underline{u}_i' = (u_{di}, u_{mi}) \end{cases}$$

where

$$d_{om}^{ii} = d_{mo}^{ii}$$

Then $\underline{\tilde{G}}^{-1}$ can be computed using simple modifications of the methods used in Henderson (1975b,1976) and Quaas (1975,1984) for inverting the numerator relationship matrix.

5.2.2. Generating $\underline{\tilde{G}}^{-1}$

Step 1

Initially, let

$$\underline{\tilde{G}}^{-1} = \underline{D}^{-1}.$$

Step 2

Determine contributions to $\underline{\tilde{G}}^{-1}$ by proceeding through the list of animals ordered so that the parents precede progeny. There will be no further contributions from the "base" animals. The contributions from the other animals are given below for different possibilities. In what follows \underline{g}_{OO}^{ij} , \underline{g}_{Om}^{ij} and \underline{g}_{mm}^{ij} refer to the elements of $\underline{\tilde{G}}^{-1}$ corresponding to the direct genetic value of i and the direct genetic value of j , the direct genetic value of i and the maternal genetic value of j and the maternal genetic value of i and the maternal genetic value of j , respectively.

- (1) $\underline{u}_i = u_{di}$; direct genetic value of one parent is included

subtract $.5d_{OO}^{ii}$ from \underline{g}_{OO}^{ij} and \underline{g}_{OO}^{ji}

add $.25d_{OO}^{ii}$ to \underline{g}_{OO}^{jj}

- (2) $\underline{u}_i = u_{di}$; direct genetic values of both parents (u_{dj} and u_{dk}) are included

subtract $.5d_{OO}^{ii}$ from \underline{g}_{OO}^{ij} , \underline{g}_{OO}^{ik} , \underline{g}_{OO}^{ji} and \underline{g}_{OO}^{ki}

add $.25d_{oo}^{ii}$ to g_{oo}^{jj} , g_{oo}^{jk} , g_{oo}^{kj} and g_{oo}^{kk}

- (3) $\tilde{u}_i^d = (u_{di}, u_{mi})$; direct genetic value of the sire is included

subtract $.5d_{oo}^{ii}$ from g_{oo}^{ij} and g_{oo}^{ji}

subtract $.5d_{om}^{ii}$ from g_{om}^{ki} and g_{mo}^{ik}

add $.25d_{oo}^{ii}$ to g_{oo}^{kk}

- (4) $\tilde{u}_i^d = (u_{di}, u_{mi})$; direct and maternal genetic values of the dam are included

subtract $.5d_{oo}^{ii}$ from g_{oo}^{ij} and g_{oo}^{ji}

subtract $.5d_{om}^{ii}$ from g_{om}^{ij} , g_{om}^{ji} , g_{mo}^{ij} and g_{mo}^{ji}

subtract $.5d_{mm}^{ii}$ from g_{mm}^{ij} and g_{mm}^{ji}

add $.25d_{oo}^{ii}$ to g_{oo}^{jj}

add $.25d_{om}^{ii}$ to g_{om}^{jj} and g_{mo}^{jj}

add $.25d_{mm}^{ii}$ to g_{mm}^{jj}

- (5) $\tilde{u}_i^d = (u_{di}, u_{mi})$; direct and maternal genetic values of the dam and the direct genetic value of the sire are included

subtract $.5d_{oo}^{ii}$ from g_{oo}^{ij} , g_{oo}^{ji} , g_{oo}^{ik} and g_{oo}^{ki}

subtract $.5d_{om}^{ii}$ from g_{om}^{ij} , g_{om}^{ji} , g_{mo}^{ij} , g_{mo}^{ji} , g_{om}^{ki} and g_{mo}^{ik}

subtract $.5d_{mm}^{ii}$ from g_{mm}^{ij} and g_{mm}^{ji}

add $.25d_{oo}^{ii}$ to g_{oo}^{jj} , g_{oo}^{jk} , g_{oo}^{kj} and g_{oo}^{kk}

add $.25d_{om}^{ii}$ to g_{om}^{jj} and g_{mo}^{jj}

add $.25d_{mm}^{ii}$ to g_{mm}^{jj}

- (6) $\underline{u}_i = (u_{di}, u_{mi})$; direct and maternal genetic values of both parents are included

subtract $.5d_{oo}^{ii}$ from g_{oo}^{ij} , g_{oo}^{ji} , g_{oo}^{ik} and g_{oo}^{ki}

subtract $.5d_{om}^{ii}$ from g_{om}^{ij} , g_{mo}^{ij} , g_{om}^{ik} , g_{mo}^{ik} , g_{om}^{ji} , g_{mo}^{ji} , g_{om}^{ki} and g_{mo}^{ki}

subtract $.5d_{mm}^{ii}$ from g_{mm}^{ij} , g_{mm}^{ji} , g_{mm}^{ik} and g_{mm}^{ki}

add $.25d_{oo}^{ii}$ to g_{oo}^{jj} , g_{oo}^{jk} , g_{oo}^{kj} and g_{oo}^{kk}

add $.25d_{om}^{ii}$ to g_{om}^{jj} , g_{mo}^{jj} , g_{om}^{jk} , g_{mo}^{jk} , g_{om}^{kj} , g_{mo}^{kj} , g_{om}^{kk} and g_{mo}^{kk}

add $.25d_{mm}^{ii}$ to g_{mm}^{jj} , g_{mm}^{jk} , g_{mm}^{kj} and g_{mm}^{kk}

However, certain conditions have to be satisfied in order to generate the exact \underline{G}^{-1} , by using this method. These conditions are :

- (1) If the maternal genetic value of an animal is included, then the direct genetic value of that animal should also be included. For instance, if the maternal genetic value of an unidentified dam is included, then the direct genetic value of the dam should also be included, although this would not be considered in the selection process.
- (2) If direct and maternal genetic values of the dam are included, then both genetic values of the sire should also be included.

When additional genetic values are included, the vectors \underline{u}_d , \underline{u}_m and the matrices \underline{A}_{dd} , \underline{A}_{dm} and \underline{A}_{mm} in (5.4) should be altered appropriately.

Examples to demonstrate how the inverse of \underline{G} is generated and to illustrate why certain conditions have to be satisfied by the vector of genetic values to be predicted are given in Appendix 4.

5.3. The inverse of the variance-covariance matrix of the residual effects

In addition to \underline{G}^{-1} , the inverse of the matrix \underline{R} (as defined in (5.3)) is required to form BLUP equations. In this section, an expression for \underline{R}^{-1} will be derived. An individual record of \underline{y} in (5.3) can also be written as

$$y_{ij} = \underline{x}_{ij}'\underline{\beta} + u_{dij} + u_{mi} + e_{ij} \quad (5.9)$$

where

u_{dij} is the direct genetic effect of the j th offspring of the i th dam;

u_{mi} is the maternal genetic effect of the dam i influencing the phenotype of her offspring; and

e_{ij} is the combined residual effect of the j th offspring of dam i .

From (5.2) the combined residual effect can be written as

$$e_{ij} = e_i^* + e_{ij}^*$$

where e_i^* is the residual effect common to full-sibs and the maternal half-sibs of dam i and e_{ij}^* is the residual effect peculiar to the j th offspring of i th dam. Then it follows that

$$\text{Cov}(e_{ij}, e_{i'k}) = \begin{cases} \sigma_{Em}^2 + \sigma_{Eo}^2 & \text{if } i=i' \text{ and } j=k \\ \sigma_{Em}^2 & \text{if } i=i' \text{ and } j \neq k \\ 0 & \text{if } i \neq i' \end{cases} \quad (5.10)$$

Therefore it is convenient to compute \underline{R}^{-1} , by writing the vector \underline{e} as

$$\underline{e}' = (e_0', e_1', \dots, e_1', \dots, e_{n_0}')$$

where \underline{e}_i for $i=1, \dots, n_0$ is an $n_i \times 1$ vector (n_i is the number of offspring of the i th dam), which is given by

$$\underline{e}_i' = (e_{i1}, \dots, e_{ij}, \dots, e_{in_i})$$

and \underline{e}_0 is the vector of combined residual effects of animals with unidentified dams and the animals with no full-sibs or maternal half-sibs. The above arrangement means that the elements of \underline{e}_i are the combined residual effects of the offspring of the i th dam. Since $\text{Cov}(e_{ij}, e_{i'k}) = 0$ when $i \neq i'$, the matrix \underline{R} can be written as

$$\underline{R} = \sum_{i=0}^{n_0} \underline{R}_i$$

where

$$\underline{R}_i = \text{Var}(\underline{e}_i).$$

But from (5.10), \underline{R}_i is an $n_i \times n_i$ matrix with $\sigma_{Eo}^2 + \sigma_{Em}^2$ as the diagonal elements and σ_{Em}^2 as the off-diagonal elements. That is, for $i=1, \dots, n_0$

$$\underline{R}_i = \sigma_{Eo}^2 \underline{I}_i + \sigma_{Em}^2 \underline{J}_i,$$

where \underline{I}_i is the identity matrix of order n_i and \underline{J}_i is the $n_i \times n_i$ matrix of "1"s. Then it follows that

$$\underline{R}_i^{-1} = a\underline{I}_i + b_i\underline{J}_i$$

where

$$a = 1/\sigma_{E0}^2$$

and

$$b_i = - \frac{\sigma_{Em}^2}{\sigma_{E0}^2 (\sigma_{E0}^2 + n_i \sigma_{Em}^2)}$$

for $i=1, \dots, n_0$. Also,

$$\underline{R}_0^{-1} = \frac{1}{\sigma_{E0}^2} \underline{I}_0.$$

Therefore \underline{R}^{-1} can be obtained as

$$\underline{R}^{-1} = \sum_{i=0}^{n_0} \underline{R}_i^{-1}.$$

5.4. A multiple-trait setting

Suppose that there are n related animals each with records on q traits whose direct genetic values and the maternal genetic values of their dams for the q traits are to be predicted. Let the vector of genetic values be written as

$$\underline{u}' = (\underline{u}'_d, \underline{u}'_m)$$

where \underline{u}'_d is the $qn \times 1$ vector of direct genetic values and \underline{u}'_m is the $qn_0 \times 1$ vector of maternal genetic values of the dams of the n animals. Then the variance-covariance matrix of \underline{u} can be written as

$$\underline{G} = \begin{bmatrix} \underline{G}_{dd} & \underline{G}_{dm} \\ \underline{G}'_{dm} & \underline{G}_{mm} \end{bmatrix}$$

where

$$\underline{G}_{dd} = \text{Var}(\underline{u}_d)$$

$$\underline{G}_{dm} = \text{Cov}(\underline{u}_d, \underline{u}'_m)$$

and

$$\underline{G}_{mm} = \text{Var}(\underline{u}_m).$$

Suppose \underline{u}_m is ordered by the dams within traits. That is

$$\underline{u}'_m = (\underline{u}'_{m1}, \dots, \underline{u}'_{mi}, \dots, \underline{u}'_{mn_0})$$

where \underline{u}_{mi} is the $q \times 1$ vector of maternal genetic values of the q traits of the i th dam. Similarly \underline{u}_d can be ordered by dams within traits which leads to

$$\underline{u}'_d = (\underline{u}'_{d1}, \dots, \underline{u}'_{di}, \dots, \underline{u}'_{dn_0})$$

where \underline{u}_{di} is the $q n_i \times 1$ vector of the direct genetic values of the q traits of the n_i offspring of the i th dam. This means that

$$\underline{G}_{dd} = \underline{\Sigma}_{dd} * \underline{A}_{dd}$$

where $\underline{\Sigma}_{dd}$ is the $q \times q$ variance-covariance matrix of the direct genetic values of the q traits and \underline{A}_{dd} is the numerator relationship matrix of the n animals. The (p, p') th element of $\underline{\Sigma}_{dd}$ is the covariance between direct genetic effects of trait p and direct genetic effects of trait p' . Similarly,

$$\underline{G}_{dm} = \underline{\Sigma}_{dm} * \underline{A}_{dm}$$

and

$$\underline{G}_{mm} = \underline{\Sigma}_{mm} * \underline{A}_{mm}$$

where \underline{A}_{dm} is the matrix of additive relationships between the n animals and the dams of the n animals and \underline{A}_{mm} is the numerator relationship matrix of the dams of the n animals. The (p,p') th elements of $\underline{\Sigma}_{dm}$ and $\underline{\Sigma}_{mm}$ give the covariance between direct genetic effects of trait p and the maternal genetic effects of trait p' and the covariance between maternal genetic effects of trait p and maternal genetic effects of trait p' , respectively. This means that \underline{G} can be expressed as

$$\underline{G} = \begin{bmatrix} \underline{\Sigma}_{dd} * \underline{A}_{dd} & \underline{\Sigma}_{dm} * \underline{A}_{dm} \\ \underline{\Sigma}'_{dm} * \underline{A}'_{dm} & \underline{\Sigma}_{mm} * \underline{A}_{mm} \end{bmatrix}. \quad (5.11)$$

5.4.1. Generating the inverse of the variance-covariance matrix of the genetic effects

The inverse of \underline{G} can be generated easily by ordering \underline{u} so that the vectors of the genetic effects of the parents precede the vectors of genetic effects of the progeny. That is

$$\underline{u}' = (\underline{u}'_1, \dots, \underline{u}'_i, \dots, \underline{u}'_n)$$

where \underline{u}'_i is a $2q \times 1$ vector if the maternal genetic values of the q traits of the i th individual are included, in addition to the direct genetic values of the q traits of the i th individual. If the maternal genetic values of the q traits are not included, \underline{u}'_i has q elements. This means

$$\underline{u}'_i = (\underline{u}'_{di}, \underline{u}'_{mi})$$

or

$$\underline{u}_i = \underline{u}_{di},$$

depending on whether the maternal genetic values of the i th individual have been included or not.

Let the vector of genetic values of the i th individual be written as

$$\underline{u}_i = \frac{1}{2}\underline{u}_j + \frac{1}{2}\underline{u}_k + \phi_i$$

where \underline{u}_j and \underline{u}_k represent the vectors of genetic values of the dam and the sire, respectively. The elements of ϕ_i represent the Mendelian sampling random variables. Then

$$\phi_i = \underline{u}_i - \frac{1}{2}\underline{u}_j - \frac{1}{2}\underline{u}_k,$$

which implies that

$$\begin{aligned} \text{Var}(\phi_i) &= \text{Var}(\underline{u}_i) - \frac{1}{2}\text{Cov}(\underline{u}_i, \underline{u}_j') - \frac{1}{2}\text{Cov}(\underline{u}_i, \underline{u}_k') - \frac{1}{2}\text{Cov}(\underline{u}_j, \underline{u}_i') \\ &\quad + \frac{1}{4}\text{Var}(\underline{u}_j) + \frac{1}{4}\text{Cov}(\underline{u}_j, \underline{u}_k') - \frac{1}{2}\text{Cov}(\underline{u}_k, \underline{u}_i') \\ &\quad + \frac{1}{4}\text{Cov}(\underline{u}_k, \underline{u}_j') + \frac{1}{4}\text{Var}(\underline{u}_k). \end{aligned}$$

Suppose direct and maternal genetic values of q traits of the i th individual are to be predicted and that direct and maternal genetic values of both parents are included. This means that

$$\underline{u}_i' = (\underline{u}_{di}', \underline{u}_{mi}')'$$

$$\underline{u}_j' = (\underline{u}_{dj}', \underline{u}_{mj}')'$$

and

$$\underline{u}'_k = (\underline{u}'_{dk}, \underline{u}'_{mk})$$

where

$$\underline{u}'_{di} = (u'_{di1}, \dots, u'_{dip}, \dots, u'_{diq})$$

and

$$\underline{u}'_{mi} = (u'_{mi1}, \dots, u'_{mip}, \dots, u'_{miq}).$$

In the above vectors, u_{dip} and u_{mip} are the direct genetic value of the p th trait of the i th individual and the maternal genetic value of the p th trait of the i th individual, respectively.

Therefore

$$(1) \text{Var}(\underline{u}_i) = a_{ii}\Sigma$$

$$(2) \text{Cov}(\underline{u}_i, \underline{u}'_j) = \text{Cov}(\underline{u}_j, \underline{u}'_i) = a_{ij}\Sigma$$

$$(3) \text{Cov}(\underline{u}_i, \underline{u}'_k) = [\text{Cov}(\underline{u}_k, \underline{u}'_i)]' = a_{ik}\Sigma$$

$$(4) \text{Cov}(\underline{u}_j, \underline{u}'_k) = [\text{Cov}(\underline{u}_k, \underline{u}'_j)]' = a_{jk}\Sigma$$

$$(5) \text{Var}(\underline{u}_j) = a_{jj}\Sigma; \text{ and}$$

$$(6) \text{Var}(\underline{u}_k) = a_{kk}\Sigma$$

where

$$\Sigma = \begin{vmatrix} \Sigma_{dd} & \Sigma_{dm} \\ \Sigma'_{dm} & \Sigma_{mm} \end{vmatrix}.$$

Then it follows that

$$\underline{D}_i = \begin{bmatrix} \alpha_{dd}\Sigma_{dd} & \alpha_{dm}\Sigma_{dm} \\ \alpha_{dm}\Sigma_{dm} & \alpha_{mm}\Sigma_{mm} \end{bmatrix}$$

where

$$\begin{aligned} \alpha_{dd} &= a_{ii} - a_{ij} - a_{ik} + 0.25a_{jj} + 0.5a_{jk} + 0.25a_{kk} \\ &= 1 - 0.25a_{jj} - 0.25a_{kk} \end{aligned}$$

and

$$\alpha_{dm} = \alpha_{mm} = 1 - 0.25a_{jj} - 0.25a_{kk}.$$

In the case where certain genetic values of the parents are excluded from the vector of genetic values to be predicted, the corresponding values of a's are considered to be zero. For example, if

$$\underline{u}_k = \underline{u}_{dk}$$

then

$$\alpha_{mm} = 1 - 0.25a_{jj}$$

Also, if only the direct genetic values of q traits of the i th individual are to be predicted and that direct genetic values of j and k are included, then

$$\underline{u}_i = \underline{u}_{di}$$

$$\underline{u}_j = \underline{u}_{dj}$$

and

$$\underline{u}_k = \underline{u}_{dk}$$

which implies that

$$\underline{D}_i = \alpha_{dd} \underline{\Sigma}_{dd}. \quad (5.12)$$

Let the matrix \underline{G} be partitioned according to the n individuals. Then the (i,j) th block of \underline{G} gives the covariance between \underline{u}_i and \underline{u}_j . Suppose \underline{u}_i and \underline{u}_j consist of direct genetic values only. Then \underline{G}_{ij} is a qxq matrix and can also be denoted as $\underline{G}_{ij}(d,d)$. If \underline{u}_i consists of direct and maternal genetic values and \underline{u}_j consists of direct genetic values only, \underline{G}_{ij} is a $2qxq$ matrix which can be further partitioned as

$$\underline{G}_{ij} = \begin{bmatrix} \underline{G}_{ij}(d,d) \\ \underline{G}_{ij}(m,d) \end{bmatrix}.$$

If \underline{u}_i and \underline{u}_j consist of both direct and maternal genetic values, \underline{G}_{ij} is a $2qx2q$ matrix which can be denoted as

$$\underline{G}_{ij} = \begin{vmatrix} \underline{G}_{ij}(d,d) & \underline{G}_{ij}(d,m) \\ \underline{G}_{ij}(d,m) & \underline{G}_{ij}(m,m) \end{vmatrix}.$$

Let \underline{G}^{-1} be partitioned according to \underline{G} . Then \underline{G}^{-1} is generated as follows.

Step 1

Let $\underline{G}^{ii} = \underline{D}_i^{-1}$ for all $i = 1, \dots, n$

Step 2

Add contributions to \underline{G}^{-1} by proceeding through the list of animals ordered so that the parents precede the progeny. The "base" animals do not make further contributions.

- (1) direct genetic values only; direct genetic values of only one parent are included

subtract $0.5\underline{\Sigma}_{dd}$ from $\underline{G}^{ij}(d,d)$ and $\underline{G}^{ji}(d,d)$

add $0.25\underline{\Sigma}_{dd}$ to $\underline{G}^{jj}(d,d)$

- (2) direct genetic values only; direct genetic values of both parents are included

subtract $0.5\underline{\Sigma}_{dd}$ from $\underline{G}^{ij}(d,d)$, $\underline{G}^{ji}(d,d)$, $\underline{G}^{ik}(d,d)$ and $\underline{G}^{ki}(d,d)$

add $0.25\underline{\Sigma}_{dd}$ to $\underline{G}^{jj}(d,d)$, $\underline{G}^{jk}(d,d)$, $\underline{G}^{kj}(d,d)$ and $\underline{G}^{kk}(d,d)$

- (3) direct and maternal genetic values; direct and maternal genetic values of the dam are included

subtract $0.5\underline{\Sigma}_{dd}$ from $\underline{G}^{ij}(d,d)$ and $\underline{G}^{ji}(d,d)$

subtract $0.5\underline{\Sigma}_{dm}$ from $\underline{G}^{ij}(d,m)$ and $\underline{G}^{ji}(d,m)$

subtract $0.5\underline{\Sigma}'_{dm}$ from $\underline{G}^{ij}(m,d)$ and $\underline{G}^{ji}(m,d)$

subtract $0.5\underline{\Sigma}_{mm}$ from $\underline{G}^{ij}(m,m)$ and $\underline{G}^{ji}(m,m)$

add $0.25\underline{\Sigma}_{dd}$ to $\underline{G}^{jj}(d,d)$

add $0.25\underline{\Sigma}_{dm}$ to $\underline{G}^{jj}(d,m)$

add $0.25\underline{\Sigma}'_{dm}$ to $\underline{G}^{jj}(m,d)$

add $0.25\underline{\Sigma}_{mm}$ to $\underline{G}^{jj}(m,m)$

- (4) direct and maternal genetic values; direct and maternal genetic values of the dam and the direct genetic values of the sire are included

subtract $0.5\underline{\Sigma}_{dd}$ from $\underline{G}^{ij}(d,d)$, $\underline{G}^{ji}(d,d)$, $\underline{G}^{ik}(d,d)$
and $\underline{G}^{ki}(d,d)$

subtract $0.5\underline{\Sigma}_{dm}$ from $\underline{G}^{ij}(d,m)$, $\underline{G}^{ji}(d,m)$, and $\underline{G}^{ik}(d,m)$

subtract $0.5\underline{\Sigma}'_{dm}$ from $\underline{G}^{ij}(m,d)$, $\underline{G}^{ji}(m,d)$ and $\underline{G}^{ki}(m,d)$

subtract $0.5\underline{\Sigma}_{mm}$ to $\underline{G}^{ij}(m,m)$ and $\underline{G}^{ji}(m,m)$

add $0.25\underline{\Sigma}_{dd}$ to $\underline{G}^{jj}(d,d)$, $\underline{G}^{jk}(d,d)$, $\underline{G}^{kj}(d,d)$ and
 $\underline{G}^{kk}(d,d)$

add $0.25\underline{\Sigma}_{dm}$ to $\underline{G}^{jj}(d,m)$

add $0.25\underline{\Sigma}_{dm}$ to $\underline{G}^{jj}(m,d)$

add $0.25\underline{\Sigma}_{mm}$ to $\underline{G}^{jj}(m,m)$

- (5) direct and maternal genetic values; direct and maternal genetic values of both parents are included

subtract $0.5\underline{\Sigma}_{dd}$ from $\underline{G}^{ij}(d,d)$, $\underline{G}^{ji}(d,d)$, $\underline{G}^{ik}(d,d)$
and $\underline{G}^{ki}(d,d)$

subtract $0.5\underline{\Sigma}_{dm}$ from $\underline{G}^{ij}(d,m)$, $\underline{G}^{ji}(d,m)$, $\underline{G}^{ik}(d,m)$
and $\underline{G}^{ki}(d,m)$

subtract $0.5\underline{\Sigma}'_{dm}$ from $\underline{G}^{ij}(m,d)$, $\underline{G}^{ji}(m,d)$, $\underline{G}^{ik}(m,d)$
and $\underline{G}^{ki}(m,d)$

subtract $0.5\underline{\Sigma}_{mm}$ from $\underline{G}^{ij}(m,m)$, $\underline{G}^{ji}(m,m)$, $\underline{G}^{ik}(m,m)$

and $\underline{G}^{ki}(m,m)$

add $0.25\underline{\Sigma}_{dd}$ to $\underline{G}^{jj}(d,d)$, $\underline{G}^{jk}(d,d)$, $\underline{G}^{kj}(d,d)$ and $\underline{G}^{kk}(d,d)$

add $0.25\underline{\Sigma}_{dm}$ to $\underline{G}^{jj}(d,m)$, $\underline{G}^{jk}(d,m)$, $\underline{G}^{kj}(d,m)$ and $\underline{G}^{kk}(d,m)$

add $0.25\underline{\Sigma}'_{dm}$ to $\underline{G}^{jj}(m,d)$, $\underline{G}^{jk}(m,d)$, $\underline{G}^{kj}(m,d)$ and $\underline{G}^{kk}(m,d)$

add $0.25\underline{\Sigma}_{mm}$ to $\underline{G}^{jj}(m,m)$, $\underline{G}^{jk}(m,m)$, $\underline{G}^{kj}(m,m)$ and $\underline{G}^{kk}(m,m)$

As in the uni-trait case, the exact \underline{G}^{-1} is obtained when similar requirements are imposed on the structure of genetic effects to be predicted. In addition direct genetic values of all traits on all animals and the maternal genetic values of all traits of the dams of the animals should be predicted. When additional genetic values are included, the matrix in (5.11) should be altered appropriately. An example to illustrate the inversion of \underline{G} for a multiple-trait setting is given in Appendix 5.

5.4.2. Inverting the variance-covariance matrix of the residual effects

Let the vector of combined residual effects be ordered by dams, so that

$$\underline{e}' = (\underline{e}'_0, \underline{e}'_1, \dots, \underline{e}'_i, \dots, \underline{e}'_{n_0})$$

where \underline{e}'_i ($i=1, \dots, n_0$) is the $qn_i \times 1$ vector of the residual effects of the q traits of the n_i offspring of the i th dam and \underline{e}'_0 is the vector of combined residual effects of the animals with unidentified dams and the animals with no full-sibs and maternal half-sibs. Let these elements be ordered by animal within traits, which means that

$$\underline{e}_i = (e_{i1}, \dots, e_{ij}, \dots, e_{in_i}).$$

Then each e_{ij} is a vector of q elements, where the p th element is the combined residual effect of trait p of the j th offspring of the i th dam. That is

$$e_{ijp} = e_{ijp}^* + e_{ip}^*$$

where e_{ijp}^* is the residual effect unique to the j th offspring of the dam i and e_{ip}^* is the residual effect common to the p th trait of the offspring of dam i . This means that

$$\text{Cov}(e_{ijp}, e_{i'jk'}) = r_{oo}^{pp'} + r_{mm}^{pp'},$$

where $r_{oo}^{pp'}$ and $r_{mm}^{pp'}$ were defined in Chapter 4. Then it follows that, for $i=1, \dots, n_o$

$$\text{Cov}(e_{ij}, e_{ik'}) = \begin{cases} \underline{R}_d + \underline{R}_m & \text{if } i=i' \text{ and } j=k \\ \underline{R}_m & \text{if } i=i' \text{ and } j \neq k \\ \underline{0} & \text{if } i \neq i' \end{cases}$$

where \underline{R}_d and \underline{R}_m are $q \times q$ matrices, the (p, p') th elements being $r_{oo}^{pp'}$ and $r_{mm}^{pp'}$, respectively. Therefore, for $i=1, \dots, n_o$

$$\underline{R}_i = \text{Var}(\underline{e}_i) = \underline{I}_i * \underline{R}_o + \underline{J}_i * \underline{R}_m$$

and

$$\text{Cov}(\underline{e}_i, \underline{e}_{i'}) = \underline{0}$$

where \underline{I}_i is the identity matrix of order n_i and \underline{J}_i is the $n_i \times n_i$ matrix of "1"s. The variance-covariance matrix of \underline{e}_o is given by

$$\underline{R}_o = \underline{I}_i * \underline{R}_d.$$

Then it follows that

$$\underline{R}^{-1} = \sum_{i=0}^{n_0} \underline{R}_i^{-1}$$

where

$$\underline{R}_i^{-1} = \begin{cases} \underline{I}_i * \underline{A} & \text{for } i=0 \\ \underline{I}_i * \underline{A} + \underline{J}_i * \underline{B}_i & \text{for } i=1, \dots, n_0 \end{cases}$$

In the above expression

$$\underline{A} = \underline{R}_d^{-1}$$

and

$$\underline{B}_i = (\underline{R}_d + n_i \underline{R}_m)^{-1} \underline{R}_m \underline{R}_d^{-1}.$$

CHAPTER 6. A STUDY OF MATERNAL EFFECTS
IN WEANING WEIGHTS OF SHEEP AND SWINE

6.1. Sheep

Weaning weights (kg) of 2174 Romney lambs born between 1971 and 1981 were analyzed. The data used were obtained from a random-bred experimental flock maintained at Massey University, Palmerston North, New Zealand.

Observations on parents and offspring are required to obtain estimates of variance components by the method described in Chapter 4. However, the data used were not from an experiment especially designed to carry out such an analysis. Therefore the following procedure was adopted for obtaining data suitable for analysis:

- (1) All sires with records, which were born between 1971 and 1981 were included. The number of sires was equivalent to the number of families.
- (2) The records of all dams which produced offspring with records were included, thereby completing information on all families. Animals with no records were deleted.

It was assumed that the sires and the dams were unrelated so that the families and the parents within the families became independent. The vector of fixed effects for the model included a general mean, 11 year-of-birth effects, 2 sex effects, 3 birth and rearing rank effects, 4 age-of-dam effects and a regression coefficient associated with the age in days at weaning. Let,

- β_1 = general mean;
 $\beta_2 - \beta_{12}$ = year of birth effects (1971 - 1981);
 $\beta_{13} - \beta_{14}$ = effects of sex (ewe, ram);
 $\beta_{15} - \beta_{17}$ = effects of birth and rearing rank (single, twin reared as single and twin, respectively);

$\beta_{18} - \beta_{21}$ = effects of age of dam (2 years - 5 years);
 β_{22} = regression coefficient associated with the age at weaning (in days).

The variance components of the model, θ_m ($m=1, \dots, 5$), were defined in Chapter 4. The phenotypic variance, and the covariances between the relatives, γ_h ($h=1, \dots, 5$), which are functions of the θ 's were also defined in Chapter 4.

A constrained maximization of the likelihood function was carried out to obtain solutions for the fixed effects and estimates of the variance components. Using initial values for the variance components ($\hat{\theta}^0$), the equations given in (4.7) were solved to find $\hat{\beta}$. The algorithm in Section 4.2.4. was used to generate the equations. Substituting these solutions for $\hat{\beta}$, the likelihood function was maximized subject to the constraints

- (i) $\theta_1, \theta_2, \theta_4, \theta_5 \geq 0$
 (to avoid negative estimates of variances) and
- (ii) $\theta_1\theta_2 - \theta_3^2 \geq 0$
 (to ensure that the estimate of the genetic correlation between direct and maternal effects lies within the range of -1 and +1)

The algorithm given in section 4.2.6. was used to generate $-F$ where $-F$ was minimized subject to the above constraints (minimizing $-F$ is equivalent to maximizing the likelihood function).

Routine EO4UAF of NAG FORTRAN library [Numerical Algorithms Group (1983)] was used to minimize $-F$ subject to the above constraints. This routine is intended for functions and constraints which have continuous first and second derivatives. However, it is not required to generate the derivatives. The computing routine uses a sequential augmented Lagrangian method,

the minimization sub-problems involved being solved by a Quasi-Newton method.

The solutions to the ML equations corresponding to the fixed effects and estimates of variance components were obtained alternately, until convergence occurred. The solutions for the fixed effects and ML estimates of variance components are given in Table 6.1 and Table 6.2, respectively. The solution values for β_{12} , β_{14} , β_{17} and β_{21} were set to zero.

Table 6.1 : ML solutions for fixed effects
resulting from a constrained optimization
using weaning weights of Romney lambs (kg)

Round	1	2	3	4	5	6
<u>general mean</u>						
β_1^0	10.2678	10.3068	10.3077	10.3077	10.3080	10.3082
<u>year-of-birth</u>						
β_2^0	-3.0860	-3.1251	-3.1264	-3.1262	-3.1271	-3.1270
β_3^0	-1.2194	-1.2669	-1.2680	-1.2678	<u>-1.2686</u>	
β_4^0	-0.7797	-0.8223	-0.8234	-0.8232	-0.8240	-0.8239
β_5^0	-0.6143	-0.6726	-0.6740	-0.6737	-0.6747	-0.6746
β_6^0	-0.5469	-0.6093	-0.6105	-0.6102	-0.6112	-0.6111
β_7^0	-0.4313	-0.4620	-0.4627	-0.4625	-0.4632	-0.4631
β_8^0	1.5950	1.6087	1.6089	1.6091	1.6087	1.6090
β_9^0	-0.4901	-0.5006	-0.5006	-0.5004	-0.5009	-0.5006
β_{10}^0	-2.8993	-2.9178	-2.9180	-2.9178	-2.9183	-2.9181
β_{11}^0	-0.7487	-0.7668	-0.7669	<u>-0.7670</u>		
<u>sex</u>						
β_{13}^0	-3.6472	-3.6104	-3.6095	-3.6098	-3.6088	-3.6091
<u>birth and rearing rank</u>						
β_{15}^0	4.1941	4.2023	4.2020	4.2020	4.2019	4.2018
β_{16}^0	2.2071	2.2236	2.2231	2.2230	2.2229	2.2228
<u>age of dam</u>						
β_{18}^0	-1.2055	-1.1949	-1.1947	-1.1948	-1.1946	-1.1947
β_{19}^0	0.2090	0.2121	0.2122	0.2122	<u>0.2123</u>	
β_{20}^0	-0.0157	<u>-0.0144</u>				
<u>age at weaning</u>						
β_{22}^0	0.1583	<u>0.1577</u>				

Table 6.2 : ML estimates of variance components
resulting from a constrained optimization using
weaning weights of Romney lambs (kg²)

Round	1	2	3	4	5
$\hat{\theta}_1$	2.5375	2.5447	2.5448	2.5498	2.5516
$\hat{\theta}_2$	6.3971	6.4209	6.4179	6.4306	6.4376
$\hat{\theta}_3$	-2.0320	-2.0466	-2.0453	-2.0517	-2.0553
$\hat{\theta}_4$	<u>0</u>				
$\hat{\theta}_5$	6.1439	6.1148	6.1144	6.1103	6.1060
$\hat{\sigma}_p^2$	13.0464	13.0319	13.0318	13.0421	13.0400

From $\hat{\theta}_1$, $\hat{\theta}_2$ and $\hat{\theta}_3$, the genetic correlation between direct and maternal effects can be estimated (-0.507). The fraction of the selection differential realized if selection is on phenotypic values [Dickerson (1947)],

$$s = (\sigma_{AO}^2 + 1.5\sigma_{AOAm} + 0.5\sigma_{Am}^2) / \sigma_p^2,$$

is 0.206. The large-sample variance-covariance matrices of the vectors of estimates for $\underline{\beta}$ and $\underline{\theta}$ were obtained using the expressions given in Section 4.7. The standard errors of the ML estimates of $\underline{\beta}$ and $\underline{\theta}$ are given in Tables 6.3 and 6.4, respectively.

Table 6.3 : Standard errors of the ML
solutions for the fixed effects

factor	solution \pm std. error
<u>general mean</u>	
β_1^0	10.3082 \pm 0.8160
<u>year-of-birth</u>	
β_2^0	-3.1270 \pm 0.7320
β_3^0	-0.2686 \pm 0.5129
β_4^0	-0.8239 \pm 0.5409
β_5^0	-0.6746 \pm 0.4709
β_6^0	-0.6111 \pm 0.4802
β_7^0	-0.4631 \pm 0.4243
β_8^0	1.6090 \pm 0.4336
β_9^0	-0.5006 \pm 0.4429
β_{10}^0	-2.9181 \pm 0.4523
β_{11}^0	-0.7670 \pm 0.5082
<u>sex</u>	
β_{13}^0	-3.6091 \pm 0.1818
<u>birth and rearing rank</u>	
β_{15}^0	4.2018 \pm 0.1958
β_{16}^0	2.2228 \pm 0.4383
<u>age of dam</u>	
β_{18}^0	-1.1947 \pm 0.2285
β_{19}^0	0.2123 \pm 0.2238
β_{20}^0	-0.0144 \pm 0.2238
<u>age at weaning</u>	
β_{22}^0	0.1577 \pm 0.0093

Note : $\beta_2^0 - \frac{1}{2}(\beta_{11}^0 + \beta_{12}^0)$ and the std. error quoted is the std. error of that contrast.

Table 6.4 : Standard errors of ML estimates
for the variance components

variance component	estimate \pm std.error
direct additively genetic variance	2.5516 \pm 0.4896
maternal additively genetic variance	6.4376 \pm 5.7070
covariance between direct and maternal genetic effects	-2.0553 \pm 2.4758
variance of the residual effects common to a litter	0.0 \pm 3.5576
variance of the residual effects unique to the individuals	6.1060 \pm 0.8999

Ch'ang and Rae (1972) estimated the genetic correlation between hogget characters and maternal environment by using dam-offspring covariance components. In addition, they estimated the fraction of the contribution from maternal sources to dam-offspring covariance (M_1), which is a function of the maternal genetic variance and the covariance between direct and maternal genetic effects. Since individual estimates of the maternal genetic variance and the covariance between direct and maternal genetic effects were not available from Ch'ang and Rae (1972), the estimates for M_1 will be compared, where

$$M_i = (1.5\sigma_{AOAm} + 0.5\sigma_{Am}^2) / \sigma_p^2.$$

The source of data for the study of Ch'ang and Rae (1972) is the same as that for this study. However, their data was obtained in the period 1955 - 1965. A comparison of some estimates from Ch'ang and Rae (1972) and this study is given in Table 6.5. The estimate of the standard deviation was obtained from Ch'ang and Rae (1970).

Table 6.5 : A comparison of estimates obtained from this study and that of Ch'ang and Rae (1970,1972)

Estimate of	Ch'ang and Rae (1970,1972)	this study
standard deviation ($\hat{\theta}_p$)	7.7	7.9
heritability ($\hat{h}^2 = \hat{\sigma}_{AO}^2 / \hat{\sigma}_p^2$)	0.30	0.20
genetic correlation between direct and maternal effects	-0.76	-0.51
M_i , a function of the amount of contribution from maternal sources to dam-offspring covariance	-0.134	0.01

The magnitudes of the heritability and the genetic correlation are lower than those for the study of Ch'ang and Rae (1972). The difference between the estimates of the standard deviation is negligible. There is a considerable difference between the estimates of M_i . Ch'ang and Rae (1961,1970) studied the effects of type of birth and rearing, age-of-dam, year-of-birth, sex and age at weaning, on weaning weights of sheep. Table 6.6 presents a comparison of the estimates obtained in both studies.

Table 6.6 : A comparison of the estimates(kg) of effects of birth and type of rearing, age of dam, sex and age at weaning on weaning weight of Romney sheep

	<u>Ch'ang and Rae</u>			1970	This study
	1961				
	flock A	flock B	flock C		
	1948-1954	1955	1956		
<u>age of dam</u>					
5-year-old - 2-year-old	2.16	1.86	1.94	2.0	1.20
5-year-old - 3-year-old	0.90	0.00	0.38	-	-0.21
5-year-old - 4-year-old	0.15	1.10	-0.10	-	0.01
<u>type of birth and rearing</u>					
single - twin	4.65	4.54	4.24	4.2	4.20
single - twin reared as single	3.04	-	1.99	2.9	1.98
<u>sex of lamb</u>					
ram - ewe	-	2.19	2.99	-	3.61
linear regression on age of lamb at weaning	0.13	-	0.08	0.12	0.16
mean - $\hat{\beta}\bar{x}$	10.96	-	14.47	-	10.31

In Table 6.6, $\hat{\beta}$ is the regression coefficient on age of lamb at weaning and \bar{x} is the average age at weaning.

Jury, Johnson and Clarke (1979) obtained adjustment factors for environmental sources of variation for weaning weights of

Romney lambs using 12 commercial flocks participating in the National Flock Recording Scheme (Sheeplan) of New Zealand. Adjustment factors were estimated for birth-rearing rank, sex, age-of-dam and age at weaning. Newman, Wickham, Rae and Anderson (1983) obtained least squares estimates for the factors affecting weaning weights of lambs. Table 6.7 compares the adjustment factors obtained by Jury et al(1979), the adjustment factors used by the Sheeplan, the adjustment factors obtained by Newman et al (1983) and the adjustment factors obtained in this study.

Table 6.7 : Adjustment factors for
Romney lamb weaning weight (kg)

source		Birth and rearing rank		dam age			sex	age at weaning
		SS-TS	SS-TT	4-2	4-3	4-5	M-F	
Jury et al (1979)	flock 1	2.3	4.3	1.3	0.2	1.0	2.5	0.21
	flock 2	1.4	4.1	1.1	0.2	0.5	1.6	0.16
	flock 3	2.1	4.6	0.7	0.3	0.2	2.9	0.15
	flock 4	1.8	4.2	1.4	0.1	-0.5	1.9	0.13
	flock 5	1.6	4.3	0.4	0.2	0.0	2.2	0.18
	flock 6	1.8	3.9	1.6	0.3	-0.2	1.7	0.17
	flock 7	1.9	4.4	0.9	0.3	0.1	2.1	0.17
	flock 8	1.9	3.8	1.3	0.4	-0.4	1.9	0.20
	flock 9	2.0	4.2	1.5	0.4	-0.1	1.9	0.18
	flock 10	2.0	3.7	1.0	0.0	-0.2	2.3	0.14
	flock 11	1.9	4.7	1.6	0.6	-0.4	2.1	0.12
	flock 12	2.7	4.6	2.2	0.2	-0.2	2.2	0.20
	average	2.0	4.2	1.3	0.3	-0.2	2.1	0.17
Sheepplan		3.2	4.5	2.3	0.9	0.0	1.8	0.14
Newman et al 1983	flock D	1.4	3.6	0.5	0.0	-	1.6	0.16
	flock E	1.9	3.9	-0.4	-1.0	-	1.3	0.18
This study		2.0	4.2	1.2	-0.2	0.0	3.6	0.16

In Table 6.7, SS, TS and TT refer to single, twin reared as single and twin, respectively.

Adjustment factors obtained in this study for birth-rearing rank, dam age and age at weaning where a maternal effects model is assumed are almost identical to the average adjustment factors obtained by Jury et al (1979). However, there is a large difference in the estimated adjustment factors for sex. The adjustment factors obtained by Newman et al (1983) are also similar to the adjustment factors obtained in this study with the exception of the adjustment for sex. The estimate of the adjustment factor obtained for sex by Jury et al (1979), by Newman et al (1983) and that used by Sheeplan are similar.

6.2. Swine

Weaning weights (8-week weights in lb) of 1035 Yorkshire or Large White pigs born between 1964 and 1971 were studied. The data used were obtained from the Animal Husbandry Department of West of Scotland Agricultural College, Auchincruive, Scotland. The families were formed as in Section 6.1., to enable use of the method of estimation described in Chapter 4. As before it was assumed that the sires and the dams were unrelated.

The vector of fixed effects of the model included a general mean, 2 sex effects, 8 year-of-birth effects, 7 parity-of-the-dam effects and a regression coefficient associated with the litter size. Let

- β_1 = general mean;
- β_2, β_3 = effects of sex (male and female respectively);
- $\beta_4 - \beta_{11}$ = effects of year (1964 to 1971 respectively);
- $\beta_{12} - \beta_{15}$ = effects of season (spring - winter);
- $\beta_{16} - \beta_{22}$ = effects of the parity of the dam (1-7); and
- β_{23} = regression coefficient associated with the litter size.

Initially, an analysis of variance was carried out using the Generalized Linear Models computing programme REG [Gilmour (1983)]. The aim was to obtain initial values for some of the

parameters. The linear equations and the nonlinear equations developed in Chapter 4 were solved alternately until the solutions converged. No restrictions were imposed on the solutions. Routine C05NAF of NAG FORTRAN library [Numerical Algorithms Group (1981)] was used to solve the nonlinear equations, the solutions to these being the estimates of variance components. The algorithm used in C05NAF is a combination of Newton-Raphson and steepest descent methods in such a way as to give a steady progress and a fast rate of ultimate convergence. In the latest NAG FORTRAN library (mark 10), C05NAF is replaced by C05NBF, which is a readily available routine for solving a system of nonlinear equations by a modification of the Powell hybrid method.

By using $\hat{\beta}^0$ (estimates obtained using REG) a set of estimates of the variance components were obtained in round 1. Several sets of initial values of θ had to be attempted before a solution to the nonlinear equations was obtained in the initial round of iterations. In the subsequent rounds of estimating variance components the solution from the previous round was used as the initial value of θ . Tables 6.8 and 6.9 present the results obtained from the unconstrained optimization of the likelihood function. The solution values for β_3 , β_{11} , β_{15} and β_{22} were set to zero.

Table 6.8 : ML estimates of variance components
resulting from an unconstrained optimization
using 8-week weights of Yorkshire pigs (lb²)

Round	1	2	3	4	5	6	7
$\hat{\theta}_1$	6.0936	10.0248	10.3964	10.3512	10.2784	10.2276	10.1956
$\hat{\theta}_2$	52.2220	88.1778	96.0844	97.4392	97.6044	97.5854	97.5502
$\hat{\theta}_3$	-24.7516	-39.0324	-42.3280	-42.8596	-42.9008	-42.8752	-42.8496
$\hat{\theta}_4$	-18.3210	-41.3268	-45.9529	-46.7473	-46.8461	-46.8363	-46.8164
$\hat{\theta}_5$	32.1190	29.0339	28.8054	28.8178	28.8665	28.8935	28.9105
$\hat{\sigma}_p^2$	47.3620	46.8773	47.0053	47.0013	47.0024	46.9950	46.9903

Table 6.8 continued

Round	8	9	10	11	12	13	14
$\hat{\theta}_1$	10.1768	10.1652	10.1588	10.1548	10.1524	10.1508	10.1500
$\hat{\theta}_2$	97.5262	97.5096	97.5024	97.4960	97.4932	97.4906	97.4894
$\hat{\theta}_3$	-42.8332	-47.8224	-42.8172	-42.8132	-42.8112	-42.8096	-42.8088
$\hat{\theta}_4$	-46.8029	-47.7933	-46.7893	-46.7857	-46.7841	-46.7825	-46.7819
$\hat{\theta}_5$	28.9206	28.9267	28.9301	28.9323	28.9336	28.9343	28.9348
$\hat{\sigma}_p^2$	46.9875	46.9858	46.9848	46.9842	46.9839	46.9836	46.9835

Table 6.9 : ML solutions for the equations corresponding to the fixed effects resulting from an unconstrained optimization using 8-week weights of Yorkshire pigs

Round	1	2	3	4	5	6	7
<u>general mean</u>							
β_1°	33.5004	33.2370	33.2389	33.2501	33.2576	33.2621	33.2647
<u>sex</u>							
β_2°	0.6237	0.5560	0.5500	0.5476	0.5465	0.5458	0.5455
<u>year-of-birth</u>							
β_4°	12.2942	11.6846	11.5410	11.4977	11.4801	11.4713	11.4664
β_5°	10.4952	10.0717	9.9941	9.9685	9.9571	9.9510	9.9476
β_6°	7.9512	8.0745	8.0050	7.9672	7.9465	7.9346	7.9277
β_7°	4.7064	4.8253	4.7790	4.7500	4.7333	4.7237	4.7180
β_8°	2.1315	2.2199	2.1698	2.1422	2.1272	2.1186	2.1136
β_9°	3.9527	3.9794	3.9490	3.9284	3.9162	3.9090	3.9047
β_{10}°	-0.8762	-0.8135	-0.8366	-0.8517	-0.8603	-0.8653	-0.8682
<u>season-of-birth</u>							
β_{12}°	0.0012	-0.0590	-0.0815	-0.0896	-0.0933	-0.0953	-0.0964
β_{13}°	-0.5943	-0.6237	-0.6467	-0.6535	-0.6561	-0.6574	-0.6581
β_{14}°	-2.5728	-2.6656	-2.6859	-2.6900	-2.6911	-2.6915	-2.6917
<u>parity of the dam</u>							
β_{16}°	-1.4694	-1.4132	-1.3737	-1.3648	-1.3622	-1.3612	-1.3607
β_{17}°	1.9579	1.7866	1.8154	1.8260	1.8306	1.8330	1.8343
β_{18}°	3.2428	3.2396	3.2759	3.2871	3.2918	3.2942	3.2956
β_{19}°	-1.1847	-1.1891	-1.1416	-1.1249	-1.1175	-1.1136	-1.1114
β_{20}°	-1.6153	-1.6745	-1.6549	-1.6481	-1.6451	-1.6436	-1.6426
β_{21}°	1.7852	1.9323	1.9644	1.9735	1.9770	1.9786	1.9796
<u>litter size</u>							
β_{23}°	-0.5553	-0.5299	-0.5275	-0.5271	-0.5270	<u>-0.5269</u>	

Table 6.9 continued

Round	8	9	10	11	12	13	
β_1^o	33.2663	33.2673	33.2678	33.2681	33.2683	<u>33.2685</u>	
β_2^o	0.5452	0.5451	<u>0.5450</u>				
β_4^o	11.4635	11.4619	11.4609	11.4603	11.4599	11.4597	11.4596
β_5^o	9.9456	9.9444	9.9437	9.9432	9.9430	9.9429	9.9428
β_6^o	7.9236	7.9212	7.9197	7.9189	7.9184	7.9181	7.9179
β_7^o	4.7147	4.7127	4.7115	4.7108	4.7104	4.7101	4.7100
β_8^o	2.1107	2.1089	2.1079	2.1073	2.1069	2.1067	2.1066
β_9^o	3.9022	3.9007	3.8999	3.8993	3.8990	3.8988	3.8987
β_{10}^o	-0.8699	-0.8709	-0.8715	-0.8719	-0.8721	-0.8722	-0.8723
β_{12}^o	-0.0971	-0.0975	-0.0977	-0.0978	-0.0979	<u>-0.0980</u>	
β_{13}^o	-0.6585	-0.6588	-0.6589	-0.6590	<u>-0.6591</u>		
β_{14}^o	-2.6918	-2.6918	<u>-2.6919</u>				
β_{16}^o	-1.3604	-1.3603	-1.3602	<u>-1.3601</u>			
β_{17}^o	1.8351	1.8355	1.8358	1.8360	1.8361		
β_{18}^o	3.2964	3.2969	3.2972	3.2974	<u>3.2975</u>		
β_{19}^o	-1.1102	-1.1094	-1.1089	-1.1087	-1.1085	<u>-1.1084</u>	
β_{20}^o	-1.6420	-1.6417	-1.6415	-1.6414	-1.6414	<u>-1.6413</u>	
β_{21}^o	1.9801	1.9804	1.9806	1.9807	<u>1.9808</u>		
β_{23}^o							

The ML estimate of the residual variance common to full-sibs and maternal half-sibs is negative (see Table 6.8). The negative estimate can be accepted as evidence that the parameter is zero which results in a truncation. If this happens, the likelihood is not maximized unless adjustments are made to other estimates. Also, these estimates result in a genetic correlation between direct and maternal effects, which lies outside the range -1 and $+1$ (-1.3609). The most unacceptable result is the estimate of the maternal genetic variance, which is approximately twice as large as the estimate of the phenotypic variance.

This problem was overcome by maximizing the likelihood function subject to the constraints given in Section 6.1. (routine E04UAF of NAG FORTRAN library was used). The ML estimates of the variance components and the ML solutions for the fixed effects are given in Tables 6.10 and 6.11, respectively.

Table 6.10 : ML estimates of the variance components
resulting from a constrained optimization (lb^2)
using 8-week weights of Yorkshire pigs

Round	1	2	3	4
$\hat{\theta}_1$	6.9364	6.7764	6.7735	6.7736
$\hat{\theta}_2$	20.5913	21.0065	21.0971	21.0972
$\hat{\theta}_3$	-11.9512	-11.9310	-11.9541	-11.9542
$\hat{\theta}_4$	0.0959	<u>0</u>		
$\hat{\theta}_5$	31.7059	30.6697	30.6558	30.6558
$\hat{\sigma}_p^2$	47.3785	46.5216	46.5723	46.5724

Table 6.11 : ML solutions to the equations corresponding to the fixed effects resulting from a constrained optimization using 8-week weights of Yorkshire pigs

Round	1	2	3	4
<u>general mean</u>				
β_1°	33.3790	33.3060	33.29860	33.29861
<u>sex</u>				
β_2°	0.6025	0.6013	<u>0.60115</u>	
<u>year-of-birth</u>				
β_4°	12.6070	12.6193	<u>12.62026</u>	
β_5°	10.4539	10.4878	10.49106	10.49105
β_6°	8.1983	8.2316	<u>8.23405</u>	
β_7°	4.8230	4.8578	<u>4.86059</u>	
β_8°	2.3556	2.3859	<u>2.38838</u>	
β_9°	3.9242	3.9365	3.93691	3.93692
β_{10}°	-0.7860	-0.7568	-0.75408	-0.75409
<u>season-of-birth</u>				
β_{12}°	0.0917	0.0902	<u>0.08986</u>	
β_{13}°	-0.4648	-0.4831	-0.48510	-0.48509
β_{14}°	-2.4422	-2.4816	-2.48587	-2.48586
<u>parity of the dam</u>				
β_{16}°	-1.7160	-1.6633	-1.65773	-1.65774
β_{17}°	1.6417	1.6688	1.67175	1.67174
β_{18}°	3.0290	3.1110	3.12004	3.12002
β_{19}°	-1.4916	-1.4496	-1.44479	-1.44480
β_{20}°	-1.7979	-1.7567	-1.75218	-1.75219
β_{21}°	1.6619	1.6562	<u>1.65442</u>	
<u>litter size</u>				
β_{23}°	-0.5443	-0.5528	<u>-0.55265</u>	

The estimate of the variance attributable to the residual effects which are common to full-sibs and maternal half-sibs is zero. The maternal genetic variance is about three times as large as the direct genetic variance. The genetic correlation between the direct and the maternal genetic effects is -1.0 which implies that there is a very strong antagonism between direct and maternal genetic effects. The fraction of the selection differential realized, if selection is on phenotypic values is 0.013 .

Ahlschwede and Robison (1971a) estimated the genetic and environmental variances and covariances relevant to birth weight, 56-day weight, 140-day weight and back fat of swine (Duroc and Yorkshire breeds). They estimated the variance components by equating the theoretical compositions to the covariances between relatives, where the covariances between relatives were estimated using analysis of variance procedures. In Table 6.12, the estimates they obtained for the 8-week weights (in kg) of Yorkshire pigs are compared with the ML estimates of the variance components obtained in this study.

Table 6.12 - A comparison of three sets of variance components (kg^2) for 8-week weights of Yorkshire pigs

estimate of	Ahlschwede and Robison (1971a)	ML estimates	
		constrained	unconstrained
phenotypic variance	13.573	9.7073	9.6224
direct additively genetic variance	-0.766	2.0971	1.3995
maternal additively genetic variance	-0.843	20.1424	4.3589
covariance between direct and maternal additively genetic variance	0.816	-8.8448	-2.4699
variance of residual effects common to a litter	4.631	-9.6657	0
variance of residual effects unique to individuals	9.736	5.9783	6.3338

The estimates for the phenotypic variance, direct additively genetic variance and the variance of the residual effects unique to the individuals obtained from the unconstrained and constrained maximization of the likelihood function are similar. In fact, the differences between the estimates for the phenotypic variance and the variance of the residual effects unique to the individuals are very small. However, the estimates obtained by Ahlschwede and Robison (1971a) and the estimates obtained in this study vary greatly. They obtained negative genetic variances for direct and maternal genetic effects and a positive, but small, estimate for

the covariance between direct and maternal genetic effects which is contrary to the ML estimates obtained in this study, for the same trait (8-week weight of Yorkshire pigs).

CHAPTER 7. DISCUSSION

Despite the computing difficulties often encountered when using maximum likelihood procedures, the maximum likelihood approach for estimating variance components has many advantages. The most common method of estimating maternal variance and covariance components has been equating covariances between relatives to their expected compositions where the covariances between relatives are estimated using analysis of variance procedures. However, the estimates obtained in this method do not always lie within the parameter space [see Ahlschwede and Robison (1971a)]. Therefore one of the advantages that maximum likelihood methods have over other methods for estimating variance components is the ability to impose constraints on the solutions obtained. However, maximization of the likelihood function without imposing constraints and truncating the solutions to certain bounds if required (truncating to zero if negative estimates of variances are obtained), is not recommended since the likelihood is not maximized unless adjustments are made to the other estimates.

The estimation of variance components by maximum likelihood methods involves the numerical solution to a constrained nonlinear optimization problem. Although this has been difficult and sometimes not feasible in the past, the availability of increased computing power and technology, means that these methods are becoming more applicable. The use of maximum likelihood methods is also becoming easier with the development of effective computing algorithms for nonlinear optimization problems. Hartley and Rao (1967) established large sample optimality properties of maximum likelihood estimators and commented that these properties should provide justification for additional computing time necessary (if any). In the case of animal breeding where large sample sizes are usually involved, even the less sophisticated methods could consume considerable amounts of computing time.

Maximum likelihood estimates are derived under the assumption of a particular distributional form for the observation vector, usually normal, which is the case in this study. This is one of the drawbacks of the maximum likelihood techniques. However, Harville (1977) suggested that the maximum likelihood estimators derived on the basis of normality assumptions may well be suitable even if the form of the distribution is unspecified.

Thompson (1976) commented that the maximum likelihood method is probably most suitable for balanced data and added that, when the data are unbalanced, the use of full ML methods can be computationally not feasible. However, there are circumstances when the special structure of the data can be exploited. In this thesis, a highly-structured variance-covariance matrix of the observation vector which can be easily inverted was utilized. In fact, explicit expressions for the inverse and the determinant of the variance-covariance matrix were developed. Therefore no iterative computing algorithm was required to obtain the determinant or the inverse of the variance-covariance matrix. This reduced the computing time required to evaluate the likelihood function and its partial derivatives.

General expressions for the large-sample variance-covariance matrices for maximum likelihood estimators exist [see (3.7) and (3.8)]. However, obtaining the large-sample variances using (3.7) and (3.8) can be computationally difficult since it involves the inverse of the variance-covariance matrix of the observation vector. This was not a problem in this study, since an explicit expression for the inverse of the variance-covariance matrix was developed.

The optimization problem in this study was carried out using two procedures for estimating variance components. The first of these solved nonlinear equations, which are the first derivatives with respect to variance components. The second procedure was to maximize the likelihood function subject to non-negativity constraints of certain functions of the variance components. The

computer time required for solving the nonlinear equations (unconstrained) was less than that for the maximization problem. However, generating the likelihood function which is essential for the second procedure, is easier than generating the partial derivative with respect to the variance components. One of the disadvantages in maximum likelihood solutions is that one is never entirely sure whether the solution is the global maximum of the likelihood. However, the fact that several starting values had to be attempted in both procedures (constrained and unconstrained) before solutions were obtained, implies that the probability that the global maximum was achieved was high.

Predicting direct and maternal genetic values of all animals is a special case of a multiple-trait evaluation where breeding values of all traits are predicted [see Quaas and Henderson (1976)]. Therefore, inverting the variance-covariance matrix of direct and maternal genetic values involves inverting the numerator relationship matrix of the animals and a matrix of order two. This means that the number of equations pertaining to the number of random effects to be predicted is twice as large as the number of animals. Also, the maternal genetic values of the unidentified animals are not predicted by this method.

In the case of meat animal species, maternal genetic ability for offspring growth is of no importance commercially. Since the total genetic effect of an individual is the sum of the direct genetic value and the maternal genetic value of its dam, it is important to distinguish the individual's genetic ability from the maternal ability of its dam. Then the animals can be selected on their individual genetic merit. This means that the objective of the prediction problem is satisfied as well as reducing the number of BLUP equations by predicting the maternal genetic values of the dams only. In practical applications, where large numbers of animals are evaluated, it is desirable to reduce the number of equations as possible. When the objective is to select for maternal ability or a linear combination of the direct and maternal genetic values, then the direct and maternal genetic

values of all animals have to be predicted.

Quaas (1975,1984) demonstrated how the inverse of the numerator relationship matrix can be derived from first principles by writing a linear model for an individual's breeding value in terms of its parents breeding values. In this thesis, this method was modified to obtain the inverse of the variance-covariance matrix of the direct genetic values of all individuals of interest and the maternal genetic values of their dams. However, additional genetic values have to be included in order to generate the correct inverse of the variance-covariance matrix and these were specified in Chapter 5. The increment in the number of equations, caused by the second condition (see also Chapter 5) is small, since there are comparatively few sires in a pedigree compared to the number of animals. The first of these restrictions causes the number of equations to increase unnecessarily, since the direct genetic values of the unidentified dams are not of any importance. This can be avoided by excluding the maternal genetic values of the unidentified dams or assuming that the dams with no records are unknown. However, such exclusions cause in a change in ranking of the predictions.

The proportion of genetic variation explained by the direct genetic and maternal genetic effects are considerably large for 8-week weight of Yorkshire pigs and for the weaning weight of Romney lambs. This means that substantial improvement of direct and maternal genetic values is possible, provided there is no negative correlation between direct and maternal genetic effects. The estimates of these proportions are 14.5%, 45.3%, 19.6% and 49.4% for direct genetic effects of 8-week weight of Yorkshire pigs, maternal genetic effects of 8-week weight of Yorkshire pigs, direct genetic effects of weaning weights of Romneys and maternal genetic effects of weaning weights of Romneys, respectively. The estimate of heritability obtained by Ch'ang and Rae (1972) for weaning weight of Romneys is 30.0%.

The genetic correlation between direct and maternal genetic effects is negative and large for 8-week weight of Yorkshire pigs and the weaning weight of Romney sheep; the constrained maximization of the likelihood resulting in the estimates -1.0 for pig data and -0.51 for sheep data. This implies that simultaneous improvement for direct and maternal genetic effects is difficult in both cases, pig breeders being confronted with the more severe problem.

The estimate of the variance of the residual effects common to a litter (that is full-sibs and maternal half-sibs) is zero in both cases. Ahlschwede and Robison (1971a) obtained an estimate of 4.631 (kg) for the variance of the environmental effects common to a litter for 8-week weight of Yorkshire pigs. The estimates they obtained for the direct additive genetic variance and the maternal additive genetic variance were -0.766 and 0.843 , respectively. This would have had some influence on their estimate of the variance of the environmental effects common to a litter.

The analyses of the sheep and pig data show that, the methods developed in this thesis for estimating genetic parameters for mixed models involving maternal effects are computationally feasible. The results obtained were generally satisfactory.

APPENDIX 1An algorithm for computing A_{i11} for a single-trait setting

Suppose the i th sire is mated to n dams. Then the matrix in (4.21) for this case can be written as

$$\begin{bmatrix} a_{i11} + b_{j11} & c_{j12} & \dots & c_{j1n} \\ c_{j21} & a_{i22} + b_{j22} & \dots & c_{j2n} \\ \vdots & \vdots & \ddots & \vdots \\ c_{jn1} & c_{jn2} & \dots & a_{inn} + b_{jnn} \end{bmatrix} \quad (A1)$$

The inverse of the above matrix has the form

$$\begin{bmatrix} p_{i11} + q_{11j} & q_{12j} & \dots & q_{1nj} \\ q_{12j} & p_{i22} + q_{22j} & \dots & q_{2nj} \\ \vdots & \vdots & \ddots & \vdots \\ q_{1nj} & q_{2nj} & \dots & p_{inn} + q_{nnj} \end{bmatrix} \quad (A2)$$

where I_{jj} is the identity matrix of order n_j and J_{jk} is the $n_j \times n_k$ matrix of "1"s.

The inverse of the matrix given in (A1) for $n \geq 3$

Multiplying the first column of matrices of (A2) by the matrix in (A1), gives

$$\begin{aligned} (a_{i11} + b_{j11})(p_{i11} + q_{11j}) + c_{j12}J_{12j}J_{21} + \dots \\ \dots + c_{jn1}J_{1n}J_{n1} = I_{11} \end{aligned} \quad (A3)$$

$$c_{j21}(p_{j11} + q_{j11}j_{j11}) + q_{j12}(a_{j22} + b_{j22})j_{j21} + \dots$$

$$\dots + c_{j1n}j_{j2n}j_{jn1} = 0 \quad (A4)$$

$$\vdots$$

$$c_{jn1}(p_{j11} + q_{j11}j_{j11}) + c_{j12}j_{j2n}j_{j21} + \dots$$

$$q_{j1n}(a_{jnn} + b_{jnn})j_{jn1} = 0 \quad (A5)$$

From (A3), two equations are obtained, namely,

$$ap_{j11} = j_{j11}$$

and

$$(bp + aq_{j11} + n_1bq_{j11} + n_2cq_{j12} + \dots + n_n cq_{j1n})j_{j11} = 0.$$

The first of these two equations gives

$$p = 1/a.$$

Then the second equation with the equations from (A4) to (A5) gives the following set of equations which can be used to find q_{1j} ($j=1, \dots, m$):

$$(a+n_1b)q_{j11} + n_2cq_{j12} + \dots + n_n cq_{j1n} = -b/a \quad (A6)$$

$$n_1cq_{j11} + (a+n_2b)q_{j12} + \dots + n_n cq_{j1n} = -c/a \quad (A7)$$

.

.

$$n_1cq_{j11} + n_2cq_{j12} + \dots + (a+n_nb)q_{j1n} = -c/a \quad (A8)$$

subtracting the j th equation from (A7) for $j=3, \dots, m$ gives

$$q_{1j} = \frac{a + n_2b - n_2c}{a + n_jb - n_jc} q_{12}.$$

Substituting this in (A6) and (A7), obtain

$$(a + n_1 b)q_{11} + [n_2 c + f(n)]q_{12} = -b/a \quad (A9)$$

and

$$n_1 c q_{11} + [a + n_2 b + f(n)]q_{12} = -c/a \quad (A10)$$

where

$$f(n) = c(a + n_2 b - n_2 c) \sum_{j=3}^n [n_j / (a + n_j b - n_j c)].$$

Equations (A9) and (A10) give

$$q_{12} = c/d$$

where

$$d = n_1 n_2 c^2 - (a + n_1 b)(a + n_2 b) - (a + n_1 b - n_1 c)f(n).$$

Then, as shown earlier q_{1j} ($j=3, \dots, m$) can be computed using

$$q_{1j} = \frac{a + n_2 b + n_2 c}{a + n_j b + n_j c} q_{12}.$$

Finally from (A6)

$$q_{11} = - \left[\frac{b}{a} + c \sum_{j=2}^n n_j q_{1j} \right] / (a + n_1 b).$$

Multiplying the second column of matrices of (A2) by the matrix in (A1), gives

$$q_{12}(a_{11} + b_{11})_{j12} + c_{j12}(p_{22} + q_{22})_{j22} + \dots + c_{2n} q_{1n} = 0 \quad (A11)$$

$$c_{j12} q_{21} + (a_{22} + b_{22})(p_{22} + q_{22})_{j22} + \dots + c_{2n} q_{2n} = I_{22} \quad (A12)$$

$$\vdots$$

$$c_{j12} q_{n1} + c_{j n_2}(p_{22} + q_{22})_{j22} + \dots + q_{2n}(a_{nn} + b_{nn})_{j n_2} = 0 \quad (A13)$$

From above, the following set of equations with $n-1$ unknowns is obtained (p and q_{12} are already known):

$$(a+n_1b)q_{12} + n_2cq_{22} + \dots + n_n cq_{2n} = -c/a \quad (A14)$$

$$n_1cq_{12} + (a+n_2b)q_{22} + \dots + n_n cq_{2n} = -b/a \quad (A15)$$

.

.

.

$$n_1cq_{12} + n_2cq_{22} + \dots + (a+n_nb)q_{2n} = -c/a \quad (A16)$$

subtracting the j th equation from (A14) for all $j=3, \dots, m$ gives

$$(a + n_1b - n_1c)q_{12} = (a + n_jb - n_jc)q_{2j}$$

which implies that

$$q_{2j} = \frac{a + n_1b - n_1c}{a + n_jb - n_jc} q_{12}.$$

Then from (A15),

$$q_{22} = - \left[\frac{b}{a} + cn_1q_{12} + c \sum_{j=3}^n n_j q_{2j} \right] / (a+n_2b).$$

i th step

Multiply the i th column of matrices of (A2) by the matrix in (A1). Then the following set of equations is obtained:

$$(a+n_1b)q_{1i} + n_2cq_{2i} + \dots + n_i cq_{ii} + \dots + n_n cq_{in} = -c/a \quad (A17)$$

$$n_1cq_{1i} + (a+n_2b)q_{2i} + \dots + n_i cq_{ii} + \dots + n_n cq_{in} = -c/a \quad (A18)$$

.

.

$$n_1cq_{1i} + n_2cq_{2i} + \dots + (a+n_ib)q_{ii} + \dots + n_n cq_{in} = -b/a \quad (A19)$$

.

.

$$n_1cq_{1i} + n_2cq_{2i} + \dots + n_i cq_{ii} + \dots + (a+n_nb)q_{in} = -c/a \quad (A20)$$

At this stage there are $m-i+1$ unknowns. subtracting (A19) from (A17), gives

$$q_{ij} = \frac{a + n_1 b - n_1 c}{a + n_j b - n_j c} q_{1i}$$

which implies that

$$q_{ij} = \frac{(a+n_1 b-n_1 c)(a+n_2 b-n_2 c)}{(a+n_i b-n_i c)(a+n_j b-n_j c)} q_{12} \cdot$$

Then from (A19)

$$q_{ii} = - \left[\frac{b}{a} + c \sum_{j=1}^{i-1} n_j q_{ji} + c \sum_{j=i+1}^n n_j q_{ij} \right] / (a+n_i b).$$

The sequence proceeds until the last column is attained. The only unknown at this stage is q_{nn} , which is

$$q_{nn} = - \left[\frac{b}{a} + c \sum_{j=1}^{n-1} n_j q_{jn} \right] / (a+n_n b).$$

The expressions for the inverses of the matrix given in (A1) when the number of dams mated to the i th sire are one and two are given below for completion, although in practice it is not recommended to use the information from such small families.

$n = 1$

Then the matrix reduces to

$$aI_{11} + bJ_{11}$$

and the inverse is given by

$$pI_{11} + q_{11}J_{11}$$

where

$$p = 1/a$$

and

$$q_{11} = -b/[a(a+n_1 b)].$$

n = 2

When $n = 2$, the inverse is given by

$$\begin{bmatrix} pI_{11} + q_{11}J_{11} & q_{12}J_{12} \\ q_{12}J_{21} & pI_{22} + q_{22}J_{22} \end{bmatrix}$$

where

$$p = 1/a$$

$$q_{12} = c/d$$

$$q_{11} = - \left[\frac{b}{a} + n_2 c q_{12} \right] / (a + n_1 b)$$

and

$$q_{22} = - \left[\frac{b}{a} + n_1 c q_{12} \right] / (a + n_2 b).$$

In the expression for q_{12}

$$d = n_1 n_2 c^2 - (a + n_1 b)(a + n_2 b).$$

Therefore, the following algorithm can be proposed to generate A_{i11} (or the values for p and q_{ijk} ($i=1, \dots, s$; $j=1, \dots, n_i$; $k=j, \dots, n_i$)).

Algorithm for computing A_{i11}

$$(1) p = 1/a$$

$$(2) d_i = \begin{cases} n_{i1} n_{i2} c^2 - (a + n_{i1} b)(a + n_{i2} b) & \text{if } n_i = 2 \\ n_{i1} n_{i2} c^2 - (a + n_{i1} b)(a + n_{i2} b) - g_i(n) & \text{if } n_i > 2 \end{cases}$$

where

$$g_i(n) = c(a + n_{i1} b - n_{i1} c)(a + n_{i2} b - n_{i2} c) \sum_{j=3}^{n_i} \{n_{ij} / (a + n_{ij} b - n_{ij} c)\}$$

$$(3) q_{i12} = c/d_i$$

$$(4) \text{ If } n_i > 2,$$

$$q_{ijk} = \frac{(a+n_{i1}b-n_{i1}c)(a+n_{i2}b-n_{i2}c)}{(a+n_{ij}b-n_{ij}c)(a+n_{ik}b-n_{ik}c)}$$

for $j=1, \dots, n_i-1$ and $k=j+1, \dots, n_i$.

$$(5) \text{ If } n_i = 1,$$

$$q_{i11} = -b/[a(a+n_{i1}b)].$$

$$\text{If } n_i = 2,$$

$$q_{i11} = - \left[\frac{b}{a} + n_{i2}cq_{i12} \right] / (a+n_{i1}b)$$

and

$$q_{i22} = - \left[\frac{b}{a} + n_{i1}cq_{i12} \right] / (a+n_{i2}b).$$

$$\text{If } n_i > 2,$$

$$q_{ijj} = - \left[\frac{b}{a} + c \sum_{k=1}^{j-1} n_{ik}q_{ikj} + c \sum_{k=j+1}^{n_i} n_{ik}q_{ijk} \right] / (a+n_{ij}b)$$

for $j = 1, \dots, n_i$.

APPENDIX 2

An algorithm to generate the determinant of the variance-covariance matrix

From (3.14),

$$|\underline{V}_i| = |\underline{V}_i^*| |\underline{V}_{i22}| |\underline{V}_{i33}| \quad (\text{A21})$$

where

$$\underline{V}_i^* = \underline{V}_{i11} - \underline{V}_{i12} \underline{V}_{i22}^{-1} \underline{V}_{i12}' - \underline{V}_{i13} \underline{V}_{i33}^{-1} \underline{V}_{i13}'.$$

Denote \underline{V}_i^* by $\underline{V}_i^*(\ell)$ where ℓ is the value of n_i .
For example, when $n_i = 1$, \underline{V}_i^* is given by

$$\underline{V}_i^*(1) = a \underline{I}_{i11} + b \underline{J}_{i11}.$$

It is well known that the determinant of $\underline{V}_i^*(1)$ is given by

$$|\underline{V}_i^*(1)| = a^{f_1(n)} (a + n_{i1} b) \quad (\text{A22})$$

where

$$f_1(n) = n_{i1} - 1.$$

For $n_i = 2$,

$$\underline{V}_i^*(2) = \begin{bmatrix} a \underline{I}_{i11} + b \underline{J}_{i11} & c \underline{J}_{i12} \\ c \underline{J}_{i21} & a \underline{I}_{i22} + b \underline{J}_{i22} \end{bmatrix}.$$

From (3.11),

$$|\underline{V}_i^*(2)| = |\underline{V}_i^*(1)| |\underline{W}_i(2)|$$

where

$$\underline{W}_i(2) = a\underline{I}_{i22} + b\underline{J}_{i22} - c\underline{J}_{i21}(a\underline{I}_{i11} + b\underline{J}_{i11})^{-1}c\underline{J}_{i12}.$$

It was shown earlier that

$$(a\underline{I}_{i11} + b\underline{J}_{i11})^{-1} = p\underline{I}_{i11} + \delta_{i11}(2)\underline{J}_{i11}$$

where

$$p = 1/a$$

and

$$\delta_{i11} = -b/[a(a+n_{i1}b)]$$

Therefore, $\underline{W}_i(2)$ can be written as

$$\underline{W}_i(2) = a\underline{I}_{i22} + \zeta_{i2}\underline{J}_{i22}$$

where

$$\zeta_{i2} = b - pc^2n_{i1} - c^2n_{i1}^2\delta_{i11}(2)$$

which implies that

$$|\underline{V}_i^*(2)| = |a\underline{I}_{i11} + b\underline{J}_{i11}| |a\underline{I}_{i22} + \zeta_{i2}\underline{J}_{i22}|.$$

This means that

$$|\underline{V}_i^*(2)| = a^{f2(n)}(a + n_{i1}b)(a + n_{i2}\zeta_{i2})$$

where

$$f2(n) = n_{i1} + n_{i2} - 2.$$

For the case $n_i = 3$,

$$|\underline{V}_i^*(3)| = |\underline{V}_i^*(2)| |\underline{W}_i(3)|$$

where

$$\underline{W}_i(3) = a\underline{I}_{i33} + b\underline{J}_{i33} - [c\underline{J}_{i31} \quad c\underline{J}_{i32}] [\underline{V}_i^*(2)]^{-1} \begin{bmatrix} c\underline{J}_{i13} \\ c\underline{J}_{i23} \end{bmatrix}.$$

But,

$$[\underline{V}_i^*(2)]^{-1} = \begin{bmatrix} p\underline{I}_{i11} + \delta_{i11}(3)\underline{J}_{i11} & \delta_{i12}(3)\underline{J}_{i12} \\ \delta_{i12}(3)\underline{J}_{i21} & p\underline{I}_{i22} + \delta_{i22}(3)\underline{J}_{i22} \end{bmatrix}$$

where

$$\delta_{i12}(3) = c/d_i$$

$$\delta_{i11}(3) = - \left[\frac{b}{a} + n_{i2}c\delta_{i12}(3) \right] / (a+n_{i1}b)$$

and

$$\delta_{i22}(3) = - \left[\frac{b}{a} + n_{i1}c\delta_{i12}(3) \right] / (a+n_{i2}b).$$

In the expression for $\delta_{i12}(3)$,

$$d_i = n_{i1}n_{i2}c^2 - (a+n_{i1}b)(a+n_{i2}b).$$

Also, $\underline{W}_i(3)$ can be written in the form

$$\underline{W}_i(3) = a\underline{I}_{i33} + \zeta_{i3}\underline{J}_{i33}$$

where

$$\zeta_{i3} = b - pc^2(n_{i1}+n_{i2}) - c^2(n_{i1}^2\delta_{i11}(3) + n_{i2}^2\delta_{i22}(3)) - 2c^2n_{i1}n_{i2}\delta_{i12}(3)$$

which means that

$$|\underline{V}_i^*(3)| = a^{f3(n)}(a+n_{i1}b)(a+n_{i2}\zeta_{i2})(a+n_{i3}\zeta_{i3})$$

where

$$f3(n) = n_{i1} + n_{i2} + n_{i3} - 3.$$

By following the above procedure, an algorithm can be proposed to compute the determinant of \underline{V}_i^* for $n_i > 3$.

Algorithm to compute $|\underline{V}_i|$ when $n_i > 3$ (n_i is the number of dams mated to the i th sire)

Step 1

$$\zeta_{i1} = b$$

Step 2

$$\zeta_{i2} = b - pc^2 n_{i1} - c^2 n_{i1}^2 \delta_{i11}(2)$$

where

$$\delta_{i11}(2) = -b/[a(a+n_{i1}b)]$$

Step 3

$$\zeta_{i3} = b - pc^2(n_{i1}+n_{i2}) - c^2(n_{i1}^2 \delta_{i11}(3) + n_{i2}^2 \delta_{i22}(3)) \\ - 2c^2 n_{i1} n_{i2} \delta_{i12}(3)$$

where

$$\delta_{i12}(3) = c/d_i$$

$$\delta_{i11}(3) = - [b/a + n_{i2}c^2/d_i]/(a+n_{i1}b)$$

and

$$\delta_{i22}(3) = - [b/a + n_{i1}c^2/d_i]/(a+n_{i2}b)$$

In the above expressions,

$$d_i = n_{i1}n_{i2}c^2 - (a+n_{i1}b)(a+n_{i2}b).$$

Step 4

Calculate $\zeta_{i\ell}$ for $4 \leq \ell \leq n_i$

where

$$\zeta_{i\ell} = b - pc^2 \sum_{j=1}^{\ell-1} n_{ij} - c^2 \sum_{j=1}^{\ell-1} n_{ij}^2 \delta_{ijj}(\ell) \\ - 2c^2 \sum_{j=1}^{\ell-2} \sum_{k=j+1}^{\ell-1} n_{ij} n_{ik} \delta_{ijk}(\ell)$$

The expressions for p and $\delta_{ijk}(\ell)$'s are the same as those in (4.22), except that ℓ is substituted for n_i .

Step 5

Then

$$|y_i^*| = a^{f_i(n)} \prod_{j=1}^{n_i} (a + n_{ij} \zeta_{ij})$$

where $f_i(n) = n_{i0} - n_i$

Since \underline{V}_{i22} is given by $\gamma_1 \underline{I}_i$, where \underline{I}_i is the identity matrix of order n_i ,

$$|\underline{V}_{i22}| = \gamma_1^{n_i}$$

V_{i33} is a scalar (γ_1). Therefore from (A21) the determinant of \underline{V}_i is given by

$$|\underline{V}_i| = \gamma_1^{g_i(n)} a^{f_i(n)} \prod_{j=1}^{n_i} (a + n_{ij} \zeta_{ij})$$

where

$$g_i(n) = n_i + 1.$$

APPENDIX 3

An algorithm for computing \underline{A}_{i11} for a multiple-trait setting

Step 1

$$\underline{P} = \underline{A}^{-1}$$

Step 2

$$\underline{D}_i = \begin{cases} n_{i1}n_{i2}C(\underline{A} + n_{i1}\underline{B})^{-1}\underline{C} - (\underline{A} + n_{i2}\underline{B}) & \text{if } n_i = 2 \\ n_{i1}n_{i2}C(\underline{A} + n_{i1}\underline{B})^{-1}\underline{C} - (\underline{A} + n_{i2}\underline{B}) - \underline{G}_i(n) & \text{if } n_i > 2 \end{cases}$$

where

$$\underline{G}_i(n) = (\underline{A} + n_{i2}\underline{B} - n_{i2}\underline{C})\underline{T}_i[n_{i1}C(\underline{A} + n_{i1}\underline{B})^{-1}\underline{C} - \underline{C}]$$

In the above expression

$$\underline{T}_i = \sum_{j=3}^{n_i} n_{ij}(\underline{A} + n_{ij}\underline{B} - n_{ij}\underline{C})^{-1}.$$

Step 3

$$\underline{Q}_{i12} = (\underline{A} + n_{i1}\underline{B})^{-1}\underline{C}\underline{D}_i^{-1}$$

Step 4

If $n_i > 2$, calculate \underline{Q}_{ijk} for $j=1, \dots, n_i$ and $k=j, \dots, n_i$, where

$$\underline{Q}_{ijk} = (\underline{A} + n_{ij}\underline{B} - n_{ij}\underline{C})^{-1}(\underline{A} + n_{i2}\underline{B} - n_{i2}\underline{C})\underline{Q}_{i12}\underline{Q}_{ik}^*$$

In the above expression

$$\underline{Q}_{ik}^* = (\underline{A} + n_{i1}\underline{B} - n_{i1}\underline{C})(\underline{A} + n_{ik}\underline{B} - n_{ik}\underline{C})^{-1}.$$

Step 5

If $n_i = 1$,

$$Q_{i11} = -\underline{A}^{-1} \underline{B} (\underline{A} + n_{i1} \underline{B})^{-1}.$$

If $n_i = 2$,

$$Q_{i11} = -[\underline{A}^{-1} \underline{B} + n_{i2} Q_{i12} \underline{C}] (\underline{A} + n_{i1} \underline{B})^{-1}$$

and

$$Q_{i22} = -[\underline{A}^{-1} \underline{C} + n_{i1} Q_{i12} \underline{C}] (\underline{A} + n_{i2} \underline{B})^{-1}.$$

If $n_i > 2$

$$Q_{ijj} = -[\underline{A}^{-1} \underline{B} + \sum_{k=1}^{j-1} n_{ik} Q_{ikj} \underline{C} + \sum_{k=j}^{n_i} n_{ik} Q_{ijk} \underline{C}] (\underline{A} + n_{ij} \underline{B})^{-1}$$

Appendix 4Examples to illustrate the inversion of the variance-covariance matrix of direct and maternal genetic effects (single-trait)

Consider the pedigree information of the example considered by Slanger (1979) [see Table A1].

Table A1 - Pedigree information of the example (from Slanger (1979))

Individuals with records	sire	dam
A	unknown	P
B	M	P
C	M	P
D	unknown	Q
E	M	R
F	A	R
G	A	R
H	A	E
I	unknown	unknown

He computed the inverse of \tilde{G} where the direct genetic values of A-I and the maternal genetic values of P, Q, R, A, E, G and M and the unidentified dam of I were included in the vector of genetic values to be predicted. The objective of this study is to predict the genetic values of the individuals A - I, free of the maternal genetic values of their dams. That is, in addition to the direct genetic values of A - I, we require the maternal genetic values of P, Q, R, E and the unidentified dam of I (U).

It was explained earlier, that if the maternal genetic value of any individual is included, then the direct genetic value of this individual should also be present in the vector of genetic values to be predicted, in order to generate the correct \underline{G}^{-1} . Therefore, it is required to include the direct genetic values of P, Q, R and the unidentified dam of I. The other option is to exclude the maternal genetic values of the unidentified dam of I, which leads to biased results. Also, since the direct and maternal genetic values of the dam and the direct genetic value of the sire of F and G are included, it is required to include the maternal genetic value of the sire of F and G. This means that, genetic values which are not present in the model are predicted (the direct genetic values of P, Q, R and U and the maternal genetic value of A). Neither genetic value of M is included in the model. Therefore let us assume that the sires of B, C and E are unknown. The following examples demonstrate how the inverse of \underline{G} is generated and also demonstrate why restrictions have to be imposed on the vector of genetic values to be predicted. The first example generates the exact \underline{G}^{-1} whereas the second generates an approximate to the inverse.

Example 1

In addition to the direct genetic values of A-I and the maternal genetic values of their dams, direct genetic values of P, Q, R and U (dams with no records) and the maternal genetic value of A (a sire) are included. Arrange the genetic values so that the direct genetic values of parents precede the direct genetic values of their progeny. The maternal genetic value of an individual, if present, will follow it's direct genetic value. For this example,

$$\underline{u}' = (P_d, P_m, Q_d, Q_m, R_d, R_m, A_d, A_m, B_d, C_d, E_d, E_m, F_d, G_d, H_d, U_d, U_m, I_d)$$

where the subscripts d and m refer to direct genetic values and maternal genetic values, respectively. Suppose that the elements

of u after they are ordered are numbered as follows:

1	2	3	4	5	6	7	8	9	10	11	12	13	14
P _d	P _m	Q _d	Q _m	R _d	R _m	A _d	A _m	B _d	C _d	D _d	E _d	E _m	F _d
15	16	17	18	19									
G _d	H _d	U _d	U _m	I _d									

It can be noted that all diagonal elements of the relationship matrix of individuals P, Q, R, U and A - I are 1.

Computation of the inverse of the matrix of the mendelian sampling random variables

P, Q, R and U

direct and maternal genetic values are required; both parents are unknown

$$\underline{D}_P^{-1} = \underline{D}_Q^{-1} = \underline{D}_R^{-1} = \underline{D}_U^{-1} = \begin{bmatrix} 108 & -36 \\ -36 & 158 \end{bmatrix}^{-1}$$

A and E

direct and maternal genetic values are required; dam's direct and maternal genetic values are included; sire is unknown

$$\underline{D}_A^{-1} = \underline{D}_E^{-1} = \frac{1}{0.75} \begin{bmatrix} 108 & -36 \\ -36 & 158 \end{bmatrix}^{-1}$$

B, C, D and I

direct genetic values only; dam's direct genetic value is included; sire is unknown

$$\underline{D}_B^{-1} = \underline{D}_C^{-1} = \underline{D}_D^{-1} = \underline{D}_I^{-1} = [0.75 \times 108]^{-1}$$

F, G and H

direct genetic value only; direct genetic values of both parents are included

$$\underline{D}_F^{-1} = \underline{D}_G^{-1} = \underline{D}_H^{-1} = [0.5 \times 108]^{-1}$$

Generating the inverse of G

Denote the (i,j)th element of \underline{G}^{-1} as $\gamma(i,j)$.

Step 1

Initially, let $\underline{G}^{-1} = \underline{D}^{-1}$. That is

<u>parents</u>	<u>individual</u>	
unknown	P	$\gamma(1,1) = 0.010020$
		$\gamma(1,2) = 2.2831 \times 10^{-3}$
		$\gamma(2,1) = 2.2831 \times 10^{-3}$
		$\gamma(2,2) = 6.8493 \times 10^{-3}$
<hr/>		
unknown	Q	$\gamma(3,3) = 0.010020$
		$\gamma(3,4) = 2.2831 \times 10^{-3}$
		$\gamma(4,3) = 2.2831 \times 10^{-3}$
		$\gamma(4,4) = 6.8493 \times 10^{-3}$
<hr/>		

unknown R $\gamma(5,5) = 0.010020$
 $\gamma(5,6) = 2.2831 \times 10^{-3}$
 $\gamma(6,5) = 2.2831 \times 10^{-3}$
 $\gamma(6,6) = 6.8493 \times 10^{-3}$

dam P,
sire unknown A $\gamma(7,7) = 0.013360$
 $\gamma(7,8) = 3.0441 \times 10^{-3}$
 $\gamma(8,7) = 3.0441 \times 10^{-3}$
 $\gamma(8,8) = 9.1324 \times 10^{-3}$

dam P,
sire unknown B $\gamma(9,9) = 0.012346$

dam P,
sire unknown C $\gamma(10,10) = 0.012346$

dam Q,
sire unknown D $\gamma(11,11) = 0.012346$

dam R,
sire unknown E $\gamma(12,12) = 0.013360$
 $\gamma(12,13) = 3.0441 \times 10^{-3}$
 $\gamma(13,12) = 3.0441 \times 10^{-3}$
 $\gamma(13,13) = 9.1324 \times 10^{-3}$

dam R,sire A F $\gamma(14,14) = 0.018519$

dam R,sire A G $\gamma(15,15) = 0.018519$

$$\text{dam E, sire A} \quad H \quad \gamma(16,16) = 0.018519$$

$$\begin{aligned} \text{unknown} \quad U \quad \gamma(17,17) &= 0.010020 \\ \gamma(17,18) &= 2.2831 \times 10^{-3} \\ \gamma(18,17) &= 2.2831 \times 10^{-3} \\ \gamma(18,18) &= 6.8493 \times 10^{-3} \end{aligned}$$

$$\begin{aligned} \text{dam U,} \quad I \quad \gamma(19,19) &= 0.012346 \\ \text{sire unknown} \end{aligned}$$

Step 2

No further contributions to \underline{G}^{-1} from the individuals P, Q, R and U. Contributions from other individuals are as follows:

(1) A

$$\gamma(1,7) = \gamma(7,1) = -0.5 \times (0.01360) = -6.68 \times 10^{-3}$$

$$\begin{aligned} \gamma(1,8) = \gamma(8,1) = \gamma(2,7) = \gamma(7,2) \\ = -0.5 \times (3.0441 \times 10^{-3}) = -1.5221 \times 10^{-3} \end{aligned}$$

$$\gamma(2,8) = \gamma(8,2) = .5 \times (9.1324 \times 10^{-3}) = -4.5662 \times 10^{-3}$$

$$\gamma(1,1) = 0.010020 + 0.25 \times (0.013360) = 0.013360$$

$$\begin{aligned} \gamma(1,2) = \gamma(2,1) &= 2.2831 \times 10^{-3} + 0.25 \times (3.0441 \times 10^{-3}) \\ &= 3.0441 \times 10^{-3} \end{aligned}$$

$$\gamma(2,2) = 6.8493 \times 10^{-3} + 0.25 \times (9.1324 \times 10^{-3}) = 9.1324 \times 10^{-3}$$

(2) B

$$\gamma(1,9) = \gamma(9,1) = -0.5 \times (0.012346) = -6.173 \times 10^{-3}$$

$$\gamma(1,1) = 0.013360 + 0.25 \times (0.012346) = 0.016447$$

(3) C

$$\gamma(1,10) = \gamma(10,1) = -0.5 \times (0.012346) = -6.173 \times 10^{-3}$$

$$\gamma(1,1) = 0.016447 + 0.25 \times (0.012346) = 0.019533$$

(4) D

$$\gamma(3,11) = \gamma(11,3) = -0.5 \times (0.012346) = -6.173 \times 10^{-3}$$

$$\gamma(3,3) = 0.010020 + 0.25 \times (0.012346) = 0.013107$$

(5) E

$$\gamma(5,12) = \gamma(12,5) = -0.5 \times (0.013360) = -6.68 \times 10^{-3}$$

$$\gamma(6,12) = \gamma(12,6) = \gamma(5,13) = \gamma(13,5)$$

$$= -0.5 \times (3.0441 \times 10^{-3}) = -1.5221 \times 10^{-3}$$

$$\gamma(6,13) = \gamma(13,6) = -0.5 \times (9.1324 \times 10^{-3}) = -4.5662 \times 10^{-3}$$

$$\gamma(5,5) = 0.010020 + 0.25 \times (0.013360) = 0.013360$$

$$\gamma(5,6) = \gamma(6,5) = 2.2831 \times 10^{-1} + 0.25 \times (3.0441 \times 10^{-3})$$

$$= 3.0441 \times 10^{-3}$$

$$\gamma(6,6) = 6.8493 \times 10^{-3} + 0.25 \times (9.1324 \times 10^{-3}) = 9.1324 \times 10^{-3}$$

(6) F

$$\begin{aligned}\gamma(5,14) &= \gamma(14,5) = \gamma(7,14) = \gamma(14,7) \\ &= -0.5 \times (0.018519) = -9.2595 \times 10^{-3}\end{aligned}$$

$$\gamma(5,5) = 0.013360 + 0.25 \times (0.018519) = 0.017990$$

$$\gamma(5,7) = \gamma(7,5) = 0.25 \times (0.018519) = 4.6298 \times 10^{-3}$$

$$\gamma(7,7) = 0.013360 + 0.25 \times (0.018519) = 0.017990$$

(7) G

$$\begin{aligned}\gamma(5,15) &= \gamma(15,5) = \gamma(7,15) = \gamma(15,7) \\ &= -0.5 \times (0.018519) = -9.2595 \times 10^{-3}\end{aligned}$$

$$\gamma(5,5) = 0.017990 + 0.25 \times (0.018519) = 0.022620$$

$$\gamma(5,7) = \gamma(7,5) = 4.6298 \times 10^{-3} + 0.25 \times (0.018519) = 9.2596 \times 10^{-3}$$

$$\gamma(7,7) = 0.017790 + 0.25 \times (0.018519) = 0.022620$$

(8) H

$$\begin{aligned}\gamma(7,16) &= \gamma(16,7) = \gamma(12,16) = \gamma(16,12) \\ &= -0.5 \times (0.018519) = -9.2595 \times 10^{-3}\end{aligned}$$

$$\gamma(7,7) = 0.02262 + 0.25 \times (0.018519) = 0.027250$$

$$\gamma(7,12) = \gamma(12,7) = 0.25 \times (0.018519) = 4.6298 \times 10^{-3}$$

$$\gamma(12,12) = 0.013360 + 0.25x(0.018519) = 0.017790$$

(9) I

$$\gamma(17,19) = \gamma(19,17) = -0.5x(0.012346) = -6.173x10^{-3}$$

$$\gamma(17,17) = -0.010020 + 0.25x(0.012346) = 0.013107$$

The exact inverse of \underline{G} generated by this method is given in Table A2.

Table A2 - The exact inverse of G for Example 1

P _d	P _m	Q _d	Q _m	R _d	R _m	A _d	A _m	B _d	C _d	D _d	E _d	E _m	F _d	G _d	H _d	U _d	U _m	I _d
1.953	.304	0	0	0	0	-.668	-.152	-.617	-.617	0	0	0	0	0	0	0	0	0
	.913	0	0	0	0	-.152	-.457	0	0	0	0	0	0	0	0	0	0	0
		1.311	.228	0	0	0	0	0	0	-.617	0	0	0	0	0	0	0	0
			.685	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
				2.262	.304	.926	0	0	0	0	-.668	-.152	-.926	-.926	0	0	0	0
					.913	0	0	0	0	0	-.152	-.457	0	0	0	0	0	0
						2.725	.304	0	0	0	-.427	0	-.926	-.926	-.926	0	0	0
							.913	0	0	0	0	0	0	0	0	0	0	0
								1.235	0	0	0	0	0	0	0	0	0	0
									1.235	0	0	0	0	0	0	0	0	0
										1.235	0	0	0	0	0	0	0	0
											1.799	.304	0	0	-.926	0	0	0
												.413	0	0	0	0	0	0
													1.852	0	0	0	0	0
														1.852	0	0	0	0
															1.852	0	0	0
																1.311	.228	-.617
																	.685	0
																		1.235

All numbers in this table are obtained by multiplying the actual numbers by 100.

Example 2

Direct genetic values of the dams with no records are removed (P_d , Q_d , R_d and U_d). The objective of this particular selection problem is to predict direct genetic values of individuals A - I and the maternal genetic values of their dams. Therefore the direct genetic values of P, Q, R and U are not required. As before the maternal genetic value of a sire (A_m) is included. Then \underline{u} for this example is given by

$$\underline{u}' = (P_m, Q_m, R_m, A_d, A_m, B_d, C_d, E_d, E_m, F_d, G_d, H_d, U_m, I_d)$$

Following is a demonstration that the exclusion of the direct genetic values of P, Q, R and U does not result in the exact \underline{G}^{-1} . The elements of \underline{G}^{-1} generated by this method and the elements of the exact \underline{G}^{-1} are given for comparison.

Suppose the genetic values are ordered so that the genetic values of parents precede the genetic values of the progeny,. For this example the order is given as follows:

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
P_m	Q_m	R_m	A_d	A_m	B_d	C_d	D_d	E_d	E_m	F_d	G_d	H_d	U_m^I	I_d

P, Q, R and U

only direct genetic values; both parents are unknown

$$D_P^{-1} = D_Q^{-1} = D_R^{-1} = D_U^{-1} = (158)^{-1}$$

The \underline{D} matrices for the other individuals are the same as those in the previous example.

Step 1

<u>parents</u>	<u>individual</u>	
unknown	P	$\gamma(1,1) = 6.3291 \times 10^{-3}$
<hr/>		
unknown	Q	$\gamma(2,2) = 6.3291 \times 10^{-3}$
<hr/>		
unknown	R	$\gamma(3,3) = 6.3291 \times 10^{-3}$
<hr/>		
dam P, sire unknown	A	$\gamma(4,4) = 0.013360$ $\gamma(4,5) = 3.0441 \times 10^{-3}$ $\gamma(5,4) = 3.0441 \times 10^{-3}$ $\gamma(5,5) = 9.1324 \times 10^{-3}$
<hr/>		
dam P, sire unknown	B	$\gamma(6,6) = 0.012346$
<hr/>		
dam P, sire unknown	C	$\gamma(7,7) = 0.012346$
<hr/>		
dam Q, sire unknown	D	$\gamma(8,8) = 0.012346$
<hr/>		

dam R,	E	$\gamma(9,9) = 0.013360$
sire unknown		$\gamma(9,10) = 3.0441 \times 10^{-3}$
		$\gamma(10,9) = 3.0441 \times 10^{-3}$
		$\gamma(10,10) = 9.1324 \times 10^{-3}$

dam R,sire A	F	$\gamma(11,11) = 0.018519$
--------------	---	----------------------------

dam R,sire A	G	$\gamma(12,12) = 0.018519$
--------------	---	----------------------------

dam E,sire A	H	$\gamma(13,13) = 0.018519$
--------------	---	----------------------------

unknown	U	$\gamma(14,14) = 6.3291 \times 10^{-3}$
---------	---	---

dam U,	I	$\gamma(15,15) = 0.012346$
sire unknown		

Step 2

As before there is no further contribution from P, Q, R and U. Also, only the direct genetic values of B,C,D and I whose parents come from the "base" population (P, Q, R and U) are included. Therefore B, C, D and I make no further contribution to \underline{G}^{-1} .

A

$$\gamma(1,4) = \gamma(4,1) = -0.5 \times (3.0441 \times 10^{-3}) = -1.5221 \times 10^{-3}$$

$$\gamma(1,5) = \gamma(5,1) = -0.5 \times (9.1324 \times 10^{-3}) = -4.5662 \times 10^{-3}$$

$$\gamma(1,1) = 6.3291 \times 10^{-3} + 0.25 \times (9.1324 \times 10^{-3}) = 8.6122 \times 10^{-3}$$

$$\gamma(3,9) = \gamma(9,3) = -0.5 \times (3.0441 \times 10^{-3}) = -1.5221 \times 10^{-3}$$

$$\gamma(3,10) = \gamma(10,3) = -0.5 \times (9.1324 \times 10^{-3}) = -4.5662 \times 10^{-3}$$

$$\gamma(3,3) = 6.3291 \times 10^{-3} + 0.25 \times (9.1324 \times 10^{-3}) = 8.6122 \times 10^{-3}$$

F

$$\gamma(4,11) = \gamma(11,4) = -0.5 \times (0.018519) = -9.2595 \times 10^{-3}$$

$$\gamma(4,4) = 0.013360 + 0.25 \times (0.018519) = 0.017990$$

G

$$\gamma(4,12) = \gamma(12,4) = -0.5 \times (0.018519) = -9.2595 \times 10^{-3}$$

$$\gamma(4,4) = 0.017990 + 0.25 \times (0.018519) = 0.022620$$

H

$$\begin{aligned} \gamma(4,13) &= \gamma(13,4) = \gamma(9,13) = \gamma(13,9) \\ &= -0.5 \times (0.018519) = -9.2595 \times 10^{-3} \end{aligned}$$

$$\gamma(4,4) = 0.022620 + 0.25 \times (0.018519) = 0.027249$$

$$\gamma(4,9) = \gamma(9,4) = 0.25 \times (0.018519) = 4.6298 \times 10^{-3}$$

$$\gamma(9,9) = 0.013360 + 0.25 \times (0.018519) = 0.017990$$

Table A3 compares the elements of the exact inverse and the approximate inverse of the variance-covariance matrix.

Table A3 - Comparison of the exact and the approximate G^{-1} for Example 2

P_m	Q_m	R_m	A_d	A_m	B_d	C_d	D_d	E_d	F_m	F_d	G_d	H_d	U_m	I
.861	0	0	-.151	-.457	0	0	0	0	0	0	0	0	0	0
.866	0	0	-.048	-.433	.096	.096	0	0	0	0	0	0	0	0
	.633	0	0	0	0	0	0	0	0	0	0	0	0	0
	.645	0	0	0	0	0	.108	0	0	0	0	0	0	0
		.861	0	0	0	0	0	-.152	-.457	0	0	0	0	0
		.872	-.125	0	0	0	0	-.062	-.436	.125	.125	0	0	0
			2.725	.304	0	0	0	.427	0	-.926	-.926	-.926	0	0
			2.118	.252	-.211	-.211	0	.736	.062	-.547	-.547	-.926	0	0
				.913	0	0	0	0	0	0	0	0	0	0
				.901	-.048	-.048	0	0	0	0	0	0	0	0
					1.235	0	0	0	0	0	0	0	0	0
					1.040	-.195	0	0	0	0	0	0	0	0
						1.235	0	0	0	0	0	0	0	0
						1.040	0	0	0	0	0	0	0	0
							1.235	0	0	0	0	0	0	0
							.944	0	0	0	0	0	0	0
		Symmetric						1.336	.304	0	0	-.926	0	0
								1.602	.259	-.273	-.273	-.926	0	0
									.913	0	0	0	0	0
									.903	-.062	-.062	0	0	0
										1.852	0	0	0	0
										1.473	-.379	0	0	0
											1.852	0	0	0
											1.473	0	0	0
												1.852	0	0
													0	0
													.633	0
													.645	.108
														1.235
														.944

The top line of each row contains the elements of approximate G^{-1} and the bottom line of each row contains the exact G^{-1} .

All numbers in this table are obtained by multiplying the actual numbers by 100.

APPENDIX 5An example to illustrate the inversion of the variance-covariance matrix of direct and maternal genetic effects (multiple-trait)

Consider two traits (trait 1 and trait 2) with the following variance-covariance matrices between direct genetic effects, between direct and maternal genetic effects and between maternal genetic effects respectively:

$$\Sigma_{dd} = \begin{bmatrix} 108 & 56 \\ 56 & 98 \end{bmatrix} \quad \Sigma_{dm} = \begin{bmatrix} -36 & -10 \\ -15 & -40 \end{bmatrix} \quad \Sigma_{mm} = \begin{bmatrix} 158 & 60 \\ 60 & 100 \end{bmatrix}$$

Also define

$$\Sigma = \begin{bmatrix} \Sigma_{dd} & \Sigma_{dm} \\ \Sigma'_{dm} & \Sigma_{mm} \end{bmatrix}.$$

Consider the individuals A - E with the pedigree information given in Table A4.

Table A4 - Pedigree information of example 3

individual	dam	sire
A	unknown	unknown
B	unknown	unknown
C	A	unknown
D	A	B
E	C	B

Predict direct genetic values of A - E and the maternal genetic values of the dams of the individuals A - E. This is equivalent to predicting direct genetic values of

A - E and the maternal genetic values of A, C and the unidentified dam of A (U). The direct genetic values of U and the maternal genetic values of B have to be included in order to generate the exact \underline{G}^{-1} .

That is,

$$\underline{u}' = (B_{d1}, B_{d2}, B_{m1}, B_{m2}, U_{d1}, U_{d2}, U_{m1}, U_{m2}, A_{d1}, A_{d2}, A_{m1}, A_{m2}, \\ C_{d1}, C_{d2}, C_{m1}, C_{m2}, D_{d1}, D_{d2}, E_{d1}, E_{d2})$$

Let

	1	2	3	4	5	6	7	8	9	10
	B_{d1}	B_{d2}	B_{m1}	B_{m2}	U_{d1}	U_{d2}	U_{m1}	U_{m2}	A_{d1}	A_{d2}
	11	12	13	14	15	16	17	18	19	20
	A_{m1}	A_{m2}	C_{d1}	C_{d2}	C_{m1}	C_{m2}	D_{d1}	D_{d2}	E_{d1}	E_{d2}

The diagonal elements of the relationship matrix of A - E and U are 1.

Expressions for the \underline{D} matrices

B,U

"base" animals; direct and maternal genetic values are to be predicted

$$[\underline{D}(B)]^{-1} = [\underline{D}(U)]^{-1} = \underline{\Sigma}^{-1}$$

$$= \begin{bmatrix} .015751 & -.010499 & .094648 & -.005413 \\ & .019292 & -.004005 & .009070 \\ & & .009635 & -.006918 \\ & & & .017238 \end{bmatrix}$$

A,C

direct and maternal genetic values; dam's direct and maternal genetic values are included

$$[\underline{D}(A)]^{-1} = [\underline{D}(C)]^{-1} = [0.75\underline{\Sigma}]^{-1}$$

$$= \begin{bmatrix} .021001 & -.013998 & .006197 & -.007217 \\ & .025723 & -.005340 & .012093 \\ & & .009635 & -.006918 \\ & & & .022983 \end{bmatrix}$$

D,E

direct genetic values only; direct genetic values of both parents are included

$$[\underline{D}(D)]^{-1} = [\underline{D}(E)]^{-1} = [0.5\underline{\Sigma}_{dd}]^{-1}$$

$$= \begin{bmatrix} .026312 & -.015038 \\ & .029002 \end{bmatrix}$$

The inverse generated by this method is given in Table A5.

Table A5 - The inverse of \mathbf{G} for Example 3

B_{d1}	B_{d2}	B_{n1}	B_{n2}	U_{d1}	U_{d2}	U_{n1}	U_{n2}	A_{d1}	A_{d2}	A_{m1}	A_{m2}	C_{d1}	C_{d2}	C_{m1}	C_{m2}	D_{d1}	D_{d2}	E_{d1}	E_{d2}
2.891	-1.802	.465	-.541	0	0	0	0	.658	-.376	0	0	.658	-.376	0	0	-1.316	.752	-1.316	.752
	3.379	-.401	.907	0	0	0	0	-.376	.725	0	0	-.376	.725	0	0	.752	-1.450	.752	-1.450
		.964	-.692	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
			1.724	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
				2.100	-1.400	.620	-.722	-1.050	.700	-.310	.361	0	0	0	0	0	0	0	0
					2.572	-.534	1.209	.700	-1.286	.267	-.605	0	0	0	0	0	0	0	0
						1.285	-.922	-.310	.267	-.642	.461	0	0	0	0	0	0	0	0
							2.298	.361	-.605	.461	-1.149	0	0	0	0	0	0	0	0
								3.283	-2.126	.775	-.902	-1.050	.700	-.310	.361	-1.316	.752	0	0
									3.941	-.668	1.512	.700	-1.286	.267	-.605	.752	-1.450	0	0
										1.606	-1.153	-.310	.267	-.642	.461	0	0	0	0
											2.873	.361	-.605	.461	-1.149	0	0	0	0
												2.758	-1.776	.620	-.722	0	0	-1.316	.752
													3.297	-.534	1.209	0	0	.752	-1.450
														1.285	-.922	0	0	0	0
															2.298	0	0	0	0
																2.631	-1.504	0	0
																	2.900	0	0
																		2.631	-1.504
																			2.900

All numbers in this table are obtained by multiplying the actual numbers by 100

BIBLIOGRAPHY

- Ahlschwede W.T. and Robison O.W. (1971a) - Maternal effects on weights and backfat of swine, Journal of Animal Science, 33(6): 1206 -1211
- Ahlschwede W.T. and Robison O.W. (1971b) - Prenatal and postnatal influences on growth and backfat in swine, Journal of Animal Science, 32(1): 10 - 16
- Aitken A.C. (1949) - On the Wishart distribution in Statistics, Biometrika, 36: 59 - 62
- Albert A. (1976) - When is a sum of squares an analysis of variance?, Annals of Statistics, 4: 775 - 778
- Alenda R., Martin T.G., Lasley J.F. and Ellersieck M.R. (1980) - Estimation of genetic and maternal effects in crossbred cattle of Angus, Charolais and Hereford parentage, I. Birth and weaning weights, Journal of Animal Science, 50(2): 226 -234
- Anderson R.D. (1978) - Studies on the estimation of variance components, Ph.D. Thesis, Cornell University
- Anderson R.D. (1979) - Estimating variance components from balanced data: Optimum properties of REML solutions and MIVQUE estimators, Proceedings of a conference in honor of C.R. Henderson, L.D. Van Vleck and S.R. Searle, Eds., 205 - 215
- Anderson R.D., Henderson H.V., Pukelsheim F. and Searle S.R. (1984) - Best estimation of variance components from balanced data, with arbitrary kurtosis, Mathematische Operationsforschung und Statistik ; Series Statistics, 15(2) : 163 - 176

- Anderson R.D., Quaas R.L. and Searle S.R. (1977) - Fourth moments in the general linear model and the variance of translation invariant quadratic forms, BU-630-M, Biometrics Unit, Cornell University, Ithaca, New York
- Baker R.L. (1980) - The role of maternal effects on the efficiency of selection in beef cattle - A review, Proceedings of the New Zealand Society of Animal Production, 40: 285 - 302
- Bateman N. (1954) - The measurement of milk production of mice through preweaning growth of suckling young, Physiological Zoology, 27: 163 - 173
- Bereskin B., Shelby C.E. and Hazel L.N. (1971) - Carcass traits of purebred Durocs and Yorkshires and their crosses, Journal of Animal Science, 32: 413 - 419
- Blunn C.T. (1969) - Preweaning growth of cross-transferred rats, Journal of Animal Science, 28: 300 - 304
- Bradford G.E. (1972) - The role of maternal effects in animal breeding : VII. Maternal effects in sheep, Journal of Animal Science, 35(6): 1324 - 1334
- Bradford G.E., Chapman A.B. and Grummer R.H. (1958) - Effects of inbreeding, selection, linecrossing and topcrossing in swine, III. Predicting combining ability and general conclusions, Journal of Animal Science, 17: 456 - 467
- Brumby P.J. (1960) - The influence of the maternal environment on growth in mice, Heridity, 14: 1 - 18
- Burris M.J. and Baugus C.A. (1955) - Milk consumption and growth of suckling lambs, Journal of Animal Science, 14: 186 - 191

- Bush N. and Anderson R.L. (1963) - A comparison of three different procedures for estimating variance components, Technometrics, 5(4): 421 - 440
- Carmon J.L. (1963) - Heterosis, combining ability, and maternal effects in mice, Journal of Genetics, 58: 225 - 231
- Ch'ang T.S. and Rae A.L. (1961) - Sources of variation in the weaning weight of Romney Marsh lambs, New Zealand Journal of Agricultural Research, 4: 578 - 582
- Ch'ang T.S. and Rae A.L. (1970) - The genetic basis of growth, reproduction and maternal environment in Romney ewes, I. Genetic variation in hogget characters and fertility of the ewe, Australian Journal of Agricultural Research, 21: 115 - 129
- Ch'ang T.S. and Rae A.L. (1972) - The genetic basis of growth, reproduction and maternal environment in Romney ewes, II. Genetic covariation between hogget characters, fertility and maternal environment of the ewe, Australian Journal of Agricultural Research, 23: 149 - 165
- Chapman A.B. (1946) - Genetic and nongenetic sources of variation in the weight response of the immature rat ovary to a gonadotrophic hormone, Genetics, 31: 494 - 507
- Cockerham C.C. and Weir B.S. (1977) - Quadratic analyses of reciprocal crosses, Biometrics, 33: 187 - 203
- Corbeil R.R. and Searle S.R. (1976a) - A comparison of variance component estimators, Biometrics, 32: 779 - 791
- Corbeil R.R. and Searle S.R. (1976b) - Restricted Maximum Likelihood (REML) estimation of variance components in the mixed model, Technometrics, 18(1): 31 - 38

- Cox D.F., Legates J.E. and Cockerham C.C. (1959) - Maternal influence on body weight, Journal of Animal Science, 18: 519 - 527
- Cox D.F. and Willham R.L. (1962) - Systematic fostering experiments in swine, Journal of Animal Science, 21: 366 - 368
- Crow G.H. and Howell W.E. (1982) - Genetic parameters of the maternal grandsire contribution to beef cattle weaning weights, Canadian Journal of Animal Science, 62: 1057 - 1062
- Crow G.H. and Howell W.E. (1983) - Evaluation of beef sires for maternal genetic effects on weaning weight and measurement of genetic trends, Canadian Journal of Animal Science, 63: 279 - 283
- Cundiff L.V. (1980) - Exploitation and experimental evaluation of breed differences, Proceedings of the World Congress on sheep and beef cattle breeding, Vol I: Technical, 71 - 85
- Deese R.E. and Koger M. (1967) - Maternal effects on preweaning growth rate in cattle, Journal of Animal Science, 26: 250 - 253
- Dickerson G.E. (1947) - Composition of hog carcasses as influenced by heritable differences in rate and economy of gain, Research Bulletin 354, Iowa Agricultural Experimental Station, 489 - 524
- Dickerson G.E. (1973) - Inbreeding and heterosis in animals, Proceedings of the Animal Breeding and Genetics Symposium in honor of Dr. J.L. Lush, Blacksburg, Virginia

- Dillard E.U., Rodriguez O. and Robison O.W. (1980) - Estimation of additive and nonadditive direct and maternal genetic effects from crossbreeding beef cattle, Journal of Animal Science, 50(4): 653 - 663
- Eisen E.J. (1967) - Mating designs for estimating direct and maternal genetic variances and direct-maternal genetic covariances, Canadian Journal of Genetics and Cytology, 9: 13 - 22
- Everett R.W. and Magee W.T. (1965) - Maternal ability and genetic ability of birth weight and gestation length, Journal of Dairy Science, 48: 957 - 961
- Falconer D.S. (1964) - Maternal effects and selection response, Genetics Today, Proceedings of the XI International Congress of Genetics, Pergamon Press, New York, 763 - 744
- Foulley J.L. and Lefort G. (1978) - Methodes d'estimation des effets directs et maternels en selection animale, Annals De Genetique et de selection animale, 10(3): 475 - 496
- Gjedrem T. (1967) - Phenotypic and genetic parameters for weight of lambs at five ages, Acta Agriculturae Scandinavica, 17: 199 - 216
- Graybill F.A. and Hultquist R.A. (1961) - Theorems concerning Eisenhart's model II, Annals of Mathematical Statistics, 32: 261 - 269
- Graybill F.A. and Wortham A.W. (1956) - A note on uniformly best unbiased estimators for variance components, Journal of the American Statistical Association, 51: 266 - 268

- Gregory K.E., Crouse J.D., Koch R.M., Laster D.B., Cundiff L.V. and Smith G.M. (1978) - Heterosis and breed maternal and transmitted effects in beef cattle, IV. Carcass traits of steers, Journal of Animal Science, 47(5): 1063 - 1079
- Gregory K.E., Cundiff L.V., Koch R.M., Laster D.B. and Smith G.M. (1978) - Heterosis and breed maternal and transmitted effects in beef cattle, I. Preweaning traits, Journal of Animal Science, 47(5): 1031 - 1041
- Gregory K.E., Koch R.M., Laster D.B., Cundiff L.V. and Smith G.M. (1978) - Heterosis and breed maternal and transmitted effects in beef cattle, III. Growth traits of steers, Journal of Animal Science, 47(5): 1054 - 1062
- Gregory K.E., Laster D.B., Cundiff L.V., Koch R.M. and Smith G.M. (1978) - Heterosis and breed maternal and transmitted effects in beef cattle, II. Growth rate and puberty in females, Journal of Animal Science, 47(5): 1042 - 1053
- Griffing B. (1956) - A generalised treatment of the use of diallel crosses in quantitative inheritance, Heridity, 10: 31 - 50
- Garwood V.A., Waltz F.A. and Heidenreich C.J. (1967) - Prenatal and postnatal influences on weight and backfat thickness of pasture-raised swine, Journal of animal Science, 26: 674 - 677
- Gilmour A.R. (1983) - REG, A Generalized Linear Models Programme, New South Wales Department of Agriculture
- Hanrahan J.P. (1976) - Maternal effects and selection response with an application to sheep data, Animal Production, 22: 359 - 369

- Hartley H.O. and Rao J.N.K. (1967) - Maximum likelihood estimation for the mixed analysis of variance model, Biometrika, 54: 93 - 108
- Harvey W.R., Casady R.B., Sutor A.E. and Mize K.E. (1961) - Prenatal and postnatal effects in rabbits, Journal of Animal Science, 20: 907
- Harville D.A. (1977) - Maximum likelihood approaches to variance component estimation and to related problems, Journal of the American Statistical Association, 72: 320 - 340
- Hayman B.I. (1954) - The theory and analysis of diallel crosses, Genetics, 39: 789 - 809
- Hazel L.N. (1943) - Genetic basis for selection indices, Genetics, 28: 476 - 490
- Hemmerle W.J. and Hartley H.O. (1973) - Computing maximum likelihood estimates for the mixed A.O.V. model using the W transformation, Technometrics, 15(4): 819 - 831
- Henderson C.R. (1950) - Estimation of genetic parameters, Annals of Mathematical Statistics, 21: 309
- Henderson C.R. (1953) - Estimation of variance and covariance components, Biometrics, 9: 226 - 252
- Henderson C.R. (1963) - Selection Index and expected genetic advance, Statistical Genetics and Plant Breeding, (W.D.Hanson and H.F.Robinson, Eds.), Washington, National Academy of Sciences, National Research Council, 141 - 163
- Henderson C.R. (1973a) - Maximum likelihood estimation of variance components, unpublished

- Henderson C.R. (1973b) - Sire evaluation and genetic trends, Proceedings of the Animal Breeding and Genetics symposium in Honor of Dr. J.L. Lush, Blacksburg, Virginia
- Henderson C.R. (1975a) - Rapid method for computing the inverse of a relationship matrix, Journal of Dairy Science, 58: 1727 - 1730
- Henderson C.R. (1975b) - Best linear unbiased estimation and prediction under a selection model, Biometrics, 31: 423 - 447
- Henderson C.R. (1975c) - Use of all relatives in intraherd prediction of breeding values and producing abilities, Journal of Dairy Science, 58: 1910 - 1916
- Henderson C.R. (1975d) - Use of relationships among sires to increase accuracy of sire evaluation, Journal of Dairy Science, 58: 1731 - 1738
- Henderson C.R. (1976) - A simple method for computing the inverse of a numerator relationship matrix used in prediction of breeding values, Biometrics, 32: 69 - 83
- Henderson C.R. (1977) - Prediction of future records, Proceedings of the International Conference on Quantitative Genetics, Iowa state university press, Ames, Iowa, 615 - 638
- Henderson C.R., Kempthorne O., Searle S.R. and Von Krosigk C.M. (1959) - The estimation of environmental and genetic trends from records subject to culling, Biometrics, 15: 192 - 218
- Henderson C.R. and Quaas R.L. (1976) - Multiple trait evaluation using relatives' records, Journal of Animal Science, 43(6): 1188 - 1197

- Henderson C.R., Searle S.R. and Schaeffer L.R. (1974) - The invariance and calculation of method 2 for estimating variance components, Biometrics, 30: 583 - 588
- Henderson H.V. and Searle S.R. (1979a) - The vec-permutation matrix; the vec operator and Kronecker products: A review, Bu-645-M, Biometrics Unit, Cornell University, Ithaca, New York
- Henderson H.V. and Searle S.R. (1979b) - Vec and vech operators for matrices, with some uses in Jacobians and multivariate statistics, Canadian Journal of Statistics, 7: 65 - 81
- Hill W.G. and Nicholas F.W. (1974) - Estimation of heritability by both regression of offspring on parent and intra-class correlation of sibs in one experiment, Biometrics, 30: 447 - 468
- Hohenboken W.D. and Brinks J.S. (1971a) - Relationships between direct and maternal effects on growth in Herefords, II. Partitioning of covariance between relatives, Journal of Animal Science, 32(1): 26 - 34
- Hohenboken W.D. and Brinks J.S. (1971b) - Relationships between direct and maternal effects on growth in Herefords, III. Covariance of paternal half-brother and sister performance, Journal of Animal Science, 32(1): 35 - 42
- Holtmann W.B. and Bernard C. (1969) - Effect of general combining ability and maternal ability of Oxford, Suffolk and North country Cheviot breeds of sheep on growth performance of lambs, Journal of Animal Science, 28: 155 - 161
- Jinks J.L. (1954) - The analysis of continuous variation in a diallel cross of *Nicotiana Rustica* varieties, Genetics, 39: 767 - 788
- Jury K.E., Johnson D.L. and Clarke J.N. (1979) - Adjustment factors for lamb weaning weight, NZ Journal of Agricultural Research, 22: 385 - 389

- Kempthorne O. (1956) - The theory of diallel cross, Genetics, 41: 451 - 459
- Kidwell J.F., Weeth H.J., Harvey W.R., Haverland L.H., Shelby C.E. and Clark R.T. (1960) - Heterosis in crosses of inbred lines of rats, Genetics, 45: 225 - 231
- Koch R.M. (1972) - The role of maternal effects in animal breeding: VI. Maternal effects in beef cattle, Journal of Animal Science, 35(6): 1316 - 1323
- Koch R.M. and Clark R.T. (1955) - Genetic and environmental relationships among economic characters in beef cattle, III. Evaluating maternal environment, Journal of Animal Science, 14: 979 - 996
- LaMotte L.R. (1973) - Quadratic estimation of variance components, Biometrics, 29: 311 - 330
- Legates J.E. (1972) - The role of maternal effects in Animal breeding: IV. Maternal effects in laboratory species, Journal of Animal Science, 35(6): 1294 - 1302
- Mangus W.L. and Brinks J.S. (1971) - Relationships between direct and maternal effects on growth in Herefords: I. Environmental factors during preweaning growth, Journal of Animal Science, 32(1): 17 - 25
- Mavrogenis A.P., Dillard E.U. and Robison O.W. (1978) - Genetic analysis of postweaning performance of Hereford bulls, Journal of Animal Science, 47(5): 1004 - 1013
- Miller J.J. (1973) - Asymptotic properties of maximum likelihood estimators in the mixed model of the analysis of variance, Technical Report, No.12, Department of Statistics, Stanford University, Stanford, California

- Miller J.J. (1977) - Asymptotic properties of maximum likelihood estimates in the mixed model of the analysis of variance, Annals of Statistics, 5: 746 - 762
- Morrison D.F. (1976) - Multivariate Statistical Methods, Second Edition, McGraw-Hill series in Probability and Statistics
- Neudecker H. (1969) - Some theorems on matrix differentiation with special reference to Kronecker matrix products, Journal of the American Statistical Association, 64: 953 - 963
- Newman S-A.N., Wickham G.A., Rae A.L. and Anderson R.D. (1983) - Weaning weight adjustments for selecting lambs born to year-old ewes, New Zealand Journal of Agricultural Research, 26: 427 - 431
- Numerical Algorithms Group (1981) - NAG FORTRAN library manual, Mark 8
- Numerical Algorithms Group (1983) - NAG FORTRAN library manual, Mark 10
- Owen J.B. (1957) - A study of the lactation and growth of hill sheep in their native environment and under lowland conditions, Journal of Agricultural Science, 48: 387 - 411
- Patterson H.D. and Thompson R. (1971) - Recovery of inter-block information when block sizes are unequal, Biometrika, 58: 545 - 554
- Pollak E.J. and Quaas R.L. (1981) - Monte carlo study of within-herd multiple trait evaluation of beef cattle growth traits, Journal of Animal Science, 52(2): 248 - 256

- Powell M.J.D. (1970) - A survey of numerical methods for unconstrained optimization, SIAM Review, 12(1): 79 - 97
- Quaas R.L. (1975) - From Mendel's laws to the A inverse, Mimeograph, Animal Science Department, Cornell University, Ithaca, New York
- Quaas R.L. (1976) - Computing the diagonal elements and inverse of a large numerator relationship matrix, Biometrics, 32: 949 - 953
- Quaas R.L. (1984) - BLUP School Hand Book : Use of mixed models for prediction and for estimation of (co)variance components, R.D.Anderson and A.R.Gilmour, Animal Genetics and Breeding Unit, University of New England, New South Wales
- Quaas R.L. and Pollak E.J. (1980) - Mixed model methodology for farm and ranch beef cattle testing programs, Journal of Animal Science, 51(6): 1277 - 1287
- Rao C.R. (1965) - Linear Statistical Inference and its applications, John Wiley and Sons
- Rao C.R. (1970) - Estimation of heteroscedastic variances in linear models, Journal of the American Statistical Association, 65: 161 - 172
- Rao C.R. (1971a) - Estimation of variance and covariance components - MINQUE theory, Journal of Multivariate Analysis, 1: 257 - 275
- Rao C.R. (1971b) - Minimum variance quadratic unbiased estimation of variance components, Journal of multivariate Analysis, 1: 445 - 456

- Rao C.R. (1972) - Estimation of variance and covariance components in linear models, Journal of the American Statistical Association, 67: 112 - 115
- Robison O.W. (1972) - The role of maternal effects in animal breeding: V. Maternal effects in Swine, Journal of Animal Science, 35(6): 1303 - 1315
- Robison O.W. (1981) - The influence of maternal effects on the efficiency of selection; A review, Livestock Production Science, 8: 121 - 137
- Roth W.E. (1934) - On direct product matrices, Bulletin of American Mathematical Society, 40: 461 - 468
- Rutledge J.J., Robison O.W., Eisen E.J. and Legates J.E. (1972) - Dynamics of genetic and maternal effects in mice, Journal of Animal Science, 35(5): 911 - 918
- Schinckel P.G. and Short B.F. (1961) - The influence of nutritional level during pre-natal and early post-natal life on adult fleece and body characters, Australian Journal of Agricultural Research, 12: 176 - 202
- Searle S.R. (1968) - Another look at Henderson's methods of estimating variance components, Biometrics, 24: 749 - 778
- Searle S.R. (1971) - Topics in variance component estimation, Biometrics, 27: 1 - 76
- Searle S.R. (1973) - Derivation of prediction formulae, BU-482-M, Biometrics Unit, Cornell University, Ithaca, New York
- Searle S.R. (1978) - A univariate formulation of the multivariate linear model, Contributions to Survey Sampling and Applied Statistics, Academic Press, 181 - 189

- Searle S.R. (1979) - Notes on variance component estimation:
A detailed account of maximum likelihood and kindred
methodology, Biometrics Unit, Cornell University, Ithaca,
New York
- Seely J. (1971) - Quadratic subspaces and completeness, Annals
of Mathematical Statistics, 42: 710 - 721
- Shelton M. (1964) - Relation of birth weight to death losses
and to certain productive characters of fall-born lambs,
Journal of Animal Science, 23: 355 - 359
- Slanger W.D. (1977) - An indirect method of forming expressions
for the inverses of genetic variance-covariance matrices
for two traits, Journal of Dairy Science, 60: 1440 - 1447
- Slanger W.D. (1979) - Genetic evaluation of beef cattle for
weaning weight, Journal of Animal Science, 48(5):
1070 - 1078
- Slanger W.D. (1980) - Comparison of within-herd genetic evaluation
procedures for beef cattle weaning weight, Journal of
Animal Science, 51(3): 595 - 603
- Thompson R. (1976a) - The estimation of maternal genetic
variances, Biometrics, 32: 903 - 917
- Thompson R. (1976b) - Design of experiments to estimate
heritability when observations are available on parents and
offspring, Biometrics, 32: 283 - 304
- Thompson R. (1977) - The estimation of heritability with
unbalanced data, I. Observations available on parents and
offspring, Biometrics, 33: 485 - 495

- Thompson W.A. (1962) - The problem of negative estimates of variance components, Annals of mathematical Statistics, 33: 273 - 289
- Townsend E.C. and Searle S.R. (1971) - Best quadratic unbiased estimation of variance components from unbalanced data in the 1-way classification, Biometrics, 27: 643 - 657
- Van Vleck L.D. (1970) - Index selection for direct and maternal genetic components of economic traits, Biometrics, 26: 477 - 483
- Van Vleck L.D. (1976) - Selection for direct, maternal and grandmaternal genetic components of economic traits, Biometrics, 32: 173 - 181
- Van Vleck L.D. and Bradford G.E. (1966) - Genetic and maternal influence on the first three lactation of Holstein cows, Journal of Dairy Science, 49: 45 - 52
- Van Vleck L.D. and Hart C.L. (1966) - Covariances among the first lactation milk records of cousins, Journal of Dairy Science, 49: 41 - 44
- Van Vleck L.D., St.Louis D. and Miller J.I. (1977) - Expected phenotypic response in weaning weight of beef calves from selection for direct and maternal genetic effects, Journal of Animal Science, 44(3): 360 - 367
- Wiener G. and Slee J. (1965) - Maternal and genetic influences on follicle and fleece development in Lincoln and Welsh mountain sheep - A study involving egg transfer, Animal Production, 7: 333 - 345
- Willham R.L. (1963) - The covariance between relatives for characters composed of components contributed by related individuals, Biometrics, 19: 18 - 27

Willham R.L. (1972) - The role of maternal effects in animal breeding: III. Biometrical aspects of maternal effects in animals, Journal of Animal Science, 35(6): 1288 - 1293

Young C.W., Legates J.E. and Farthing B.R. (1965) - Prenatal and postnatal influences on growth, prolificacy and maternal performance in mice, Genetics, 52: 553 - 561