Chapter 1

Introduction

Success when selecting livestock for a particular breeding goal depends upon correctly identifying the superior animals from among their contemporaries. During the last twenty-five years significant improvements have been made in the process of evaluating livestock for their genetic potential. These improvements result from the use of Best Linear Unbiased Prediction (BLUP). Its use is now widespread among species and countries.

The development of BLUP is largely due to Henderson (1973). Among other properties BLUP is able to combine information from a variety of sources - observations of the chosen trait and correlated traits on self and relatives - in the 'best' way. Its general acceptance is due to two developments. Firstly, Henderson's (1975, 1976) discovered a method to write the inverse of the covariance matrix between animal effects directly from a list of animals and their parents. Secondly, rapid developments in the power of computers have allowed the evaluation of large numbers of animals with more complicated and multiple-trait models.

The aim of this thesis is to develop some algorithms that implement BLUP procedures more efficiently than has been done in the past and therefore add to the size and complexity of models that can be analysed.

It begins with a review of the literature relating to BLUP, its properties and algorithms

commonly employed in its application in Chapter 2. Chapter 3 presents an alternative method of inverting **A** using partitioned matrix theory. This method is used in Chapter 4 to demonstrate how gametes can be analysed with an animal model. Chapter 5 describes an efficient method for finding inbreeding coefficients of the animals in a population. The following three chapters (6-8) describe methods for representing, factoring and transforming the mixed model equations (MME) which allow significant savings in both the time and memory required to find solutions to the MME. The study is concluded with a discussion of the relative value of these methods as compared with other available methods and the scope for other improvements in efficiency.

Because chapters 4-8 have been published as papers, there is some overlap of contextual settings contained in the introductions and also with Chapter 2. Some alterations to the published forms of these chapters have been made so that the nomenclature throughout the thesis is consistent. As well as a general appendix, there is an appendix to Chapter 5 that was part of the published paper. Chapters 3 and 4 describe work completed with Johann Sölkner and Chapters 6 and 8 with Hans-Ulrich Graser. In all cases the fundamental ideas contained therein were mine, but the contribution of both Johann and Hans in developing these ideas and with the proofs and examples I gratefully acknowledge.

Chapter 2

Literature Review

2.1 Introduction

The mechanism of inheritance - whereby offspring receive half of each of their parents' genetic material - provides animal breeders with a powerful tool for the manipulation of livestock populations. This tool is selection and it is the process of choosing, from among the available candidates, superior animals to be the parents of the next generation. Successful selection depends on accurate predictions of the genetic worth of the available animals.

For many industries and species, the method of choice for evaluating livestock is Best Linear Unbiased Prediction (BLUP). It was derived by Henderson (1949, 1950, 1953, 1963, 1973, 1984, 1990) between 1949 and 1973 from selection index theory. This review considers the basis for BLUP as the method of choice and examines some of the practical problems associated with its implementation.

2.2 Best Linear Unbiased Prediction

BLUP is a method of estimating random effects based upon a mixed linear model such as:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Zu} + \mathbf{e} \tag{2.1}$$

where $\mathbf{y}$ is the vector of observations, $\mathbf{b}$ is the vector of fixed effects, $\mathbf{X}$ and $\mathbf{Z}$ are incidence matrices, $\mathbf{u}$ is a random vector of additive genetic effects and $\mathbf{e}$ is the random vector of residuals such that

$$\begin{aligned} E(\mathbf{u}) &= 0, \\ E(\mathbf{e}) &= 0 \end{aligned}$$

and

$$Var \begin{bmatrix} \mathbf{u} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{G} & \mathbf{0} \\ \mathbf{0} & \mathbf{R} \end{bmatrix}$$

where $\mathbf{G}$ and $\mathbf{R}$ are known positive definite matrices.

$\hat{\mathbf{b}}$ is the best linear unbiased estimate (BLUE) of $\mathbf{b}$ and $\hat{\mathbf{u}}$ is the BLUP of $\mathbf{u}$. $\hat{\mathbf{b}}$ and $\hat{\mathbf{u}}$ are the solutions to the mixed model equations (MME):

$$\begin{bmatrix} \mathbf{X'R^{-1}X} & \mathbf{X'R^{-1}Z} \\ \mathbf{Z'R^{-1}X} & \mathbf{Z'R^{-1}Z + G^{-1}} \end{bmatrix} \begin{bmatrix} \hat{\mathbf{b}} \\ \hat{\mathbf{u}} \end{bmatrix} = \begin{bmatrix} \mathbf{X'R^{-1}y} \\ \mathbf{Z'R^{-1}y} \end{bmatrix} \tag{2.2}$$

which result from differentiating the joint density of $\mathbf{y}$ and $\mathbf{u}$ with respect to $\mathbf{b}$ and $\mathbf{u}$ and equating them to zero (Henderson, 1973).

BLUP is best in that the mean square error of the residuals is minimised; it is linear in that the elements of $\mathbf{u}$ are a linear combination of the data and it is unbiased in the sense that the mean of the estimate is equal to the mean of the quantity being estimated. Proofs of these properties were developed by Henderson et al. (1959) and Henderson (1963).

For single trait models the matrix $\mathbf{G}$ is commonly assumed to be $\mathbf{A}\sigma_u^2$, where $\mathbf{A}$ is the numerator relationship matrix and σ_u^2 is the additive genetic variance, and $\mathbf{R}$ is assumed to be $\mathbf{I}\sigma_e^2$, where $\mathbf{I}$ is the identity matrix and σ_e^2 is the residual variance. In multiple trait models these are assumed to be $\mathbf{A} * \mathbf{G}_0$ and $\mathbf{I} * \mathbf{R}_0$ where $\mathbf{G}_0$ and $\mathbf{R}_0$ are the genetic and residual covariances among traits respectively and * symbolises the Kronecker product.

Before Henderson (1973) derived BLUP, selection indexes were widely used to combine information from an individual and its relatives and from correlated traits as a predictor of an animal's performance, viz.

$$\hat{\mathbf{w}}_i = E(\mathbf{w}|\mathbf{y}) = \alpha + \mathbf{C}'\mathbf{V}^{-1}(\mathbf{y} - \theta) \tag{2.3}$$

where $\hat{\mathbf{w}}$ is the index, α is the column vector of means of $\mathbf{w}$, $\mathbf{C}$ is the covariance matrix between $\mathbf{w}$ and $\mathbf{y}$, $\mathbf{V}$ is the covariance matrix of $\mathbf{y}$ and θ is the vector of means of $\mathbf{y}$. When calculating the selection index, it was generally assumed that the means of $\mathbf{y}$ and $\mathbf{w}$ were known, which was valid when equal information was available on all candidates but not so when the information available on candidates was unequal. When the generalised least square (GLS) estimates of these means obtained from the data were used in their place such that $\hat{\theta} = \mathbf{X}\hat{\mathbf{b}}$ and $\hat{\alpha} = P\hat{\mathbf{b}}$, an estimable function of the data, then Equation 2.3 is the BLUP of $\mathbf{w}$ (Henderson, 1973).

The $\hat{\mathbf{b}}$ were obtained as one set of solutions to the GLS equations

$$(\mathbf{X}'\mathbf{V}^{-1}\mathbf{X})^{-}\mathbf{X}'\mathbf{V}^{-1}\mathbf{y} = \hat{\mathbf{b}} \tag{2.4}$$

where $\mathbf{V} = \mathbf{ZGZ}' + \mathbf{R}$. With Equation 2.2, Henderson (1973) demonstrated that $\hat{\mathbf{u}} = \hat{\mathbf{w}}$ and $\mathbf{X}\hat{\mathbf{b}}$ could be obtained without inverting $\mathbf{V}$ which, for large populations, would even now be infeasible.

2.3 The Numerator Relationship Matrix A and its inverse

The numerator relationship matrix, **A**, describes the genetic relationships between all animals in a population as described by the pedigree. It is a matrix with the following properties (Henderson, 1975, 1976):

1. it is symmetric.
2. $a_{ii} = 1 + F_i$ where a_{ii} is the i^{th} diagonal of **A** and F_i is the inbreeding coefficient of the i^{th} animal, Wright (1922).
3. $a_{ij} = \rho_{ij}\sqrt{(a_{ii}a_{jj})}$ where ρ_{ij} is Wrigh 's (1922) coefficient of relationship between animals i and j.

Thus it describes the probability that one allele chosen at random from each of the ith and jth animals are identical by descent.

Recursive rules for building **A** require that animals are numbered so that parents precede their progeny and are:

$$a_{ii} = 1 + F_i \tag{2.5}$$

$$a_{ij}, a_{ji} = 0.5(a_{jp} + a_{jq}), j < i. \tag{2.6}$$

where $F_i = 0.5a_{pq}$ is the inbreeding coefficient of animal i with parents p and q. i and j are rows and columns in **A** corresponding to the ith and jth animals. If either parent is unknown then a_{jp} (a_{jq}) and a_{pq} are omitted and $F_i = 0$.

Quaas (1984) and Dempfle (1990) describe how **A** is used in the interpretation of the random variables in **u**. Consider an animal's breeding value $\mathbf{u}_i$ as a function of its parents' breeding values u_{sire} and u_{dam}, viz.

$$u_i = 0.5u_{sire} + 0.5u_{dam} + \phi_i$$

where ϕ_i represents the deviation of the ith animal from the mean breeding value of its parents due to mendelian sampling. In matrix form

$$\mathbf{u} = 0.5\mathbf{P}\mathbf{u} + \mathbf{\Phi} \tag{2.7}$$

where $\mathbf{P}$ is a lower triangular matrix with 1s in the columns of each row relating to the parent of the animal represented by that row and zeroes elsewhere. Rearranging

$$\mathbf{u} = (\mathbf{I} - 0.5\mathbf{P})^{-1}\mathbf{\Phi}$$

and

$$\begin{aligned} var(\mathbf{u}) &= (\mathbf{I} - 0.5\mathbf{P})^{-1} Var(\Phi)(\mathbf{I} - 0.5\mathbf{P}')^{-1} \\ &= (\mathbf{I} - 0.5\mathbf{P})^{-1}\mathbf{D}(\mathbf{I} - 0.5\mathbf{P}')^{-1}\sigma_u^2 \end{aligned}$$

where $\mathbf{D}\sigma_u^2$ is the variance matrix of $\mathbf{\Phi}$.

The elements of $\mathbf{D}$ are $(0.5 - 0.25(F_{sire} + F_{dam}))$ when both parents are known, $(0.75 - 0.25(F_{parent}))$ when one parent is known and 1 for base animals (Henderson 1975, 1976). Alternatively Quaas (1984) showed that

$$\begin{aligned} d_i &= var(\phi_i)/\sigma_u^2 \\ &= 1 + F_i - 0.25a_{pp} - 0.5a_{pq} - 0.25a_{qq} \\ &= 1 - 0.25(a_{pp} + a_{qq}) \end{aligned} \tag{2.8}$$

Because the elements of Φ are independent, $\mathbf{D}$ is diagonal. Now

$$\mathbf{A} = (\mathbf{I} - 0.5\mathbf{P})^{-1}\mathbf{D}(\mathbf{I} - 0.5\mathbf{P}')^{-1}$$

and

$$\mathbf{A}^{-1} = (\mathbf{I} - 0.5\mathbf{P}')\mathbf{D}^{-1}(\mathbf{I} - 0.5\mathbf{P})$$

Because $(\mathbf{I}-0.5\mathbf{P}')^{-1}$ is triangular and $\mathbf{D}$ is diagonal, $\mathbf{A}$ is readily invertible as Henderson's (1976) simple rules show. These rules require generating a lower triangular matrix $\mathbf{L}$ such

that $\mathbf{LL}' = \mathbf{A}$ ($\mathbf{L}$ could also be obtained from a more computationally expensive Cholesky decomposition of $\mathbf{A}$). Henderson (1976) also showed that $\mathbf{L} = \mathbf{T}D$ where $\mathbf{T}$ is derived on a row by row basis as

$$\mathbf{T}_i = \begin{bmatrix} \mathbf{T}_{i-1} & \mathbf{0} \\ \mathbf{s}_i' \mathbf{T}_{i-1} & 1 \end{bmatrix}.$$

D is the diagonal of $\mathbf{L}$ and $\mathbf{s}_i$ is half the ith row of $\mathbf{P}$ up to, but not including, the diagonal element. Now $D^2 = \mathbf{D}$ (Quaas, 1984).

Quaas (1976) demonstrated how two vectors the length of the number of animals in the population could be used to build $\mathbf{D}$ and subsequently $\mathbf{A}^{-1}$. Golden et al. (1991) modified this algorithm so that operations involving zeroes were avoided, but this algorithm required a considerable amount of sorting once the ancestors of each animal were identified. One limitation of this approach was that all d_i needed to be recomputed each time $\mathbf{A}^{-1}$ was required.

Meuwissen and Luo (1992) used an approach based on the rows of $\mathbf{T}D$ and were thus able to avoid recomputing old d_is unless new ancestors had been added to the population. Quaas (as cited by Mrode, 1996) implemented a more efficient algorithm, based upon lists of ancestors for this method.

(The source code of such a list based implementation of the column approach for this method is shown in the appendix together with my source code as published by Meuwissen and Luo (1992))

Computing $\mathbf{D}$ is the only difficult part of computing $\mathbf{A}^{-1}$ and it is trivial if the F_i are known. Until methods for computing $\mathbf{D}$ were available, two methods for computing F_i were commonly employed. The first was the path coefficient method (Wright, 1922) which required identifying all the ancestors that each animal's parents had in common and determining the length of each path between the animal's sire and dam through all common ancestors (Falconer, 1981). This method was adequate when pedigrees were short and animals had few common ancestors but became very complicated once there were many common ancestors and pedigrees were deep. (Source code for this method can

be found in the appendix.) The second method for computing the F_is was the tabular method outlined in equations 2.5 and 2.6.

2.4 Solving the Mixed Model Equations

One reason which delayed implentation of BLUP was the lack of sufficient computing power. Although Henderson originally derived BLUP in 1949, it was not until the early 1970's that it was first applied to industry (Henderson, 1990). Schaeffer (1976) describes how to build and solve the MME. In his example a simple sire model with one fixed effect per animal was used and the fixed effects were absorbed into the sires' equations. By processing the animal records in order of fixed effects, most memory was retained for the sires' equations and hence the number of sires evaluated was maximised. Because the coefficient matrix is symmetric, only one triangle needed to be stored. Nevertheless, matrices were frequently constructed by computing contributions to elements and right hand sides, writing them to tape and then accumulating them once they had been sorted. This was even done when building $\mathbf{A}^{-1}$ as described by Quaas (1976). If the order of the coefficient matrix was large then solutions to the MME would be found by iteration.

By absorbing animals without progeny the reduced animal model (Quaas and Pollak, 1980) reduced both the number of equations and the number of (non-zero) elements in the coefficient matrix. This method was developed for use in the beef industry in which the majority of animals have no progeny. This is one example of how the use of equivalent models (Henderson, 1985) can expedite finding predictions of genetic merit.

Quaas (1983, pers. comm.) demonstrated how the non-zero elements in a triangle of the coefficient matrix of the MME could be stored as a series of linked lists. This allowed the available memory to be used more efficiently and could also reduce the amount of computation in each round of iteration.

A new method, commonly called *iterating on the data*, was described by Schaeffer and Kennedy (1986a, 1986b). In this implementation only parts of the MME are stored and

the data are read from memory or disk at least once per iteration. Combining Gauss-Seidel and Jacobi iteration can limit the number of times data need to be read to once each iteration. Although Schaeffer and Kennedy's (1986a, 1986b) description concerned a single trait model, they indicated how it could be applied to models with multiple traits.

Other methods, all designed to reduce either the time or memory required to obtain solutions have been proposed. One package (PEST, Groeneveld et al., 1990) allows the practitioner to choose from a variety of ways of both representing and solving the MME. The different strategies for solving the MME usually amount to different methods of iteration. Gauss-Seidel or Jacobi iteration are used frequently with some form of over-relaxation. 'Block' iteration is sometimes used to update parts of $\mathbf{u}$ and expedite convergence. In some implementations (Schaeffer and Kennedy, 1986; Groeneveld et al., 1990) new solutions to small parts of the solution vector are found simultaneously which can also result in faster convergence of the equation system.

2.5 Multiple Trait Models

Multiple trait models are preferred to single trait models because they increase the accuracy of the predictions as information from other traits is included, provided that good estimates of the correlations among traits in the base population are available. This is particularly important for animals with limited information, but may have little effect for parents with many progeny. Multiple trait models also account for selection bias if the trait(s) which was used as the basis for selection is included in the analysis (Sorensen and Kennedy, 1984).

Multiple trait analyses impose a significant computational cost as although the number of equations increases in proportion to the number of traits, the number of (non-zero) elements in the coefficient matrix of the MME increases in proportion to the square of the number of traits. There is also a significant cost in the number of parameters that are required as that also increases with the square of the number of traits (Quaas, 1984).

2.6 Transformations of the Mixed Model Equations

Significant effort has been aimed at reducing the cost of multiple trait analyses. These methods have focussed largely on ways to transform the MME. One method is the use of canonical transformation. The use of this transformation turns a t-trait multiple trait analysis to t single trait analyses by transforming the set of correlated traits into a set of new traits with uncorrelated genetic effects and residuals. Solutions from the t single trait analyses are then 'backtransformed' to obtain solutions on the original scale.

Quaas (1984) describes a triangular (Cholesky) transformation which can be useful when data are recorded sequentially such that all animals with the ith trait observed have all previous traits observed. Quaas (1984) described a similar, triangular transformation that could be used when there were some traits observed on all animals, and different subsets of the remaining traits recorded on different subsets of animals.

Until recently the use of a canonical transformation was unfortunately limited to situations with:

1. only one random effect,
2. all traits observed on all measured animals, and
3. the same incidence matrices used for all fixed effects and traits (Ducroq and Besbes, 1993).

Methods which relax these constraints are described by Ducroq and Chapuis (1997). Gengler and Misztal (1996) proposed augmenting the fixed effects to remove the third restriction. Their implementation required replicating the data as many times as there were traits, requiring additional (dummy) fixed effects. Ducroq and Besbes (1993) describe a method to augment the data vector when some data are missing. Missing data are replaced by their expected values and then canonical transformation can be applied. It should then be preferred to the triangular transformation. Ducroq and Chapuis (1997) extended the canonical transformation for use with reduced animal models and more than

one random effect. By constraining the augmented effects to be zero, they extended the method of Gengler and Misztal (1996) so that replicating the records was not required. The transformations of Lin and Smith (1990) also allowed the analysis of models with more than one random effect.

Ducroq and Chapuis (1997) found that when some data were missing and the data permitted use of the triangular transformation (Quaas, 1984) then augmenting the data and using the canonical transformation is preferable. Wiggans and Goddard (1997) take the canonical transformation to its logical conclusion whereby they transform the traits for analysis into a smaller subset of traits by setting all but the largest eigenvalues in the transformation matrix to zero.

2.7 Conclusion

The statistical properties of BLUP together with the power of computers have made BLUP the method of choice for the evaluation of livestock for additive genetic effects. Developments in the way that the MME are stored and solved have evolved and the ratio of computing power to computing cost has increased. Improved methods for solving the MME will continue to be useful as more complicated models and larger amounts of data are used.

Much of the emphasis on the canonical transformation arises from applications in the dairy industry where cows are recorded often and whole herds are recorded simultaneously. In this situation, models for analysis and incidence matrices are frequently similar for different traits and missing records are unusual. In more extensive industries than the dairy industry, data available for analysis may not be so well structured.

Chapter 3

Inverting A using partitioned matrix theory

3.1 Introduction

This chapter illustrates how partitioned matrix theory can be used to build the inverse of the relationship matrix. This method is used in chapter 4 as the basis for analysing gametic variation with an animal model.

3.2 Rules for A in matrix form

The recursive rules in Equations 2.5 and 2.6 for building **A** require that animals are numbered so that parents precede their progeny. They are:

$$\begin{aligned} a_{ii} &= 1 + F_i \\ a_{ij}, a_{ji} &= 0.5(a_{jp} + a_{jq}), j < i. \end{aligned}$$

where p and q are the parents of animal i and i and j are rows and columns in **A** corresponding to the ith and jth animals.

A matrix representation of these rules when building $\mathbf{A}$ row by row is:

$$\mathbf{A}_i = \begin{bmatrix} \mathbf{A}_{i-1} & \mathbf{A}_{i-1}\mathbf{s}_i \\ \mathbf{s}_i'\mathbf{A}_{i-1} & a_{ii} \end{bmatrix} \tag{3.1}$$

where $\mathbf{s}_i$ is a vector containing two elements, $\frac{1}{2}$ corresponding to the sire or dam (if known) and zeroes elsewhere ($\mathbf{s}_i$ corresponds to half the ith row of the matrix $\mathbf{P}$ in Equation 2.7 up to but not including the diagonal element).

When computing the diagonal elements of $\mathbf{A}$, it is useful to consider $\mathbf{s}_i$ as the sum of two vectors $\mathbf{p}_i$ and $\mathbf{q}_i$, $\mathbf{s}_i = \mathbf{p}_i + \mathbf{q}_i$, which are vectors of zeroes except for one half at the position of the animal's sire or dam respectively. The expected inbreeding coefficient of an individual is: $F_i = \mathbf{p}_i'\mathbf{A}_{i-1}\mathbf{q}_i + \mathbf{q}_i'\mathbf{A}_{i-1}\mathbf{p}_i$ which is equivalent to $0.5a_{pq}$.

3.3 Inverting the numerator relationship matrix: the partitioned matrix approach

Rather than decomposing $\mathbf{A}$, we may investigate the effect of adding each additional row (animal) to $\mathbf{A}$ on the elements of $\mathbf{A}^{-1}$ via partitioned matrix theory.

Applying the standard matrix result (e.g. Searle, 1982)

$$\begin{bmatrix} \mathbf{A} & \mathbf{B} \\ \mathbf{C} & \mathbf{D} \end{bmatrix}^{-1} = \begin{bmatrix} \mathbf{A}^{-1} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} \end{bmatrix} + \begin{bmatrix} -\mathbf{A}^{-1}\mathbf{B} \\ \mathbf{I} \end{bmatrix} (\mathbf{D} - \mathbf{C}\mathbf{A}^{-1}\mathbf{B})^{-1}[-\mathbf{C}\mathbf{A}^{-1} \quad \mathbf{I}]$$

to $\mathbf{A}_i$ in Equation 3.1 we get

$$\begin{aligned} \mathbf{A}_i^{-1} &= \begin{bmatrix} \mathbf{A}_{i-1}^{-1} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} \end{bmatrix} + \begin{bmatrix} -\mathbf{A}_{i-1}^{-1}\mathbf{A}_{i-1}\mathbf{s}_i \\ 1 \end{bmatrix} (a_{ii} - \mathbf{s}_i'\mathbf{A}_{i-1}\mathbf{A}_{i-1}^{-1}\mathbf{A}_{i-1}\mathbf{s}_i)^{-1}[-\mathbf{s}_i'\mathbf{A}_{i-1}\mathbf{A}_{i-1}^{-1} \quad 1] \\ &= \begin{bmatrix} \mathbf{A}_{i-1}^{-1} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} \end{bmatrix} + \begin{bmatrix} -\mathbf{s}_i \\ 1 \end{bmatrix} (a_{ii} - \mathbf{s}_i'\mathbf{A}_{i-1}\mathbf{s}_i)^{-1}[-\mathbf{s}_i' \quad 1] \end{aligned}$$

$$= \begin{bmatrix} \mathbf{A}_{i-1}^{-1} & \mathbf{0} \\ \mathbf{0} & 0 \end{bmatrix} + (a_{ii} - \mathbf{s}_i'\mathbf{A}_{i-1}\mathbf{s}_i)^{-1} \begin{bmatrix} \mathbf{s}_i\mathbf{s}_i' & -\mathbf{s}_i \\ -\mathbf{s}_i' & 1 \end{bmatrix} \tag{3.2}$$

Since a_{ii} is assumed to be $1+0.5a_{pq}$ and $\mathbf{s}_i'\mathbf{A}_{i-1}\mathbf{s}_i$ is equal to $0.25(a_{pp}+a_{pq}+a_{qp}+a_{qq})$, when $\mathbf{s}_i$ is defined as a vector of zeroes except for two halves at the positions of the parents, this may be rewritten as

$$\mathbf{A}_i^{-1} = \begin{bmatrix} \mathbf{A}_{i-1}^{-1} & \mathbf{0} \\ \mathbf{0} & 0 \end{bmatrix} + (1 - 0.25(a_{pp} + a_{qq}))^{-1} \begin{bmatrix} \mathbf{s}_i\mathbf{s}_i' & -\mathbf{s}_i \\ -\mathbf{s}_i' & 1 \end{bmatrix}$$

This is equivalent to the result of Henderson (1975, 1976) as was shown implicitly by Smith and Mäki-Tanila (1990).

An alternative, equivalent reduction of the scalar term in Equation 3.2 is given by

$$\begin{aligned} d^i &= (1 + \mathbf{p}_i'\mathbf{A}_{i-1}\mathbf{q}_i + \mathbf{q}_i'\mathbf{A}_{i-1}\mathbf{p}_i - \mathbf{s}_i'\mathbf{A}_{i-1}\mathbf{s}_i)^{-1} \\ &= (1 + \mathbf{p}_i'\mathbf{A}_{i-1}\mathbf{q}_i + \mathbf{q}_i'\mathbf{A}_{i-1}\mathbf{p}_i - (\mathbf{p}_i + \mathbf{q}_i)'\mathbf{A}_{i-1}(\mathbf{p}_i + \mathbf{q}_i))^{-1} \\ &= (1 - \mathbf{p}_i'\mathbf{A}_{i-1}\mathbf{p}_i - \mathbf{q}_i'\mathbf{A}_{i-1}\mathbf{q}_i)^{-1} \end{aligned} \tag{3.3}$$

This derivation of $\mathbf{A}^{-1}$ identifies the terms that contribute to d^i explicitly. The result is the same as that of Equation 2.8 and is essentia to the next chapter. The ability to describe alternative forms for $\mathbf{p}$ and $\mathbf{q}$ has been applied by others (e.g. Van Arendonk et al., 1994) to modify $\mathbf{A}$ for different probabilities that alleles might be inherited. Equation 3.3 illustrates simply the terms that need to be calculated to compute $\mathbf{A}^{-1}$ when modifying $\mathbf{p}$ for multiple-sire mating (Henderson, 1988; Dempfle, 1990; Famula, 1992 and Kerr, 1993).

This technique also illustrates that if the animals from the base population are not a random sample, then Henderson's (1975, 1976) rules can be applied to descendants of the base population once the partition of $\mathbf{A}$ relating to the base population has been inverted, as shown by Henderson (1984).