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GENETIC ASSESSMENT OF
BIOLOGICAL MERIT IN CATTLE

By
Just Jensen

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ABSTRACT

GENETIC ASSESSMENT OF BIOLOGICAL MERIT IN CATTLE

By

Just Jensen

The goal of this work was the construction of a total merit selection criterion for use in cattle populations. The topics addressed relate to estimation of genetic parameters, the genetics of beef production and its energetic efficiency, and between and within breed genetic parameters for dairy production and calving traits.

The estimation of genetic parameters from large populations poses severe computing problems. Algorithms that reduce the computer resources needed were reviewed. Strategies for sampling data from populations undergoing selection were compared using a model of breeding events in cattle populations. Genetic parameters estimated using recent data only were unbiased if all relationships between animals were taken into account.

Genetic parameters of beef production and its energetic efficiency were estimated in an experiment with 650 calves from 31 sires. No interactions between sire and proportion of roughage in the diet were found. Daily gain was negatively correlated with feed conversion ratio, but positively correlated with daily feed intake.

Residual intake and partial requirements for productive and nonproductive use of energy were estimated for each bull. There was considerable genetic variation in residual intake and partial energy requirement for both productive and nonproductive use of energy. Consideration of body composition had no significant influence on residual intake. Feed conversion ratio and partial energy requirements were phenotypically uncorrelated to body composition. Selection for leaner animals would increase partial energy requirements. Milk production had a positive genetic correlation to daily gain and nonproductive use of energy, but was not correlated with appetite of the growing bull.

The effect of immigration of Brown Swiss genes into the Red Dane population on dairy production and calving traits were estimated from data on 170,166 cows. Heterosis was 7.1 to 7.7% for production traits. Brown Swiss were 2.6 to 6.2% inferior to Red Dane. Heterosis effects for calving traits were small compared to additive breed differences.

Genetic improvement of calving traits was possible. Dairy production was not genetically correlated with maternal effects on calving traits but had antagonistic correlations to direct effects on calving traits.

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INTRODUCTION

Selection of parents of the next generation of animals is the tool that has been used for the genetic improvement of cattle populations. The goal of selection is to ensure that future animals will outperform the current animals in production.

There are several alternative breeding schemes that can accomplish a set of defined breeding goals, but in order to choose the most efficient one, alternative schemes must be compared. Stochastic modeling, which simulates real events is a useful tool in comparing breeding schemes. Also, data generated from stochastic models can be used to test the properties of statistical models and methods used in estimation of genetic parameters.

Crossbreeding or immigration of genes have been popular for genetic improvement in many European dual purpose and dairy cattle breeds. In Danish Red Cattle genes have been imported from the Brown Swiss breed. Data have been accumulated that makes it possible to evaluate the impact of crossbreeding in terms of, additive genetic and heterotic effects.

Efficiency, defined as either economic efficiency or biological efficiency has received increased attention in recent years as a desirable selection goal in cattle. However, maximizing efficiency of producing dairy and beef products is not necessarily the same as maximizing the output of milk and beef per animal or production unit. A major obstacle in selection for biological efficiency is that it requires measures of feed intake. Such measures are expensive or impossible to obtain on a large scale under commercial conditions.

Intake and other measures for efficiency may be possible in dual purpose populations, however, since relatively few animals are performance tested for beef production. Selection for biological efficiency may therefore be incorporated in the performance test, if efficiency can be measured on the young bull, and is genetically related to overall biological efficiency of males and females in the production system.

Efficiency of whatever trait is a ratio of output to input. Groups of traits other than dairy and beef traits, that are related to economic merit, may be calving traits, fertility, and type or management traits.

In order to make selection decisions based on many traits simultaneously, information on these traits must be combined into an overall index for economic merit. This means that each trait should have assigned a weight according to its importance relative to the overall economic merit. Determination of such weights requires extensive economic analysis and long term projection of the dairy and beef production enterprises and also requires knowledge of biological parameters of the underlying genetics of the traits of interest. Such biological knowledge, especially relationships among traits of different groups, is not available. Therefore, the first step in a study of economic merit should be to obtain such biological information, while deferring economic considerations.

Knowledge of genetic parameters are also necessary in predicting the results of various breeding programs. Selection decisions made today have their main impact several years in the future. It is

therefore important to be able to predict genetic changes accurately and study alternatives before implementation. Since exact knowledge of genetic parameters is not possible in reality, they must be estimated. Most of the data available for such estimation are field data. There are several problems in the estimation of genetic parameters from field data that need to be addressed.

The improvement of beef traits in dual purpose populations relies mainly on tests of future artificial insemination bulls based on their own performance. Bulls selected after the performance test would then be tested for breeding value for milk production based on a progeny test. Those bulls would have daughters producing in commercial herds. These daughters would be measured for all other traits of interest. Selection occurs both after the performance test for beef production and after progeny test for dairy production. The very best bulls are selected as sires of the next batch of bulls to be performance tested. The use of field data from populations undergone such a selection scheme can potentially cause bias in estimates of genetic parameters. The current method of choice for the estimation of genetic parameters is restricted maximum likelihood (REML) due to the desirable statistical properties of this method. In order to account for biases due to selection, all data that led to the current population should ideally be included in the analysis. Use of all data on several traits in REML estimation often leads to models that require amounts of computation that cannot be done with current computers. It is therefore necessary to develop strategies for sampling of data for use in analyses. This sampling should be done in such a way that resulting

models are computationally manageable and biases in estimates is minimized.

This thesis is organized in eight chapters covering three main topics. The first topic is computation algorithms and data sampling in alleviating computation difficulties in the estimation of genetic parameters. The second topic relates to beef production and its biological efficiency and the genetic relationships between these traits measured on the growing young bulls and the dairy production of female relatives. The third topic deals with estimation of crossbreeding effects and genetic parameters on dairy production and calving performance in a population importing genetic material.

Chapter 1 reviews transformation algorithms in the estimation of genetic parameters in a class of single and multiple trait models. Chapter 2 describes a stochastic model which simulates breeding events in dual purpose and dairy populations. The model was used in Chapter 3 for the purpose of generating data used to compare different strategies of data sampling for the estimation of genetic parameters in populations undergoing selection.

Chapter 4, 5, and 6 reports on an experiment designed to study 1) the possibility of including selection for energy efficiency in the performance testing of young bulls, 2) alternative expressions for energy efficiency of growing young bulls, and 3) the relationships of beef characteristics in growing young bulls with the dairy production of female halfsibs.

In Chapter 7, between breed additive genetic and heterotic effects on dairy production and calving traits is reported. Chapter 8 presents

genetic parameters of dairy production and calving traits.

CHAPTER 1

Transformation Algorithms in Analysis of Single Trait and of Multitrait Models With Equal Design Matrices and One Random Factor per Trait: A Review

Introduction

Estimation of (co)variance components by use of restricted maximum likelihood (REML) methods as proposed by Patterson and Thompson (1971) has become increasingly popular due to its desirable statistical properties. However, it often requires heavy computing due to its iterative nature and the need for inverting one or more large matrices in each iteration round. Several algorithms for obtaining REML estimates of (co)variance components exist, but the expectation maximization (EM) algorithm (Dempster et al. 1977) has been most frequently used due to the relative ease of programming required, and expressions that are intuitively easy to understand. Unfortunately, the EM algorithm in general converges slowly. Several suggestions have been made to speed up convergence such as the common intercept approach (Schaeffer, 1979) or nonlinear adjustment (Misztal and Schaeffer, 1986). However, application of these techniques in multitrait models is unclear, because more parameters usually must be estimated than in single trait models. Also, the convergence rate generally decreases as the number of parameters to be estimated increases.

Other algorithms for REML estimation of (co)variance components such as Fisher scoring (Patterson and Thompson, 1971), Newton Raphson (Jennrich and Sampson, 1976) or a procedure developed in principle by Anderson (1973) and used by Meyer (1985) generally converge in fewer rounds, but each round requires more computation and more complex programming than the EM algorithm. In order to avoid inverting large matrices, an algorithm for single trait models developed by Smith

(1986) and Graser et al. (1987) maximizes the likelihood function directly using a grid search. For multitrait models, maximization of the likelihood function directly becomes more complicated. Yet another approach has been the use of transformations applied to different elements in the EM algorithm. For a large class of models these transformations offer an alternative that drastically reduce the computational requirements of the EM algorithm.

The purpose of this paper is to review recent developments in the use of transformation algorithms in single and multiple trait models with equal design matrices. The model is assumed to contain only one random factor per trait. The models studied represent a limited subset of all possible multitrait models, but a large proportion of the models usually used in single trait analysis. The single trait analysis will be presented as a special case of the multitrait analysis.

Models

Let Y be a $n \times t$ matrix of observations on n individuals each with records on t traits. Now, let the model for the i^{th} trait, i.e., the i^{th} column in Y , be

$$y_i = Xb_i + Zu_i + e_i$$

where b_i is a $f \times 1$ vector of fixed effects, u_i is a $q \times 1$ vector of random effects, X and Z are known matrices relating observations in y_i to classes in b_i and u_i ; and e_i is a $n \times 1$ vector of random residuals. The model for all t traits simultaneously would then be:

$$y = (I_t * X)b + (I_t * Z)u + e$$

where $y = \text{vec } Y$, "*" denotes the direct product operation (Searle, 1982),

$$\mathbf{b}' = [b'_1, b'_2, \dots, b'_t],$$

$$\mathbf{u}' = [u'_1, u'_2, \dots, u'_t], \text{ and}$$

$$\mathbf{e}' = [e'_1, e'_2, \dots, e'_t].$$

The expectations, $E()$, and (co)variances matrices, $V()$, are

$$E(\mathbf{y}) = (\mathbf{I}_t * \mathbf{X})\mathbf{b}, E(\mathbf{u}) = 0, E(\mathbf{e}) = 0,$$

$$V(\mathbf{y}) = \mathbf{G} * \mathbf{Z} \mathbf{A} \mathbf{Z}' + \mathbf{R} * \mathbf{I}_n; V(\mathbf{u}) = \mathbf{G} * \mathbf{A}; \text{ and } V(\mathbf{e}) = \mathbf{R} * \mathbf{I}_n$$

where $\mathbf{G}$ and $\mathbf{R}$ are (co)variances matrices of the t traits for the random factor and the residual, respectively, and $\mathbf{A}$ is the numerator relationship matrix for elements in $\mathbf{u}_1$. Under these assumptions the mixed model equations that would yield the best linear unbiased estimator (BLUE) of the fixed effects and the best linear unbiased predictor (BLUP) of the random effects can be written as (Henderson, 1973):

$$\begin{bmatrix} \mathbf{R}^{-1} * \mathbf{X}'\mathbf{X} & \mathbf{R}^{-1} * \mathbf{X}'\mathbf{Z} \\ \mathbf{R}^{-1} * \mathbf{Z}'\mathbf{X} & \mathbf{R}^{-1} * \mathbf{Z}'\mathbf{Z} + \mathbf{G}^{-1} * \mathbf{A}^{-1} \end{bmatrix} \begin{bmatrix} \hat{\mathbf{b}} \\ \hat{\mathbf{u}} \end{bmatrix} = \begin{bmatrix} (\mathbf{R}^{-1} * \mathbf{X}')\mathbf{y} \\ (\mathbf{R}^{-1} * \mathbf{Z}')\mathbf{y} \end{bmatrix} \quad [1]$$

As in practice, (co)variances are unknown, $\mathbf{G}$ and $\mathbf{R}$ in [1] contain a priori estimates.

Let $\mathbf{C}$, a generalized inverse of the coefficient matrix in [1], be partitioned by denoting the ij^{th} submatrix of $\mathbf{C}$ corresponding to the i^{th} and j^{th} subvectors of $\mathbf{u}$ as $\mathbf{C}_{ij}$.

Utilizing expressions by Dempster et al. (1977), the EM algorithm to estimate the ij^{th} element in $\mathbf{G}$ and $\mathbf{R}$ are:

$$\hat{g}_{ij(k+1)} = [\hat{\mathbf{u}}'_{i(k)} \mathbf{A}^{-1} \hat{\mathbf{u}}_{j(k)} + \text{tr}(\mathbf{A}^{-1} \mathbf{C}_{ij(k)})]/q \quad [2]$$

$$\hat{r}_{ij(k+1)} = [\hat{\mathbf{e}}'_{i(k)} \hat{\mathbf{e}}_{j(k)} + \text{tr}(\mathbf{B}_{ij(k)})]/n \quad [3]$$

for the k^{th} round of iteration, where B_{ij} is the submatrix of WCW' corresponding to the ij^{th} pair of traits, where $W = [X; Z]$. These expressions are due to Henderson (1984), and correspond to the REML estimators given by Patterson and Thompson (1971) and Harville (1977) but extended to multiple traits.

In estimation of (co)variance components or in prediction of the random elements in u , we are not interested in solutions for the fixed effects. Therefore, the equations in [1] corresponding to fixed effects can be absorbed to give

$$[R^{-1}Z'MZ + G^{-1}A^{-1}]u = (R^{-1}Z'M)y \quad [4]$$

where $M = I - X(X'X)^{-1}X'$ is a projection matrix. In cases where X describes more than one classification factor or includes covariates, it can typically be partitioned as $X = [X_1 : X_2]$ such that $X_1'X_1$ is diagonal and thus can be absorbed easily. Equations corresponding to X_2 must then be absorbed either as a block or generally easier by using Gaussian elimination or sweeping operations (Dempster, 1969, Goodnight, 1978). A detailed [4] denoting parts by t traits is

$$\begin{bmatrix} r^{11}Z'MZ + g^{11}A^{-1} & r^{12}Z'MZ + g^{12}A^{-1} & \dots & r^{1t}Z'MZ + g^{1t}A^{-1} \\ r^{21}Z'MZ + g^{21}A^{-1} & r^{22}Z'MZ + g^{22}A^{-1} & \dots & r^{2t}Z'MZ + g^{2t}A^{-1} \\ \vdots & \vdots & \ddots & \vdots \\ r^{t1}Z'MZ + g^{t1}A^{-1} & r^{t2}Z'MZ + g^{t2}A^{-1} & \dots & r^{tt}Z'MZ + g^{tt}A^{-1} \end{bmatrix} \begin{bmatrix} \hat{u}_1 \\ \hat{u}_2 \\ \vdots \\ \hat{u}_t \end{bmatrix}$$

$$= \begin{bmatrix} r^{11}Z'My_1 + r^{12}Z'My_2 + \dots + r^{1t}Z'My_t \\ r^{21}Z'My_1 + r^{22}Z'My_2 + \dots + r^{2t}Z'My_t \\ \vdots \\ r^{t1}Z'My_1 + r^{t2}Z'My_2 + \dots + r^{tt}Z'My_t \end{bmatrix} \quad [5]$$

where r^{ij} and g^{ij} are the ij^{th} elements of R^{-1} and G^{-1} , respectively.

Simplifications of the EM-REML estimators in [2] and [3] are possible in many cases:

1) If the individuals in u are unrelated, then $A = I$, and [2] becomes

$$\hat{g}_{ij(k+1)} = [\hat{u}'_{i(k)}\hat{u}_{j(k)} + \text{tr}(C_{ij(k)})]/q;$$

2) If there is only one trait in the analysis (single trait analysis)

the (co)variance matrices G and R are scalars. The computations

necessary to evaluate [3] reduce to:

$$\text{tr}(B_{11}) = r(X) + q - \alpha \text{tr}[(Z'MZ + \alpha A^{-1})^{-1}] \quad [6]$$

$$\text{and } \hat{e}'\hat{e} = y_1'y_1 - \hat{b}'Z'My - \hat{u}'Z'My - \alpha\hat{u}'\hat{u} \quad [7]$$

where $r(X)$ is the column rank of X and $\alpha = r_{11}/g_{11}$. Proof of equation [6] can be found in Schaeffer (1983), and equation [7] is due to Thompson (1969).

Transformation Algorithms

Canonical Transformation

It is clear from [5] that if covariances were zero, the multitrait analysis would split into t single trait analyses. The purpose of the canonical transformation is to obtain a set of canonical variates, between which, all covariances are zero, without loss of any information contained in the original variables.

Let data for the j^{th} individual observation be arranged in a $tx1$ vector y_j , and let $P = G + R$ be the phenotypic (co)variance matrix, $V(y_j) = P$. If a linear transformation on y_j is performed with a transformation matrix Q , i.e., $y_{cj} = Qy_j$; then:

$$\begin{aligned} V(y_{cj}) &= Q(P)Q' = Q(G + R)Q' = QGQ' + QRQ' \\ &= G_c + R_c \end{aligned} \quad [8]$$

where subscript c denotes canonical scale hereonafter.

If Q is chosen such that G_c is diagonal and $R_c = I_t$, the variables in y_{cj} are called canonical variates which have unit residual variances and are uncorrelated. Such a transformation was first suggested for animal breeding problems by Thompson (1976) and has been applied to practical animal breeding data in several publications (Arnason, 1982, Arnason, 1984, Taylor et al., 1985, Schaeffer, 1986 and Meyer et al., 1987).

The diagonal elements of G_c are the eigenvalues of RG^{-1} and Q is the matrix of corresponding eigenvectors. The matrix RG^{-1} is generally not symmetric, which complicates the calculation of eigenvalues and eigenvectors. Schaeffer (1986) gave an alternative method of computing Q which only involves obtaining eigenvalues and eigenvectors of symmetric matrices.

After transformation to the canonical scale, the mixed model equations in [5] contain t diagonal blocks corresponding to the t canonical variates. The equations for the i^{th} block are:

$$[Z'MZ + \lambda_i^{-1}A^{-1}]\hat{u}_{ci} = Z'My_{ci} \quad [9]$$

where λ_i is the i^{th} diagonal element of G_c . Expressions for estimating the variances now reduce to the single trait form. Formulas for estimating the covariances reduce to crossproducts of the solution vectors and the residuals. At convergence such crossproducts are expected to be zero. Let

$$G_c = (Z'MZ + \lambda_i^{-1}A^{-1})^{-1}.$$

Then, for the (k+1)th round of iteration, estimators of the elements in G_c are:

$$\hat{g}_{cii}(k+1) = [\hat{u}'_{ci} \mathbf{A}^{-1} \hat{u}_{ci} + \text{tr}(\mathbf{A}^{-1} \mathbf{C}_c)]/q \quad [10]$$

$$\hat{g}_{cij}(k+1) = [\hat{u}'_{ci} \mathbf{A}^{-1} \hat{u}_{cj}]/q, \text{ for } i \neq j \quad [11]$$

and those in $\mathbf{R}$ are:

$$\hat{r}_{cii}(k+1) = [\hat{e}'_{ci} \hat{e}_{ci} + r(X) + q - \lambda_i^{-1} \text{tr}(\mathbf{A}^{-1} \mathbf{C}_c)]/n \quad [12]$$

$$\hat{r}_{cij}(k+1) = [\hat{e}'_{ci} \hat{e}_{cj}]/n, \text{ for } i \neq j \quad [13]$$

where $\hat{e}'_{ci} \hat{e}_{cj} = \mathbf{y}'_{ci} \mathbf{M} \mathbf{y}_{cj} - \hat{u}'_{ci} \mathbf{Z}' \mathbf{M} \mathbf{y}_{cj} - \lambda_i \hat{u}'_{ci} \hat{u}_{cj}$, for all i and j .

The estimation of the covariances is much simplified, because the traces in [2] or [3] for that case reduce to zero due to the block diagonal structure of the multitrait mixed model equations on the canonical scale.

The (co)variance estimates on the canonical scale are in $\hat{\mathbf{G}}_c$ and $\hat{\mathbf{R}}_c$, which must be transformed back to the original scale by:

$$\hat{\mathbf{G}}_{(k+1)} = \mathbf{Q}^{-1} \hat{\mathbf{G}}_c \mathbf{Q}^{-T} \quad [14]$$

$$\text{and } \hat{\mathbf{R}}_{(k+1)} = \mathbf{Q}^{-1} \hat{\mathbf{R}}_c \mathbf{Q}^{-T} \quad [15]$$

where $\mathbf{Q}^{-1}$ is the transpose of $\mathbf{Q}^{-1}$. In practice $\hat{\mathbf{G}}$ and $\hat{\mathbf{R}}$ may be very close to positive semi-definite of the conclusion of an iteration. However, they can be very close to, but never be positive semi-definite.

The new estimates of $\mathbf{G}$ and $\mathbf{R}$ are then used to obtain a new $\mathbf{Q}$ transformation matrix and a new $\mathbf{G}_c$, the diagonal matrix of corresponding eigenvalues, so the process from [9] through [15] can be iterated until a convergence criterion is met.

This procedure yields the same results as the straightforward multitrait estimators in [3] and [4], and a proof of such equivalence was given in principle by Meyer (1985).

Other algorithms that incorporate the canonical transformation in

REML procedures for estimating the (co)variance matrices G and R have been presented by Meyer (1985) and Schaeffer (1985). The algorithm by the latter author estimated only the genetic and residual variances on the canonical scale. The variance estimates at convergence were then backtransformed to obtain both variances and covariances on the original scale by use of the inverse of the initial Q transformation matrix. Such a procedure would generally yield estimates that are dependent on the initial values chosen for G and R , Buttazzoni and Mao, (1987, unpublished results). Meyer (1985) showed another algorithm which estimate the off-diagonal elements of G_c and R_c and utilize a new Q in each round of the iteration process. She also used an alternative algorithm given in principle by Andersen (1973), mainly to speed up convergence. However, it requires the inversion and storing of $t \times t$ matrices in each iteration so the procedure tends to be computationally demanding.

"Cholesky" Transformation

After canonical transformation, a multitrait analysis of t traits can be accomplished by t separate single trait analyses.

The model for the i^{th} canonical variate could be written as:

$$y_{ci} = Xb_{ci} + Zu_{ci} + e_{ci} \quad [16]$$

The (co)variance matrices of the random vectors are

$$V(u_{ci}) = \lambda_i A \text{ and } V(e_{ci}) = I_n.$$

Further we have $Cov(e_{ci}, e_{cj}) = 0$ and $Cov(u_{ci}, u_{cj}) = 0$, i.e., residual variances are unity and all covariances between traits are zero. The goal of the "Cholesky" transformation is to diagonalize

$V(u_{ci})$. To do so, the relationship matrix is decomposed such that $A = LL'$, where L is a lower triangular positive definite matrix and $LL^{-1} = I$. The model [16] is rewritten as:

$$\begin{aligned} y_{ci} &= Xb_{ci} + ZLL^{-1}u_{ci} + e_{ci} \\ &= Xb_{ci} + Z^*u_{cli} + e_{ci} \end{aligned} \quad [17]$$

where $Z^* = ZL$, and $u_{cli} = L^{-1}u_{ci}$, and subscript l denotes "Cholesky" scale.

The variance of u_{cli} is

$$\begin{aligned} V(u_{cli}) &= V(L^{-1}u_{ci}) = L^{-1}(\lambda_i A)L^{-T} \\ &= \lambda_i I_q. \end{aligned} \quad [18]$$

The mixed model equations for the i^{th} canonical variate after absorption of fixed effects are now:

$$[Z^*MZ^* + \lambda_i^{-1}I]\hat{u}_{cli} = Z^*My_{ci} \quad [19]$$

The quadratic and bilinear forms used in the estimation of (co)variance components [10] through [15] are in principle not altered by the "Cholesky" transformation but computations in each round become easier. This is illustrated by the following:

$$\hat{u}'_{cli}\hat{u}_{cli} = \hat{u}'_{ci}L^{-T}L^{-1}\hat{u}_{cj} = \hat{u}'_{ci}A^{-1}\hat{u}_{cj} \quad [20]$$

$$\hat{u}'_{cli}Z^*My_{cj} = \hat{u}'L^{-T}L^{-1}Z^*My_{cj} = \hat{u}'_{ci}Z^*My_{cj} \quad [21]$$

$$\begin{aligned} \text{tr}(A^{-1}C_c) &= \text{tr}[A^{-1}(Z'MZ + \lambda_i^{-1}A^{-1})^{-1}] \\ &= \text{tr}[L^{-T}L^{-1}(Z'MZ + \lambda_i^{-1}A^{-1})^{-1}] \\ &= \text{tr}[L^{-1}(Z'MZ + \lambda_i^{-1}A^{-1})^{-1}L^{-T}] \\ &= \text{tr}[(L'Z'MZL + \lambda_i^{-1}L'A^{-1}L)^{-1}] \\ &= \text{tr}[(Z^*MZ^* + \lambda_i^{-1}I)^{-1}]. \end{aligned} \quad [22]$$

The computational advantage of the "Cholesky" transformation is, therefore, that A^{-1} drops out of the expressions used in estimating the

elements of G and R (Meyer, 1987). This can also be seen in [20], [21], and [22]. Thus, the inverse of A no longer needs to be computed and stored. The matrix L can easily be computed from a list of pedigree information following rules given by Henderson (1976) and Quaas (1976). As shown by Meyer (1987), L can be processed one column at a time, overwriting the original arrays. The use of the "Cholesky" transformation of the solution vectors in [17] was first suggested for animal breeding problems by Smith (1986) and by Smith and Graser (1986).

Householder transformation

In order to evaluate the traces in [22], a matrix of order qxq would still need to be inverted for each trait in each round of the iteration process. To ease the computational burden in obtaining these inverses, Dempster et al. (1984) suggested the unique spectral factorization of the coefficient matrix. Let the coefficient matrix in [19] be $[H + \lambda_1^{-1}I]$ then the unique spectral factorization of H is

$$H = PDP' \quad [23]$$

where D is a diagonal matrix with the eigenvalues of H as diagonal elements and P is the matrix of corresponding normalized mutually orthogonal eigenvectors of H , i.e., $P' = P^{-1}$. Hence, $P'HP = D$ is an orthogonal similarity transformation of H into D .

By applying this transformation to the coefficient matrix in [19] we get:

$$P'[H + \lambda_1^{-1}I]P = [D + \lambda_1^{-1}I] \quad [24]$$

The coefficient matrix is now diagonal. However, finding the eigenvalues and eigenvectors of a large matrix can be computationally

very demanding, and as shown by Smith and Graser (1986) not necessary. A series of $q-2$ Householder transformations (Householder, 1958) is a less demanding alternative, and is usually an initial step in finding eigenvalues and eigenvectors. A description of the Householder transformation can be found in most textbooks on linear algebra. Programs for performing the transformation are available on all reasonably equipped computer installations. Computing algorithms can be found in textbooks on numerical analysis such as Kennedy and Gentle (1980) or Stoer and Bulisch (1980). Other advantages of the Householder transformation are that it is numerically stable and can be employed on matrices too large to store in computer memory (Hansen and Lawson, 1969).

Let P be the product of $q-2$ Householder transformation matrices. Then $P'P = PP' = I$, i.e., P is orthogonal. The idea of the Householder transformation is to choose a matrix, P , such that by premultiplying by P' on both sides of the equation in [19]:

$$P'[Z^*MZ^* + \lambda_i^{-1}I]PP'\hat{u}_{cli} = P'Z^*My_{ci}$$

$$\text{or} \quad [T + \lambda_i^{-1}I]\hat{u}_{clhi} = P'Z^*My_{ci} \quad [25]$$

the resulting $T = P'Z^*MZ^*P$ is symmetric and tridiagonal and $\hat{u}_{clhi} = P'\hat{u}_{cli}$, where subscript h denotes Householder scale. The estimates of G_c and R_c can now be computed using [10] through [15] but with $\hat{u}_{ci}$ being replaced by $\hat{u}_{clhi}$, $Z'My_{ci}$ by $P'Z^*My_{ci}$, and $\text{tr}(A^{-1}C)$ by $\text{tr}[(T + \lambda_i^{-1}I)^{-1}]$.

Once T is found, the equation system in [25] can be solved in linear time by Gaussian elimination. The expression $\text{tr}[(T + \lambda_i^{-1}I)^{-1}]$ can be computed in linear time by the following recursion formulas, as

shown by Smith and Graser (1985) who attributes the derivation to R.L. Quaas:

$$\text{tr}[(T + \lambda_i^{-1}I)^{-1}] = \sum w_i$$

where $w_1 = t_{11}$, $d = t_{11}$, and $u = t_{21}/d$, for $i = 1$, [26]

and for $i > 1$, $d = t_{ii} - t_{i(i-1)} u$,

$$w_i = (1 + t_{i(i-1)} u w_{(i-1)})/d,$$

and $u = t_{i1}/d$. [27]

where t_{ij} is the ij^{th} element of $(T + \lambda_i^{-1}I)$. Smith and Graser (1985) also showed that the evaluation of $\text{tr}[(T + \lambda_i^{-1}I)^{-1}]$ can be incorporated easily into an algorithm for solving [25] by Gaussian elimination so that solutions and traces can be obtained in linear time.

The tridiagonal matrix T needs to be found only once no matter how many traits are included in the analysis or how many iterations are needed to obtain convergence of the (co)variance estimates.

The proof that the quadratic and bilinear forms and the traces calculated on this new scale are the same as if they were calculated on the canonical scale directly follows the same logical steps as the proof that the "Cholesky" transformation did not alter these quantities. Smith and Graser (1985) also proved this for the Householder transformation directly.

Application of transformation in single trait analysis

The mixed model equations for a single trait analysis corresponding to [19] are

$$[Z^* M Z^* + \alpha I] \hat{u} = Z^* M y \quad [28]$$

where $\alpha = \sigma_e^2 / \sigma_u^2$. If we let $C = (Z^* M Z^* + \alpha I)^{-1}$, then the EM-REML

estimates of the variances are:

$$\sigma_{u(k+1)}^2 = [\hat{u}'\hat{u} + \sigma_{e(k)}^2 \text{tr}(C)]/q \quad [29]$$

$$\sigma_{e(k+1)}^2 = [\hat{e}'\hat{e} + \sigma_{e(k)}^2 (r(X) + q - \alpha \text{tr}(C))]/n \quad [30]$$

$$\text{where } \hat{e}'\hat{e} = y'My - \hat{u}'Z^*My - \alpha\hat{u}'\hat{u} \quad [31]$$

The only difference in [29] and [30] from [2] and [3] is the appearance of $\sigma_{e(k)}^2$, since this was factored out of the single trait mixed model equations in [28]. If $A = I$, Z^* reduces to Z . Instead of iterating from [28] through [31], a better alternative would be to apply the Householder transformation on [28] so that solutions and traces can be obtained in linear time.

Backtransformation

At convergence the estimates of G_c and R_c are transformed back to the original scale using [14] and [15]. The solutions to the tridiagonal systems in [28] can be backtransformed to the original scale using a two-step procedure:

1. To undo the Householder and the "Cholesky" transformation, multitrait solutions from [25], or single trait solutions from [28], are premultiplied by the inverse of the transformation matrices, L^{-1} from [17] and P' from [25]:

$$\tilde{u}_{ci} = LP \tilde{u}_{clhi} \quad [32]$$

where a "~" superscript denotes a solution obtained at convergence.

The corresponding prediction error variances estimated as if parameter (co)variances were known are computed as (Jensen and Mao, 1987):

$$V(u_{ci} - \tilde{u}_{ci}) = LP[T + \lambda_1^{-1}I]^{-1}P'L' = C_{ii} \quad [33]$$

The inverse of $[T + \lambda_1^{-1}I]$ can be obtained with minimal computational effort (Smith and Graser, 1986). The diagonal elements in C_{ii} and $\tilde{u}_{ci}$

will be used in the next step.

2. Solutions on the canonical scale are backtransformed to the original scale: Let the solutions for the j th individual be arranged in a txl vector $\bar{u}_{cj}$ and the corresponding estimated prediction error variances in a txt diagonal matrix C_j .

$$\text{Then } \bar{u}_j = Q_{(k)}^{-1} \bar{u}_{jc} \quad [34]$$

$$\text{and } V(u_j - \bar{u}_j) = Q_{(k)}^{-1} C_j Q_{(k)}^{-T} \quad [35]$$

The solutions contained in $\bar{u}_j$ at convergence are not BLUP, but in the case where the (co)variance matrices are unknown, they are the best approximations when uncertainty about fixed effects and the unknown variances are taken into account (Gianola et al., 1986).

Numerical Example

This numerical example demonstrates the equivalence of the straight-forward multitrait approach and the multitrait approach that uses the three transformations.

Consider the data in Table 1, which is a modified subset of data used by Meyer (1986). The same starting parameters were also used here:

$$G = \begin{bmatrix} 12 & 9 \\ 9 & 10 \end{bmatrix} \quad \text{and} \quad R = \begin{bmatrix} 160 & 75 \\ 75 & 140 \end{bmatrix}$$

The three sires were assumed to be related according to the following relationship matrix:

$$\mathbf{A} = \begin{bmatrix} 1.00 & 0.25 & 0.25 \\ 0.25 & 1.00 & 0.50 \\ 0.25 & 0.50 & 1.00 \end{bmatrix}$$

Table 1.
Data used in numerical example^a.

Trait	Sire 1		Sire 2		Sire 3	
	1	2	1	2	1	2
Herd 1	106	31	115	40	127	51*
					120	49*
					129	60*
					145	59*
Herd 2	105	21	109	30		
	120	50	121	48		
	98	32	132	55		
	111	48				
	117	29				
	101	22				
Herd 3			132	53	137	49
			117	41	139	67
			129	49	131	44
			125	55		
			119	37		

^aData consist of paired subset of data used by Meyer (1986) with two modifications. Observations marked * were moved from herd 3 and all records for trait 2 were reduced by 100.

The solutions to the usual multiple trait mixed model equations from [1] are:

$$\hat{\mathbf{b}}' = [122.337, 113.961, 127.393, 47.163, 38.3732, 48.2362],$$

$$\text{and } \hat{\mathbf{u}}' = [-2.20238, 0.52125, 2.41526, -2.00205, 0.551105, 2.1183].$$

First round estimates of $\mathbf{G}$ and $\mathbf{R}$ using [2] and [3] are, respectively,

$$\hat{\mathbf{G}}_{(1)} = \begin{bmatrix} 15.0460 & 11.7839 \\ 11.7839 & 12.3598 \end{bmatrix} \text{ and } \hat{\mathbf{R}}_{(1)} = \begin{bmatrix} 106.4670 & 81.6079 \\ 81.6079 & 120.7820 \end{bmatrix}$$

These values would then be used in [1] and the process iterated until convergence.

The matrix Q computed from the initial values of G and R and used to transform the data into the canonical scale for the first round of the iteration process was:

$$Q = \begin{bmatrix} 0.048206 & 0.0459666 \\ -0.0776011 & 0.0861689 \end{bmatrix}$$

with $G_c = \begin{bmatrix} 0.0889006 & 0 \\ 0 & 0.0261515 \end{bmatrix}$

The Cholesky decomposition of the relationship matrix is:

$$L = \begin{bmatrix} 1.0 & 0 & 0 \\ 0.25 & 0.968246 & 0 \\ 0.25 & 0.451848 & 0.856349 \end{bmatrix}$$

The matrix Z^*MZ^* is:

$$Z^*MZ^* = \begin{bmatrix} 1.59375 & -1.79932 & -0.428174 \\ -1.79932 & 2.84514 & -0.866008 \\ -0.428174 & -0.866008 & 2.35278 \end{bmatrix}$$

In this case, only the elements (3, 1) and (1, 3) with the value -0.428174 need to be annihilated by the Householder transformation in order to tridiagonalize the above matrix. The corresponding P matrix is

$$P = \begin{bmatrix} 1 & 0 & 0 \\ 0 & -0.972835 & -0.231500 \\ 0 & -0.23150 & 0.972835 \end{bmatrix}$$

In practice the matrix P would not be computed. Instead, vector valued functions of $q-2$ individual transformation matrices should be computed and stored. These vectors can be stored as q columns in a triangular qxq matrix.

After applying the Householder transformation we obtain:

$$T = \begin{bmatrix} 1.59375 & 1.84957 & 0 \\ 1.84957 & 2.42868 & 0.88407 \\ 0 & 0.88407 & 2.76923 \end{bmatrix}$$

The mixed model equations for the first canonical variate shown in [25] are:

$$\begin{bmatrix} 12.8423 & 1.84957 & 0 \\ 1.84957 & 13.6772 & 0.88407 \\ 0 & 0.88407 & 14.0177 \end{bmatrix} \begin{bmatrix} \hat{s}_{c11} \\ \hat{s}_{c12} \\ \hat{s}_{c13} \end{bmatrix} = \begin{bmatrix} -2.83947 \\ -2.34557 \\ 2.97471 \end{bmatrix}$$

which have solutions

$$\hat{s}'_{c1} = [-0.198195 \quad -0.159058 \quad 0.222242].$$

The solutions for the second variate is:

$$\hat{s}'_{c2} = [-0.0016072 \quad -0.00532212 \quad -0.0108284]$$

The corresponding traces of the inverse coefficient matrices for the first and second variates are 0.225935 and 0.0742087, respectively. So the first round estimates of G_c and R_c become, respectively,

$$\hat{G}_{c(1)} = \begin{bmatrix} 0.113302 & -0.00041382 \\ -0.00041382 & 0.0247856 \end{bmatrix}, \text{ and } \hat{R}_{c(1)} = \begin{bmatrix} 0.864277 & 0.126558 \\ 0.126558 & 0.446563 \end{bmatrix}.$$

Backtransformation to the original scale using [14] and [15] yields exactly the same results as the straightforward multiple trait procedure.

Numerical Strategies

Numerous numerical strategies can be employed in order to make procedures as efficient as possible in terms of numerical stability and amount of computation involved. Most of these strategies can be found elsewhere in the literature. A couple of "tricks" probably not found in the literature in relation to the canonical transformation are discussed below.

In the iteration process, transformations must be performed in each round. To ease these computations, compute first $Y'MY$, the matrix of sum of squares and crossproducts, and $P'Z^*MY$ a $q \times t$ matrix of "single trait" left hand sides. These matrices can then be transformed to the canonical scale using:

$$P'Z^*MY_c = P'Z^*MYQ' \quad [36]$$

$$\text{and } Y_c'MY_c = QY'MYQ'. \quad [37]$$

Let $Q_{(k+1)}$ be the canonical transformation matrix for the next round in the iteration process, a "round to round" transformation matrix can then be computed as $Q_r = Q_{(k+1)} Q^{-1}$, which can be used after the initial round in [36] and [37] in place of Q in order to minimize the numerical effort involved.

An algorithm applying the "Cholesky" transformation directly from

a list of pedigree information was given by Meyer (1987). Stoer and Bulirsch (1980) outline an algorithm for the Householder transformation that avoids actually setting up the transformation matrix. Instead, $q-2$ vector valued functions of P are computed. These vectors can be stored in the same space as the original matrix to be reduced, thus saving both computer time and memory.

Convergence Criteria

The purpose of this section is to illustrate the effect of choice of convergence criteria on the estimates obtained. The algorithm employing the transformations requires limited computational effort in each round of the iteration process which allows for a conservative convergence criteria without excessive computing costs. The estimates of G and R are generally updated in an approximate geometric progression (Misztal and Schaeffer, 1986). This means that the changes in the estimates of G and R become smaller and smaller in later rounds of iteration. Small changes per round, however, can accumulate to a considerable amount over many rounds of iteration.

A simulation study was conducted to illustrate the effect of choosing a conservative stopping criteria instead of a fixed number of iterations. A total of 600 observations on two traits using true population parameters as the starting values was simulated. The 600 individuals simulated were descendants from 30 unrelated sires and were distributed in 100 herds. The number of herds per sire group was on average 7.97. The parameters generally slowest to converge are the genetic covariances or equivalently the genetic correlations, so this

parameter was used to illustrate convergence rates. The true population genetic correlation was 0.82. Estimates from round 30 and at convergence along with the number of rounds necessary to reach convergence are shown for 10 replicates in Table 2.

The norm of the matrix of differences of the parameter estimates was used as a convergence criterion, i.e.,

$$\|\hat{G}_{(k+1)} - \hat{G}_{(k)}\|$$

and

$$\|\hat{R}_{(k+1)} - \hat{R}_{(k)}\|.$$

Both norms were required to be less than 10^{-6} . As can be seen from Table 2, dramatic changes in parameter estimates can occur even after round 30. Also that the number of rounds needed to reach convergence vary wildly from sample to sample.

Table 2.

Estimates of genetic correlation from round 30 and at convergence in a small simulated population^a.

Replicate	Genetic Correlation		No. of rounds ^b for convergence
	Round 30	Convergence	
1	0.43	0.42	400
2	0.84	0.95	2200
3	0.21	-0.02	4400
4	0.67	0.67	100
5	0.89	0.91	400
6	0.70	0.79	500
7	0.96	1.00	4800
8	0.52	0.60	500
9	0.51	0.51	200
10	0.78	0.83	400

^aSee text for description of population

^bConvergence only tested for each 100 rounds.

Discussion

The transformation algorithms reviewed in this paper offer a very useful alternative for EM-REML estimation of (co)variance components for a class of models frequently used in animal breeding. The class includes all single trait models with two variance components. Also included are multitrait models with equal design matrices and one random factor per trait.

By employing a series of transformations, the problem of slow convergence of the EM algorithm would be largely alleviated since the computations necessary in each round of the iteration process can be performed in linear time. However, there are some initial computing efforts necessary. If the relationship matrix is included, a Cholesky decomposition of the relationship matrix must be found. This can be done directly from a list of pedigree information. Further, if the Householder transformation is used, it would require about the same amount of numerical work as computing an inverse of the same matrix but this has to be done only once, no matter how many rounds of iteration the problem requires. If (co)variance components are to be estimated from an animal model, which tends to have a coefficient matrix that is large and sparse, the Householder transformation is not well suited for sparse matrix methods. In this case, tridiagonalization may be obtained by other transformations such as the Givens rotations which is better suited for sparse methods. A comparison of these transformation techniques applied to sparse matrices in animal breeding problems is needed.

When the computations necessary in each round of the iteration

process can be evaluated in linear time, the use of conservative convergence criteria is possible. As demonstrated by the simulation example, the number of iterations needed to reach a certain degree of convergence can vary a great deal from sample to sample, and that considerable change in parameter estimates can accumulate in later rounds. These factors stress the need for a conservative convergence criteria. More research work needs to be done to determine optimum convergence criteria.

CHAPTER 2

A Stochastic Model of Breeding Schemes in Cattle Populations

Introduction

Traditional methods of optimizing breeding schemes have generally involved the maximization of discounted economic returns in deterministic models. Such models predict expected genetic gain by the use of gene flow theory (Hill, 1974) or by the use of asymptotic theory (Rendel and Robertson, 1950).

The expected genetic gain from a genetic improvement program is influenced by many factors. Some of these factors relates to the population itself such as average genetic production potential and amounts of phenotypic and genetic variation present in the population. Other factors are more external to the population and includes factors such as climate, economic environment, skills of producers, availability of infrastructure to provide test results, etc. All these factors can be accounted for in both deterministic and stochastic models.

However, some important factors are more difficult to take into account in deterministic models. These factors include the variance of the expected genetic gain due to random genetic drift (Falconer, 1981), the buildup of inbreeding and the reduction of genetic variance due to both inbreeding and linkage disequilibrium or Bulmer effect (Bulmer, 1971).

Many researchers today are facing the task of analyzing data originating from populations undergoing intense selection. Statistical models for such analyses need to take the selection incurred into account. To test and validate such models, data from simulated populations are a very useful tool.

This chapter reports on the construction of a stochastic model of breeding events in dual purpose and dairy cattle populations.

Overview of Model

Cattle are primarily used for production of milk and beef. The model constructed can be used to simulate either populations reared solely for the production of milk (Single purpose populations) or populations used for the simultaneous production of milk and beef (Dual purpose populations). Genetic improvement of dual purpose cattle poses problems beyond what is faced in single purpose populations, since more traits must be taken into consideration.

Genetic improvement in cattle populations have four pathways: cows to bulls, bulls to bulls, cows to cows and bulls to cows. The importance of these pathways differ, due to generation interval, selection intensity and accuracy of prediction of the genetic merit of animals.

Young bulls, that are sampled for possible use in artificial insemination (AI), are born out of contract matings. A contract mating is usually an agreement between an AI organization and the owner of a cow with outstanding credentials. Such cows are usually found in commercial herds. Upon agreement, the cow is mated to a bull proven to be superior and the resulting young bull is transferred to a central testing facility at about six weeks of age in order to be tested for beef production traits. This test is based on his own performance. The performance test is concluded when the bull is around one year of age so his breeding value for beef production can be predicted. Young

bulls who meet the criteria are then progeny tested for milk production and other traits that can only be measured on females. Each bull is mated to a random sample of cows from the population, and his breeding value for direct calving difficulty can be predicted when the offspring are born. Most of the female progeny will be bred shortly after one year of age and start lactating after two. At this time, bulls can be evaluated for effect on maternal calving difficulty and on female fertility. When the progeny have concluded their first lactations, the bulls can then be evaluated for milk production. Earlier evaluations on milk production may be done on records in progress. Those bulls that are promising in the preliminary evaluations are further progeny tested for management traits on a subsample of their daughters. These daughters are recorded for management traits during their first lactations. Commonly management traits are those related to the ease with which the cow can be managed in the herd or to her ability to function in the herd. In some populations some of these traits are traditionally called type traits.

After breeding values of a bull are predicted for all traits, a total merit index is computed by weighing each trait according to its partial economic importance. The best bulls is then used in the bull to cow path and the very top bulls are used in the bull to bull path, i.e. in the contract matings to produce the next generation of young bulls.

In the cow to cow path, selection is usually less accurate and less intense due to the low reproductive rate in the bovine. Another reason is the large rate of replacement of cows due to reasons not

directly related to production, such as disease or infertility. However, milk production in the first lactation receive the primary selection emphasis.

The most intense selection is in the cow to bull path since very few cows are needed to produce bulls for future use in AI. These cows are selected among those with the highest predicted breeding values. Contract matings between these cows and the very best bulls are then arranged to start the next cycle.

The model, called DPSIM, is simulated at the animal level and is aggregated such that year can be used as the unit of time. Similar breeding schemes were also studied by deterministic models using asymptotic theory by e.g. Petersen et al. (1973).

Model Description

Traits

The selection process in both single and dual purpose cattle takes many traits into consideration. These traits can be grouped into the following categories:

- (1) Growth traits measured during performance testing of males;
- (2) Calving ease and stillbirth;
- (3) Female fertility traits;
- (4) Milk production traits;
- (5) Management traits;

The traits in the categories (2) and (3) are lowly heritable, and can be strongly influenced by management in the herd. These traits were therefore not considered in the model. Each of the trait categories would normally consist of several traits, but heretofore each were

modeled as one trait. The three remaining traits were denoted as GROWTH for growth traits, YIELD for milk production traits and TYPE for management traits.

Parameters

The program starts by calling subroutine DPPARL that reads basic parameters chosen for this particular run of the model. The parameters that can be varied in the model are defined in Table 3, together with abbreviations subsequently used. Typical values for these parameters are also shown in Table 3. Typical population means, heritabilities, phenotypic standard deviations, phenotypic and genetic correlations, and partial economic weights of the three traits are shown in Table 4. Genetic parameters shown for growth traits were estimated by Jensen and Andersen (1984) and for type traits by Jensen (1985). For milk production, genetic parameters were estimated by Pedersen (1985) and Pedersen and Gjørl Christensen (1984).

The genetic parameters are converted into additive genetic and environmental (co)variance matrices called V_G and V_E , respectively. In order for V_G and V_E to be valid (co)variance matrices they must be positive definite. Therefore, the eigenvalues of V_G and V_E is computed. If any eigenvalue is negative, the corresponding (co)variance matrix is invalid and the computations cannot proceed.

Table 3.
Basic parameters for simulation model.

Name	Description	Typical value
NYEAR	No. of years to be simulated	25
NT	No. of traits to be simulated	3
NBSIRE	No. of sires in base population	25
NYBPET	Performance test capacity for beef	25
NBDPET	No. of bull dams required to produce one young bull for performance testing.	3
NBSY	No. of bull-sires per year	2
NBCY	No. of cow-sires per year	4
NHERD	No. of herds	50
NCPH	Avg. no of cows per herd	40
PYBPGTY	Pct. of young bulls tested for yield	.50
PYBPGTT	Pct. of young bulls also tested for type	.50
PCTT	Pct. of progeny recorded for type	.50
INVCR	Involuntary culling rate for cows	.20
SRDTM	Survival rate of daughters from test matings	.75
SRDCTM	Survival rate of daughters from contract matings	.85
SRDNM	Survival rate of daughters from normal matings	.75
SRYB	Survival rate of young bulls on performance test	.85

Table 4.
Typical population means, heritabilities, standard deviations, partial economic weights, phenotypic (above diagonal) and genetic (below diagonal) correlations to be used in simulation models.

<u>Trait</u>	Population	<u>Heritability</u>	<u>SD</u>	Economic	Correlations		
	<u>mean</u>			<u>weight</u>	<u>GROWTH</u>	<u>YIELD</u>	<u>TYPE</u>
GROWTH	1200	.50	75	3	---	.10	.10
YIELD	250	.25	35	50	.40	---	.10
TYPE	7	.40	1	500	.30	.20	---

Base population

The subroutine DPBASE is used to simulate the base or founder population. For males the base population consists of NBSIRE individuals born in year zero and NYBPET individuals born in year one. The bulls born in year zero is to be performance tested for GROWTH in

year zero and the bulls born in year one provide for the utilization of the performance testing facility in year one. For females, first NHERD herds with an average of NCPH lactating cows per herd are simulated. The herd sizes are sampled from a Poisson distribution with a mean equal to NCPH. The total number of females in a herd is usually about twice the number of lactating cows due to the rearing of replacement stock. Therefore, twice as many females as lactating cows are simulated in each herd according to an age distribution of 30%, 20%, 25% and 25% percent of the females is born in year -2, -1, 0 and 1, respectively. The cows born in or before year -2 would be lactating in year 0, so that information for selection decisions on females is available in year 1. The females born in year 1 makes up for the time lag between the first matings and the birth of the first batch of calves. All animals simulated in the base population are assumed to be unrelated and sampled from a large population of females.

The true breeding value of an individual in the base population is computed as:

$$\mathbf{a}_i = \mathbf{L}_G \mathbf{z}_i \quad [1]$$

where $\mathbf{a}_i$ is a 3 by 1 vector of true additive breeding values for the i^{th} animal, $\mathbf{z}_i$ is a vector of trivariate normal deviates with mean zero and (co)variance matrix $\mathbf{I}_3$; and $\mathbf{L}_G$ is a matrix satisfying $\mathbf{L}_G \mathbf{L}'_G = \mathbf{V}_G$. The phenotypic values for the i^{th} animal is then computed as:

$$\mathbf{p}_i = \mathbf{m} + \mathbf{a}_i + \mathbf{L}_E \mathbf{e}_i \quad [2]$$

where $\mathbf{p}_i$ is the 3 by 1 vector of phenotypic values, $\mathbf{m}$ is the 3 by 1 vector of population means, $\mathbf{e}_i$ is a vector of trivariate normal deviates with mean zero and (co)variance matrix $\mathbf{I}_3$, and $\mathbf{L}_E$ is a matrix

satisfying $L_E L'_E = V_E$. All random variables in the model are simulated using IMSL STAT/LIBRARY subroutines (IMSL, 1987).

All traits are simulated simultaneously for all animals although in reality a trait cannot be measured before certain events have occurred. However, the phenotypic values are never used until these events have occurred. For males, only GROWTH is possible and only at the conclusion of the performance test. For females only YIELD and TYPE are possible since these traits are sex limited with YIELD being measured at the conclusion of first lactation. TYPE is measured on a cow only if her sire is selected to be progeny tested for TYPE, and only if the cow belongs to the subgroup of cows in the progeny group that is recorded for TYPE.

Prediction of breeding values

After the base population is generated, and at the end of each year, the breeding values of all living animals are predicted using single trait selection index procedures (Hazel, 1943). The procedure used is an approximation of a true multiple trait selection index (Hazel, 1943), but was chosen due to its popularity in practice. In fact the most appropriate procedure would have been the use of multiple trait mixed linear models (Henderson, 1973). However, use of such models would drastically increase the computational requirements of the model. The mixed models, however, could easily be incorporated if certain research projects would require this.

For males an index for growth (I_G) is computed as:

$$I_G = h_G^2(p_G - m_G) \quad [3]$$

where, h_G^2 is the heritability for GROWTH, p_G is the individuals phenotype for growth and m_G is the population mean for GROWTH. The breeding values of bulls for YIELD (I_Y) and TYPE (I_T) are computed based on progeny data as:

$$I_Y = b_Y(\bar{x}_Y - m_Y) \quad [4]$$

$$I_T = b_T(\bar{x}_T - m_T) \quad [5]$$

where $\bar{x}_Y$ and $\bar{x}_T$ are the average of the phenotypic values of the progeny, m_Y and m_T are the population means for YIELD and TYPE, respectively. The coefficients b_Y and b_T are computed as:

$$b_Y = 2n_Y / (n_Y + (4 - h_Y^2) / h_Y^2) \quad [6]$$

$$b_T = 2n_T / (n_T + (4 - h_T^2) / h_T^2) \quad [7]$$

where, respectively, n_Y and n_T are the number of progeny recorded for YIELD and TYPE, and h_Y^2 and h_T^2 are the corresponding heritabilities.

A total merit index is computed for each bull by linearly weighing the predicted breeding value for each trait by a partial economic weight as:

$$I_P = v_G I_G + v_Y I_Y + v_T I_T \quad [8]$$

where v_G , v_Y and v_T are the partial economic weights for GROWTH, YIELD and TYPE, respectively. If an index for a trait is missing the corresponding term in [8] is dropped.

Females are evaluated for YIELD only. The index for YIELD (I_Y) in females is computed as:

$$I_Y = h_Y^2(p_Y - m_Y) \quad [9]$$

where p_Y is the phenotypic value of YIELD in first lactation. Females that not yet have finished a lactation are evaluated as:

$$I_Y = .5(I_{YS} + I_{YD}) \quad [10]$$

where I_{YS} and I_{YD} are the predicted breeding values for YIELD of the individual's sire and dam. The index I_Y is then transformed into economic units by multiplying it by the economic weight for YIELD. This provides for the possibility of avoiding selection for any trait, by setting the corresponding partial economic weight equal to zero. If all economic weights are set equal to zero, the model will perform random matings.

Simulation of Yearly Breeding Events

Culling

Culling of animals is performed by subroutine DPCULL. Voluntary culling is culling of low producing excess cows, while involuntary culling is culling due to other factors such as disease or infertility.

A cow is culled due to involuntary reasons if a unit uniform random variable is less than INVCR. Voluntary culling of cows is then done on a within herd basis. The total number of lactating cows in each herd is counted and compared to the herd size determined in DPBASE. If there are excess cows, those with the lowest I_Y indexes are culled.

No culling of young stock is simulated directly, but only progeny surviving until breeding age are generated, as will be described in section 3.5.2. Also males that survive the performance test for GROWTH are not culled either. It is assumed, that semen is collected after the performance test as an insurance against the possible loss of a bull due to disease or accidents etc. However, no bull is allowed to be used in breeding if he is more than seven years old.

Mating

Subroutine DPMAPR simulates mating and production, and is the core of the model. Matings are of three kinds and will be described in the sequel.

Test Matings. The number of young bulls that finish the performance test for GROWTH in the current year is counted, and the total number is called NYBAV. The number of young bulls to be progeny tested is then computed as:

$$NSIPGT = NYBPET * PYBPGTY \quad [11]$$

The variables NYBPET and PYBPGTY is defined in Table 3. If NSIPGT is greater than NYBAV, all performance tested young bulls are also progeny tested, thus no selection for GROWTH takes place. If NSIPGT is smaller than NYBAV, then the NSIPGT bulls with the highest I_G indexes are chosen for test matings. The cows to be used in test matings can be chosen in several ways. Most populations use strategies such that a bull is mated to a random sample of cows from the population. The strategy chosen here is to use all first lactation cows (two year olds) in the test matings. The bulls to be progeny tested are mated at random to the first lactation cows using a uniform discrete random variable.

The sex of offspring is determined by a unit uniform random distribution with the sex ratio assumed to be .5. Only female offspring of test matings that survives to breeding age are generated. The offspring is determined to survive if a unit uniform random variable is less than SRDTM (Defined in Table 3).

Contract Matings. The objective of contract matings is to produce

young bulls which are to be performance tested for GROWTH next year. In dairy populations only young bulls which are to be progeny tested for milk yield are produced. This is the only type of mating in the model where both male and female progeny are generated. The test capacity on the performance test station is NYBPET. The bull sires to be used in contract matings are selected as the NBSY sires with the highest I_p indexes, as long as the sire is seven years old or younger. The cows for contract matings are selected among cows that are more than two years old, i.e. second or later lactation, based strictly on I_Y . The number of cows required for contract matings is computed as:

$$NCCM = NYBPET * NBDPET \quad [12]$$

If NCCM is smaller than the number of cows available for contract matings, all available cows is used in the contract matings. The selected sires and dams are mated at random by use of a uniform discrete random variable. Again sex of the offspring is determined by a unit uniform distribution with a sex ratio of .5. Male offspring survives to breeding age if a unit uniform random variable is less than SRYB, and female offspring survives to breeding age if a unit uniform random variable is less than SRDCTM. These survival rates, as defined in Table 1, thus include survival from birth and to breeding age.

Matings to generate producing females. For these matings the top NBCY sires are selected based on I_p . Only sires seven years or younger are used. All females of breeding age, not used in test matings or contract matings, are mated to these sires. Again, the selected sires and the cows are mated at random using a discrete uniform distribution and only female offspring are generated. The survival rate employed

for female offspring of normal matings is SRDNM as defined in Table 3.

Control of inbreeding

Close inbreeding is avoided. As explained in the preceding section groups of selected sires and dams are mated at random within the group. However, if they happen to involve matings between father-daughter, dam-son, or full- or half-sibs, the mating is avoided. Instead the cow is assigned to the best bull in the group that meets the above mentioned requirements against mating of close relatives. If no such bull can be found in the group, the cow is culled. This generally only happens in very small populations. After a mating is accepted and the offspring survives to breeding age, the inbreeding coefficient of the offspring is calculated using a modified version of the algorithm given by Quaas (1976).

Generation of progeny records

The true breeding value of a surviving offspring is computed as:

$$\mathbf{a}_0 = .5(\mathbf{a}_S + \mathbf{a}_D) + CF * \mathbf{L}_M \mathbf{z}_1 \quad [13]$$

where, $\mathbf{a}_0$ is a 3 by 1 vector of true additive breeding values of the offspring for the three traits; $\mathbf{a}_S$ and $\mathbf{a}_D$ are the corresponding vectors of true additive breeding values of its sire and dam, respectively; $\mathbf{L}_M$ is a matrix satisfying $\mathbf{L}_M \mathbf{L}_M' = .5\mathbf{V}_G$, the (co)variance matrix of Mendelian deviations in a non-inbred population, and $\mathbf{z}_1$ is a vector of trivariate normal deviates with zero means and (co)variance matrix $\mathbf{I}_3$. The factor CF accounts for the inbreeding present in the parents and is computed as:

$$CF = (1 - .5(F_S + F_D))^{.5} \quad [14]$$

where, F_S and F_D , respectively, is the inbreeding coefficient of the sire and dam.

The vector of phenotypic values of an offspring is then computed as:

$$p_0 = m + a_0 + L_E e_1. \quad [15]$$

Progeny testing for type

The main selection pressure when selecting bulls is usually on milk production. Therefore, only bulls with acceptable predicted breeding values for YIELD are progeny tested for TYPE. Such schemes are practiced in order to save costs by avoiding testing bulls that would not be used anyway. Each year bulls are evaluated for YIELD on a preliminary basis using the DPEVAL routine, The number of sires with new progeny test results for YIELD is counted as NSPGTY. The number of sires to be progeny tested for TYPE is then computed as:

$$NSPTTR = NSPGTY * PYBPGTT \quad [16]$$

The NSPTTR bulls out of the NSPGTY that have the highest I_Y indexes in the preliminary evaluation is then progeny tested for TYPE. The number of progeny recorded for TYPE in each progeny group is computed as:

$$NPRT = NPROG * PCTT \quad [17]$$

where, NPROG is the number of cows in the progeny group that were recorded for YIELD.

Example

Description of example

As a genetic improvement program progresses, some buildup of inbreeding is inevitable. Inbreeding reduces the genetic variance, the

very factor a genetic improvement program tries to exploit. Another factor that reduces genetic variance is Bulmer effect (Bulmer, 1971), which arises from the mating of selected parents. Chance plays an important role, especially in small populations. Random fluctuation in the genetic level due to chance is called genetic drift (Falconer, 1981). Such genetic drift induces a variance in the expected genetic gain from a selection program. Inbreeding and genetic drift are strongly influenced by the number of males and females used as parents in each generation. The model was therefore used to study the effects of cow population size and number of tested bulls used per year on the genetic response, the buildup of inbreeding, reduction of genetic variance and genetic drift.

The size of a cow population in the model is determined by the number of herds (NHERD) and average herd size (NCPH). Tested bulls that are used in the bull to bull and the bull to cow paths are denoted, respectively, NBSY and NBCY (Table 3). A total of nine situations were investigated. Three cow population sizes were selected by setting (NHERD,NCPH) to (50,40), (25,40) and (25,20), which correspond to cow population sizes of 2,000, 1,000 and 500 cows, respectively. For each cow population size, three levels of bull use were simulated by setting (NBSY,NBCY) to (1,2), (2,4) and (4,8) for each of the three cow population sizes.

Results of example runs

Each of the nine situations were simulated 10 times and comparisons were made, based on the data on animals born in year 25. The following characteristics were computed for each replicate:

Genetic mean and standard deviation for GROWTH, YIELD and TYPE and average inbreeding coefficient. Genetic drift was measured as the standard deviation of the genetic means in year 25 calculated from the 10 replicates within a given situation.

The genetic means, genetic standard deviations and the average inbreeding coefficients from each replicate, a total of 90 observations, were subjected to a two way analysis of variance to determine the effect of cow population size, level of bull use and interaction between the two effects. The significance levels obtained are shown in Table 5. There were no effect of interaction for any of the characteristics studied. Population size had a significant influence on the genetic mean for YIELD and on the genetic standard deviation for TYPE. Level of bull use had a significant influence on the genetic mean in GROWTH, on the genetic standard deviation for YIELD and TYPE, and on the average inbreeding coefficient.

Table 5.
Level of significance for effects of population size, bull use and interaction between population size and bull use.

Characteristics	Population size	Bull use	Interaction
Genetic mean			
male GROW	.1231	.0078	.8202
female YIELD	.0001	.3262	.1984
female TYPE	.2907	.7335	.4076
Genetic stand. dev.			
GROWTH	.2522	.1346	.8435
YIELD	.6469	.0073	.2607
TYPE	.0608	.0001	.9701
Avg. inbreeding	.7010	.0001	.4549

The genetic means in year 25 for GROWTH, YIELD and TYPE are shown in Table 6. All situations showed a considerable progress for all three traits. There were no differences among population sizes in genetic progress made in GROWTH. However, the intermediate level of bull use of (2,4) gave a higher response in GROWTH than that of (1,2) or (4,8) bull sires and cow sires per year. This was in contrast to standard theory for deterministic models that would predict the highest response for models with the highest selection intensity, i.e. (1,2) in this comparison. The same tendency, although insignificant, can be seen for YIELD. The reason for the highest response at the intermediate level of bull-use is probably due to a greater risk in relying on very few bulls per year in the (1,2) case. On the other hand, if (4,8) bulls are used, the selection intensity becomes too low.

Table 6.
Genetic level in year 25, averaged over 10 replicates.

Situation		Male	Female	
Cow-population size <u>NHERD, NCPH</u>	Bull use <u>NBSY, NBCY</u>	<u>GROWTH</u>	<u>YIELD</u>	<u>TYPE</u>
50,40	1,2	151	62.8	1.02
50,40	2,4	160	64.3	1.02
50,40	4,8	159	60.8	.93
25,40	1,2	138	52.3	.82
25,40	2,4	158	57.7	.91
25,40	4,8	147	56.2	.98
25,20	1,2	134	51.6	.94
25,20	2,4	156	49.5	.94
25,20	4,8	148	48.0	.80

For the genetic progress in YIELD, population size was a highly significant factor, such that the genetic progress obtained increased

with increasing population size. The number of young bulls progeny tested per year was the same in all situations. Decreasing the population size meant that the number of cows available for test matings also decreased, leading to a reduction of the accuracy in which breeding values of the bulls were predicted. Lower accuracy means more mistakes in the selection decisions, with the result that genetic progress is reduced.

None of the factors studied had a significant effect on the genetic progress in TYPE.

The genetic standard deviations in year 25, averaged over the 10 replicates are shown in Table 7. Level of bull-use had a significant effect on the genetic variation in YIELD and TYPE such that use of fewer bulls reduced the genetic standard deviation with up to 15 percent of the genetic standard deviation in the base population. Most of the reduction is due to Bulmer effect, since the inbreeding accumulated only would reduce the genetic standard deviation with a fraction $(1-F)^5$, where F is the average inbreeding coefficient.

The average inbreeding in year 25 is also shown in Table 7. Population size had no effect on the accumulated inbreeding, but inbreeding increased markedly as fewer bulls were used per year as bull sires and cow sires.

Table 8 shows the estimates of the variation due to genetic drift. The number of replicates simulated per situation was too low to obtain accurate estimates of this variation. However, results showed that there were considerable genetic drift in all the situations investigated. This means that the genetic progress made in a

particular improvement program can deviate substantially from the expected progress, due to random genetic drift.

Table 7.
Genetic standard deviations in year 25, averaged over 10 replicates.

Situation		Genetic SD			Avg. Inbreeding
Cow-population size <u>NHERD, NCPH</u>	Bull use <u>NBSY, NBCY</u>	<u>GROWTH</u>	<u>YIELD</u>	<u>TYPE</u>	
50,40	1,2	47.1	15.3	.58	.074
50,40	2,4	47.7	16.1	.62	.063
50,40	4,8	48.4	16.0	.63	.040
25,40	1,2	47.1	15.5	.55	.075
25,40	2,4	49.1	15.3	.60	.059
25,40	4,8	48.3	16.2	.60	.043
25,20	1,2	46.3	15.1	.56	.078
25,20	2,4	46.9	15.7	.60	.066
25,20	4,8	47.8	15.9	.61	.042
Base population		53.0	17.5	.63	---

Table 8.
Total genetic drift accumulated in year 25. SD on 10 replicates.

Situation		SD of genetic mean		
Cow-population size <u>NHERD, NCPH</u>	Bull use <u>NBSY, NBCY</u>	<u>GROWTH</u>	<u>YIELD</u>	<u>TYPE</u>
50,40	1,2	23.0	6.14	.33
50,40	2,4	18.4	7.63	.24
50,40	4,8	15.5	4.14	.13
25,40	1,2	14.0	5.46	.14
25,40	2,4	19.0	5.51	.28
25,40	4,8	23.1	5.96	.28
25,20	1,2	16.7	5.32	.25
25,20	2,4	15.8	7.37	.38
25,20	4,8	11.9	2.80	.23

CHAPTER 3

Estimation of Genetic Parameters Using Sampled Data From Populations Undergoing Selection

Introduction

Genetic parameters of economically important traits in livestock populations are usually estimated from field data. Such data often originates from populations that have been subjected to intense selection for one or more traits. The selection over time alters genetic (co)variances due to accumulation of inbreeding and gametic phase disequilibrium (Bulmer, 1971, Falconer, 1981). However, genetic parameters of the base population prior to selection must be known in order to draw general inferences about the population in terms of genetic and phenotypic relationships among traits, to predict gains from breeding programs, and to predict breeding values of animals.

Henderson (1975) and Goffinet (1983) argued that in prediction of breeding values, all data used in the selection decisions that led to the current populations must be included in analysis in order to alleviate selection bias.

The problem of genetic parameter estimation under a selection model was considered by Schaeffer (1987). He showed that for certain translation invariant selection rules the usual REML estimation is not biased by selection. However, in most practical situations the selection rule is not translation invariant, i.e. selection is across fixed effects in the model. Sorensen and Kennedy (1984) showed that minimum variance quadratic unbiased estimation (MIVQUE) of variance components was not biased by selection from an animal model with a complete relationship matrix. A practical problem with MIVQUE, however, is its dependency on the prior values assumed for iteration.

Most livestock populations undergo selection for more than one

trait simultaneously. An example is the simultaneous selection for beef and milk production traits in many European cattle breeds. However, multitrait selection has been practiced also in single purpose cattle populations. Therefore, data on multiple traits should be included in simultaneous analyses.

In many practical situations only more recent data from the current population is available, and thus raise the question of applicability of analysis results to the unselected population. A population undergoing selection for several traits can be thought of as existing in a three dimensional space defined by time, animals, and the traits under selection. Data from a population can be stratified according to one or a combination of these dimensions. Common ways of sampling have been to analyze only data from a certain time period. For example, analyzing data on type traits on Holstein cows who calved between 1982 and 1988 in Michigan and Wisconsin can be thought of as sampling according to a combination of time, space and traits. Using only sample data could be due to limited data source in some cases. However, if a large volume of data is available, sampling of data can be repeated and estimates from different samples can be averaged and can be used to compute SE of estimates.

For most estimation problems in animal breeding the model of choice would be a multiple trait animal model. However, use of such models to estimate genetic parameters can be impossible due to computational difficulties or the animal model might not be feasible due to lack of pedigree information. In such cases simplified operational models, usually sire models, are used.

Another common concern has been the use of data on progeny of highly selected sires, since the variance among those sires is smaller than among unselected sires. Van Vleck (1985) suggested the inclusion of these sires but to treat the effect of them as fixed in the model. The advantage would be a more precise estimation of other fixed effects in the model and more degrees of freedom in the estimation of residual variances.

The objective of this study was to investigate different methods of sampling data from populations undergoing selection in estimating genetic parameters and to investigate the efficiency of different operational models.

Materials and Methods

Simulation of Data

Data was simulated for a small dual purpose population, selecting for both beef and milkfat, and for a larger dairy population selecting for milkfat only. A traditional AI breeding scheme was simulated for both populations, each for a 15 y period. A detailed description of the simulation model was given in Chapter 2 so only a brief description of the simulated populations is given below.

The simulation model was designed to generate data that resembled the data structure found in real cattle populations. Basic parameters describing the simulated populations are given in Table 9. The traits simulated were assumed to be affected by a large number of loci, each with small effects (Infinitesimal model). Only additive genetic effects were considered and all loci were assumed to be unlinked. The

base population were in Hardy-Weinberg equilibrium. For a dual purpose population, the traits simulated were growth measured on young bulls sampled as potential future AI sires and first lactation milkfat production on cows in commercial herds. The genetic parameters assumed for the unselected base populations were heritabilities of .25 and .50 for milkfat production and growth, respectively, and corresponding phenotypic standard deviations were 35 kg and 75 g. The genetic correlation between milkfat production and growth was assumed to be .20 and the relative economic importance of the two traits were 8:1. The performance test for growth of future AI bulls at a central test station was concluded before one year of age so that selection on growth were possible before the bulls were used in breeding. The final selection of bulls was based on a total merit index weighing each trait with the corresponding economic weight. For dairy populations only milkfat production in commercial herds was simulated. The populations were simulated over a 15 y time horizon. The simulation of both the dual purpose and the dairy populations were replicated 15 times.

Since data were simulated, the breeding value and residual deviation was known for each animal. These values were used to obtain direct estimates of genetic and residual variance. The animals were grouped according to year of birth and the mean and variance of true breeding values and residual deviations were computed for each year of birth. The variances for each year of birth were used to compute true heritabilities for each year, and used as reference for the values to be estimated later.

Table 9.
Parameters used in simulation of dual purpose and dairy populations.

	Dual Purpose	Dairy
No. of years to be simulated	15	15
No. of traits	2	1
No. of sires in base population	25	25
Performance test capacity for beef	25	---
No. of bull-dams selected/year	75	36
No. of bull-sires selected/year	2	2
No. of cow-sires selected/year	2	2
No. of herds	4	20
No. of cows	200	1000
No. of young bulls tested for milkfat/yr	4	12
Involuntary culling rate/cow/year	.20	.20
Survival rate of daughters from test matings	.75	.75
Survival rate of daughters from contract matings	.85	.85
Survival rate of daughters from normal matings	.75	.75
Survival rate of young bulls < 1 yr	.85	.85

Sampling of Data for Estimation

In this study, only data sampling in term of time was considered. The 15 y of data were divided into three consecutive 5 y periods. A total of three schemes of sampling data over time were compared:

Scheme 1: All data over time and all relationships between animals were used;

Scheme 2: Only data in the last 5 y was used, but relationships were traced all the way back to the base population;

Scheme 3: Only data from the last 5 y were used and relationships were only traced for the last 5 y, also.

Models

Simulated data were analyzed for each of the three sampling schemes according to the following three models. For dairy populations, of course all matrices pertaining to growth were deleted.

$$\begin{bmatrix} y_G \\ y_M \end{bmatrix} = \begin{bmatrix} X_G & 0 \\ 0 & X_M \end{bmatrix} \begin{bmatrix} b_G \\ b_M \end{bmatrix} + \begin{bmatrix} Z_{G1} & 0 \\ 0 & X_{M1} \end{bmatrix} \begin{bmatrix} a_{G1} \\ a_{M1} \end{bmatrix} + \begin{bmatrix} e_G \\ e_M \end{bmatrix} \quad [1]$$

$$\begin{bmatrix} y_G \\ y_M \end{bmatrix} = \begin{bmatrix} X_G & 0 \\ 0 & X_M \end{bmatrix} \begin{bmatrix} b_G \\ b_M \end{bmatrix} + \begin{bmatrix} Z_{G2} & 0 \\ 0 & Z_{M2} \end{bmatrix} \begin{bmatrix} a_{G2} \\ s_{M2} \end{bmatrix} + \begin{bmatrix} e_G \\ e_M \end{bmatrix} \quad [2]$$

$$\begin{bmatrix} y_G \\ y_M \end{bmatrix} = \begin{bmatrix} X_G & 0 \\ 0 & X_M \end{bmatrix} \begin{bmatrix} b_G \\ b_M \end{bmatrix} + \begin{bmatrix} 0 & 0 \\ 0 & X_s \end{bmatrix} \begin{bmatrix} 0 \\ s_{Mf} \end{bmatrix} + \begin{bmatrix} Z_{G2} & 0 \\ 0 & Z_{M3} \end{bmatrix} \begin{bmatrix} a_{G2} \\ s_{M3} \end{bmatrix} + \begin{bmatrix} e_G \\ e_M \end{bmatrix} \quad [3]$$

where y_G and y_M were vectors of observations on growth and milkfat production, respectively; b_G and b_M were, respectively, vectors of fixed effects of management groups for growth and milkfat production with X_G and X_M the corresponding incidence matrices.

Model [1] was a full animal model, where a_{G1} and a_{M1} were random vectors of additive breeding values for growth and milkfat, respectively, for all animals either with or without own performance record, and Z_{G1} and Z_{M1} were the corresponding incidence matrices.

Model [2], was a combined animal-sire model, where a_{G2} was a random vector of additive breeding values for growth for all males, s_{M2} was a random vector of additive sire effects for milkfat, and Z_{G2} and Z_{M2} were the corresponding incidence matrices. This model was practical, since growth was measured on bulls during the performance test before being used in AI and milkfat was measured on female offspring of these bulls. The computational requirement for Model [2] is much less than that for Model [1].

Model [3] was a modification of Model [2]. The submodel for growth was unchanged but in the submodel for milkfat s_{Mf} was a vector of fixed sire effects on second crop daughters, s_{M3} was a vector of random sire effects on first crop daughters, X_s and Z_{M3} were the corresponding incidence matrices. A sire that had both first and second crops of daughters in data would thus have two effects in the model. The fixed sire effects were included in an attempt to control selection bias, but still use records of daughters of selected sires to obtain better estimates of the fixed effects and the residual variance in the model.

In the absence of selection, assumptions first moments of random vectors in the models were

$$E \begin{bmatrix} y_G \\ y_M \end{bmatrix} = \begin{bmatrix} X_G b_G \\ X_M b_M \end{bmatrix} \quad \text{for Model [1] and [2],}$$

and

$$E \begin{bmatrix} y_G \\ y_M \end{bmatrix} = \begin{bmatrix} X_G b_G \\ X_M b_M + X_s s_{Mf} \end{bmatrix} \quad \text{for Model [3].}$$

The expectation of all other random vectors in the models were zero. The second moments of these random vectors in the models were assumed to be:

$$V \begin{bmatrix} a_{G1} \\ a_{M1} \end{bmatrix} = \begin{bmatrix} \sigma_{G,a}^2 & \sigma_{GM,a} \\ \sigma_{GM,a} & \sigma_{M,a}^2 \end{bmatrix} * A$$

$$V \begin{bmatrix} a_{G2} \\ s_{M2} \end{bmatrix} = \begin{bmatrix} \sigma_{G,a}^2 & (\sigma_{GM,a})/4 \\ (\sigma_{GM,a})/4 & (\sigma_{M,a}^2)/4 \end{bmatrix} * A_m$$

$$V \begin{bmatrix} e_G \\ e_M \end{bmatrix} = \begin{bmatrix} \sigma_{G,e}^2 & 0 \\ 0 & \sigma_{M,e}^2 \end{bmatrix} * I$$

and

$$V \begin{bmatrix} e_G \\ e_M \end{bmatrix} = \begin{bmatrix} \sigma_{G,e}^2 & 0 \\ 0 & \sigma_{M,e}^2 + (3\sigma_{M,a}^2)/4 \end{bmatrix} * I$$

where $\sigma_{G,a}^2$, $\sigma_{M,a}^2$ were the additive genetic variances for growth and milkfat production. respectively and $\sigma_{GM,a}$ is the additive genetic covariance between the two traits, $\sigma_{G,e}^2$ and $\sigma_{M,e}^2$ were the environmental variances for growth and milkfat, respectively, and $*$ denotes direct product. All residual covariances were assumed to be zero since all males were measured for growth only and females for milkfat only. In Model [1], the relationship matrix A considered all known sires and dams, but for Model [2] and [3], A_m considered only sires and maternal grandsires.

Estimation Algorithm

Heritabilities, genetic and phenotypic correlations and phenotypic SD were estimated using a multivariate restricted maximum likelihood (REML) algorithm. The multivariate restricted likelihood function were maximized using derivative free methods as described by Meyer (1989).

Let the model for t traits be:

$$\mathbf{y} = \mathbf{X}\mathbf{b} + \mathbf{Z}\mathbf{u} + \mathbf{e} \quad [4]$$

where $\mathbf{y}$ is a vector of observation vectors for all traits; $\mathbf{b}$ is a vector of fixed effects for all traits; $\mathbf{u}$ is a vector of random additive genetic effects of the same animals for the t traits; and $\mathbf{e}$ is a vector of random residuals corresponding to $\mathbf{y}$. $\mathbf{X}$ and $\mathbf{Z}$ are known design matrices corresponding to, respectively, $\mathbf{b}$ and $\mathbf{u}$; since $V(\mathbf{u}) = \mathbf{G}$ and $V(\mathbf{1}) = \mathbf{R}$, $V(\mathbf{y}) = \mathbf{Z}\mathbf{G}\mathbf{Z}' + \mathbf{R} = \mathbf{V}$.

Assuming normality, the log likelihood is:

$$L = c - .5[\ln|\mathbf{V}| + \ln|\mathbf{X}^*\mathbf{R}^{-1}\mathbf{X}^*| + (\mathbf{y} - \mathbf{X}\hat{\mathbf{b}})'\mathbf{V}^{-1}(\mathbf{y} - \mathbf{X}\hat{\mathbf{b}})] \quad [5]$$

where c is a constant and $\mathbf{X}^*$ is the largest submatrix of $\mathbf{X}$ with full column rank. Following the notation of Meyer (1989) and dropping c , an alternative form of [5] is:

$$-2L = \ln|\mathbf{R}| + \ln|\mathbf{G}| + \ln|\mathbf{C}| + \mathbf{y}'\mathbf{P}\mathbf{y} \quad [6]$$

where $\mathbf{C}$ is the largest full rank submatrix of the coefficient matrix of the mixed model equations from [4] and

$$\mathbf{P} = \mathbf{V}^{-1} - \mathbf{V}^{-1}\mathbf{X}^*(\mathbf{X}^*\mathbf{V}^{-1}\mathbf{X}^*)^{-1}\mathbf{X}^*\mathbf{V}^{-1}.$$

The form of the likelihood function given in [6] was minimized using a quasi-Newton method given by Dennis et al. (1983) and using code from IMSL (1987). This method requires many evaluations of [6] in order to locate its minimum. The four elements in [6] were computed in each evaluation following the strategy outlined by Meyer (1989), which involves, in each iteration setting up the mixed model equations from [4] in tableau form followed by the elimination of all equations by absorption or Gauss-elimination.

Information accumulated on the estimation algorithm

Since use of multiple trait derivative free REML is relatively new, it was considered useful to accumulate information on the convergence pattern of the algorithm. For each model run the total number of rounds to convergence and the number of rounds until a specified degree of convergence was obtained. The degree of convergence was computed by [7] which is modified from Misztal et al (1988):

$$C_t^{(n)} = \frac{|| \mathbf{x}^{(n+1)} - \mathbf{x} ||}{|| \mathbf{x} ||}, \quad [7]$$

where $\mathbf{x}^{(n+1)}$ was the vector containing the intermediate solution from the n 'th evaluation and $\mathbf{x}$ was the vector containing the final solution obtained at convergence. The absolute value of $\log_{10} C_t^{(n)}$ is approximately the number of significant digits in $\mathbf{x}$. The convergence criteria was chosen such that the estimates were accurate to approximately 5 significant digits. Expression [7] was then used to obtain the number of rounds iterated when estimates were accurate to 1, 2, 3, or 4 significant digits.

Results and Discussion

Biases in Genetic Parameter Estimates Due to Data Sampling

Table 10 shows the average number of bulls and cows included in analysis. Estimates of the genetic parameters for the dual purpose populations are shown in Table 11. For milkfat all heritability estimates were unbiased, regardless of model, if all data and all relationships were included in the analysis. However, SE of the heritability estimate increased from .06 in the full animal model to .12 in the combined animal-sire model and further to .15 if sire

effects on second crop daughters were treated as fixed. If only recent data, were used, but relationships were traced all the way back to the base population, estimates from the full animal model were still unbiased.

Table 10.

No. of animals included in analysis, averaged over 15 replicates.

Years included	Dual Purpose		Dairy	
	1-15	11-15	1-15	11-15
Bulls	420	147	198	70
Cows	2198	741	10588	3519

Table 11.

Average estimates of genetic parameters in dual purpose populations.

Model	Sampling scheme	Milkfat		Growth		r _A	SD
		h ²	SD	h ²	SD		
(True parameters		.25		.50		.20	)
[1]	1	.25	.06	.64 ^b	.17	.26	.21
	2	.25	.09	.62	.22	.06 ^b	.28
	3	.20 ^a	.10	.50	.24	.04	.34
[2]	1	.25	.12	.78 ^b	.12	.32	.32
	2	.21	.17	.48	.26	.34	.41
	3	.21	.16	.60	.31	.20	.42
[3]	1	.27	.15	.77 ^b	.14	.25	.38
	2	.36 ^b	.20	.56	.28	-.11 ^b	.24
	3	.36 ^b	.22	.55	.31	.16	.52

^aSignificant at 10% α -level.

^bSignificant at 5% α -level.

If only recent data and recent relationships were used there was a tendency ($P < .10$) for both the full animal model and the combined animal-sire model to yield estimates that were biased downwards.

However, this tendency was not significant for the combined animal size due to the large variance among estimates. Use of recent data and relationships only in the combined animal-sire model with sire effects on second crop daughters treated as fixed surprisingly yielded an upward bias in the heritability estimate for milkfat. This finding was the main reason for also simulating the larger single purpose dairy population in order to check if this result could be repeated in a larger population. Results are shown in Table 12. In all cases for dairy population, heritability estimates were biased downwards, even if all data were included in the analysis. Treating sire effects of second crop daughters as fixed did not alleviate any bias due to selection.

All estimates of heritability of growth were biased upwards when all data and all relationships were included in the analysis. Again this was an unexpected result, and we lack a reasonable explanation. On the other hand the estimates from analyses using recent data only were all essentially unbiased.

The genetic correlations estimated from all data were all unbiased regardless of models used, but were associated with large SE, therefore no definitive trend could be observed. When only recent data were included in the analysis, SE were even greater and in fact there were not enough information in the simulated data to estimate the correlation with reasonable precision.

Table 12.
Average estimate of heritability of milkfat in dairy populations.

Model	Sampling Scheme	Heritability	SD
(True parameter		.25	)
[2]	1	.20*	.06
	2	.20*	.08
	3	.19*	.08
[3]	1	.22*	.07
	2	.20*	.08
	3	.20*	.08

Changes in Underlying Genetic Parameters Due to Selection

The additive genetic variance would decrease over time due to buildup of inbreeding and gametic phase disequilibrium or Bulmer effect caused by directional selection (Bulmer, 1971, Falconer, 1981). Inbreeding was negligible in our simulated breeding schemes so only Bulmer effect needs to be considered. In simulated populations, additive genetic variance can be computed from the true breeding values and residual variance from the residual deviations of each individual. Average heritability, based on true breeding values and residual deviations, were plotted as a function of time in Figure 1 for dual purpose populations and in Figure 2 for dairy populations. In both cases a considerable decrease in heritability was observed. The magnitude of such decreases is dependent on the selection intensity among parents and the mating structure.

Estimated parameters were compared to the expected or true underlying parameters using heritability estimates for milkfat. Use of recent data only gave estimates which essentially reflect the

Figure 1.
Heritability based on true BV Avg. of 15 dual purpose pops.

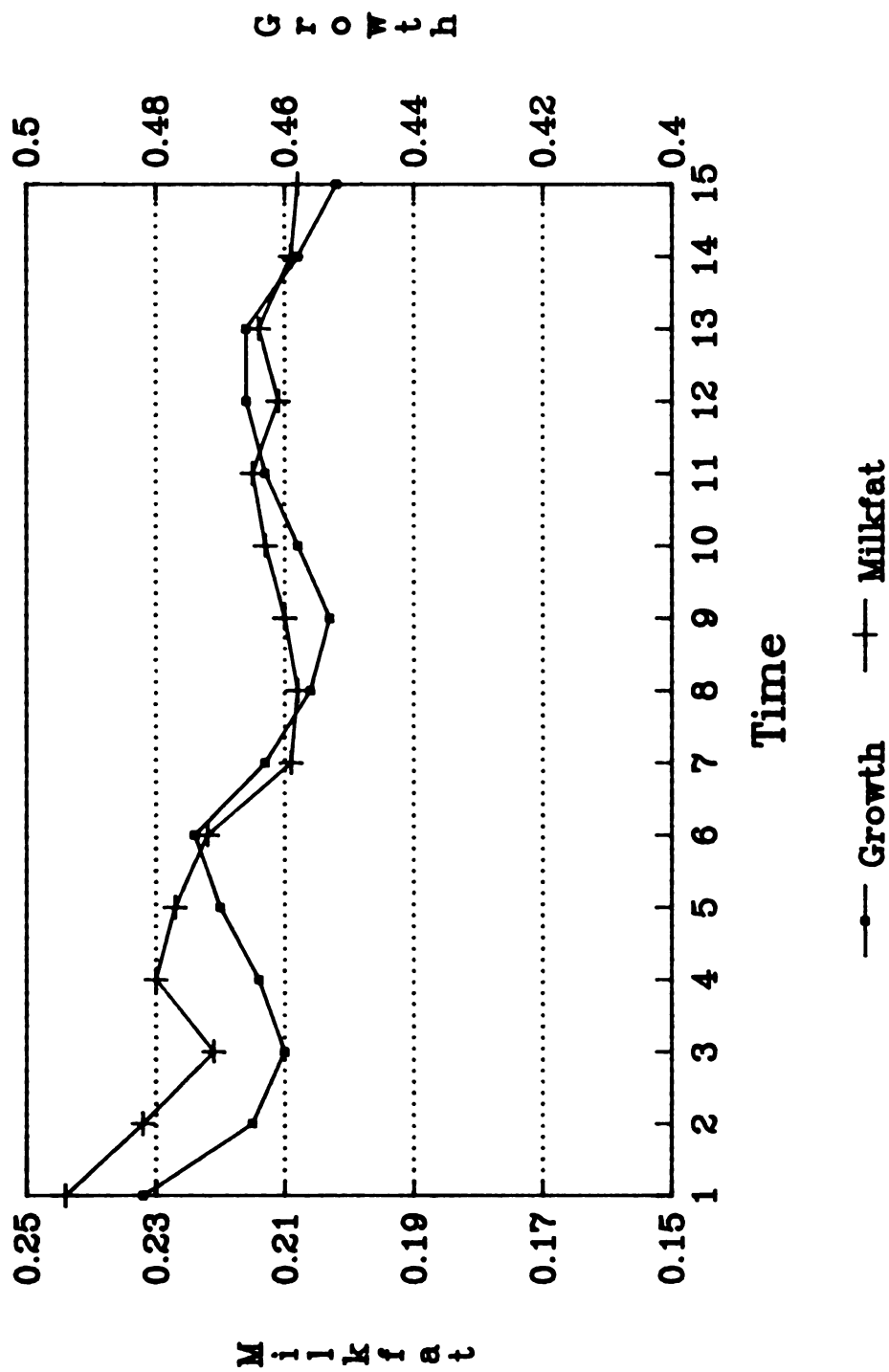
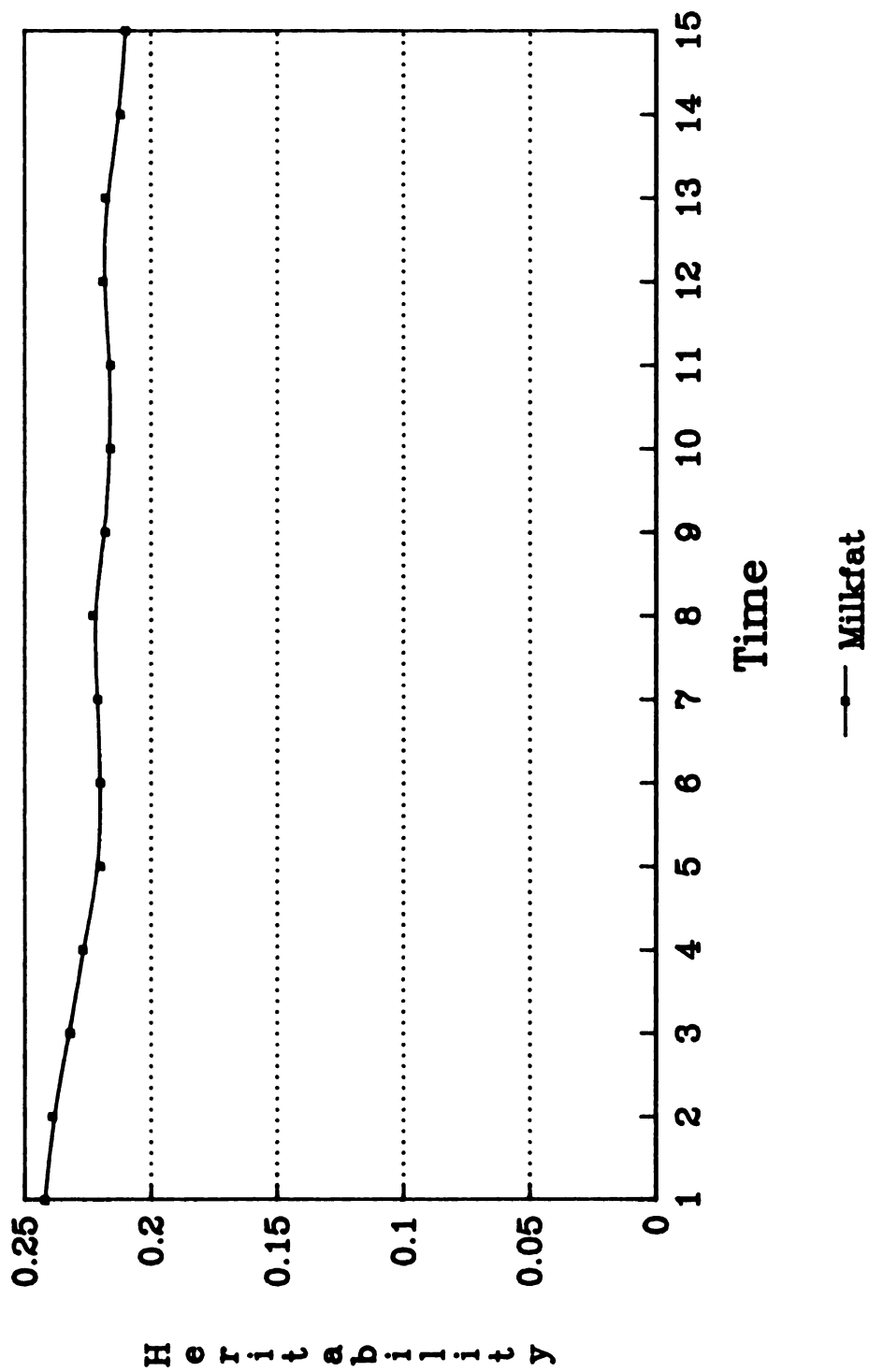


Figure 2.
Heritability based on true BV Avg. of 15. Dairy Populations.



population of the same time period, since the estimate obtained is an unbiased estimate of the heritability in the population of the same period. Even the use of a relationships matrix which tied recent animals to the original base population, failed to produce unbiased estimates of the base population parameters.

Convergence Pattern of the Estimation Algorithm

Table 13 shows the average number of iteration rounds needed to obtain a certain number of significant digits in the estimates of the genetic parameters. The analysis on the dual purpose populations with two traits in the analysis required considerable more iterations than the single trait analysis on the dairy populations. Changing the model from a full animal model to a combined animal-sire model also increased the number of iterations. Thus, although the amount of computation per round is less for the combined model the total amount of computation for a given analysis was not reduced significantly. Changing the model such that sire effects of second crop daughters were treated as fixed increased the number of iterations in the dual purpose populations, but not in the dairy populations. By comparing the number of iterations in Table 13 and SE of estimates in Table 11 and 12 it appears that the number of iterations is inversely related to SE of the estimates. In other words, the more information available on the set of parameters the less rounds of iteration is necessary.

Table 13.

Average no. of rounds to obtain a certain number of significant digits in estimates of genetic parameters.

Model	Sampling scheme	No. of significant digits				
		1	2	3	4	5
Dual purpose populations						
1	1	55	78	98	118	125
	2	74	92	117	121	121
	3	84	100	117	128	128
2	1	73	99	116	119	119
	2	112	144	196	221	239
	3	114	172	219	236	293
3	1	72	99	113	114	114
	2	127	158	206	253	279
	3	175	200	230	255	273
Dairy populations						
2	1	9	16	24	26	26
	2	12	21	28	31	31
	3	12	21	28	31	31
3	1	9	17	24	25	26
	2	12	23	28	29	29
	3	11	22	28	29	29

Conclusions

Selecting parents of following generations would change the variance in the progeny generation from what could be expected in a random mating population. Sorensen and Kennedy (1984) showed that for an infinitesimal model with selection within fixed effects, that a MIVQUE estimator using models that took all relationships into account yielded unbiased estimates of base population parameters. Results from this investigation using a REML estimator confirms this result, even though selection in this case resembled real populations with selection across fixed effects. However, this conclusion might be dependent of

the selection intensities applied, a factor that was kept constant in the present investigation.

The combined animal-sire models also seemed to provide unbiased estimates of base population heritability for milkfat in the dual-purpose situations if all data were included in the analysis. The inclusion of a trait recorded on the bulls themselves might be the reason for this observation. The single trait sire models for the dairy populations were unable to yield unbiased estimates of base population parameters in any of the cases.

If only recent data, but a complete relationship matrix were incorporated in the model, the estimates of heritability for milkfat were still unbiased, albeit with a greater SE.

Using recent data only and recent relationships only is essentially equivalent to redefining the base population to be the selected population. The estimates obtained were unbiased estimates of the genetic parameters in this redefined base population. Sorensen and Kennedy (1984) discussed methods of obtaining the genetic parameters in the current selected population. However, such an approach does not seem useful in practice, since it is dependent on the selection intensity among the ancestors to the current generation, the mating structure used, and the amount of inbreeding present in the current population. If these factors can be quantified, a more practical approach might be to develop correction factors to adjust the estimate results for biases due to selection. This subject seems to warrant further research. Treating sire effects on second crop daughters as fixed did not reduce selection bias in the populations investigated.

The reason for this might be that a large proportion of the populations was used for testing so that the number of second crop daughters was relatively low.

CHAPTER 4

Performance Testing of Dual Purpose Bulls for Beef
Traits. Genetic Parameters for Growth, Feed Intake,
Appetite and Carcass Composition

Introduction

Genetic parameters for growth traits of young bulls are well documented, e.g., Andersen, 1977, and Hanset et al., 1987. However only few estimates of genetic parameters exist for feed intake, appetite and carcass composition due to the high costs associated with measuring these traits. Also the genetics of the partial energy requirements of young bulls for maintenance and growth are not well understood.

In most European countries milk and beef are, to a large extent, produced from dual purpose cattle. To facilitate selection for beef traits most countries have established test stations, where future AI bulls are tested mostly for growth traits based on own performance. Due to the relatively small number of animals tested it is possible to measure feed intake without excessive cost. This may facilitate selection for feed conversion ratio and appetite expressed as average daily feed intake. Appetite may be an important trait since energy and protein intake might be a major limiting factor of production in the lactating cow. (Andersen, 1989, Holmes, 1988, Korver, 1988). The total utility of measuring feed intake during the performance test depends on the genetic correlation between feed intake of the growing bull and the overall merit in the production system.

An experiment was carried out to estimate genetic parameters of growth, feed intake, feed conversion ratio, appetite and carcass composition. Furthermore the experiment was designed such that partial energy requirements for growth and maintenance could be estimated. This paper presents the experimental plan and genetic parameters for

growth, feed intake, feed conversion ratio, appetite and carcass composition of young bulls. In subsequent Chapters we examined alternative ways of describing energy requirements and estimate their relations to the aforementioned production traits and the milk yield of female halfsibs.

Materials and Methods

Animals

The experiment was conducted in Denmark at the experiment station "EGTVED" under supervision of the National Institute of Animal Science. From 1978 to 1982, it was planned to purchase 144 bull calves each year from commercial dairy herds. In each of the first three years the calves were the progeny of six sires of Holstein Friesian (HF) descent. In 1981 they were the progeny of three HF and three Brown Swiss (BS) sires, and in 1982 the calves were progeny of seven BS sires. Very little variation in the proportion of HF or BS genes existed among the bulls used in the experiment. The effect of proportion of HF or BS genes, therefore, could not be studied. Sires were used in one year only. Therefore, over the 5 yrs a total of 31 sires were used. All the sires were young bulls sampled either in Denmark or in North America. Very few genetic relationships existed among the bulls, and they were assumed unrelated in all analyses.

Feeding

All calves were brought to the test station before three weeks of age and started on test at an age of 28 days. In the first production period (P1) from 28 d to a live weight (LW) of 200 kg, all calves were

fed restricted amounts according to live weight, such that energy intake was about 75% of expected ad libitum intake for animals of similar weight. In the second production period (P2) from 200 kg liveweight until slaughter, the calves were randomly placed on four different treatments. Treatment 1 was concentrates fed ad libitum from automatic feed hoppers. Treatments 2, 3 and 4 were all rations based on concentrates and roughages fed ad libitum, which were composed such that 75%, 50% and 25% of expected energy intake were from the concentrate component, respectively. In 1978 and 1979 concentrates were fed in fixed amounts based on weight, and roughages were fed ad libitum. In the last 3 yrs roughages and concentrates were fed as total mixed rations. The roughage component in the diet was changed every year as indicated in Table 14. Also shown in Table 14 is the energy and dry matter content of the major feedstuffs used. A detailed description of procedures used in feeding and handling of the animals was given by Bailey et al. (1985), who used data from the first two years to estimate effects of treatment and slaughter weight on growth, feed efficiency and carcass composition.

The animals also were randomly assigned to three slaughter weight groups. Target slaughter weights were 340, 470 and 600 kg liveweight. Thus it was planned to have two calves in each sire by treatment by slaughter weight subclass.

Table 14.
Energy Content (Mj) and Dry Matter Content of Diets Used.

<u>Year</u>	<u>Treatment^a</u>	<u>Mj/kg</u>	<u>DM/kg</u>
1978	1	6.07	.862
	2	2.71	.420
	3	1.74	.293
	4	1.29	.232
1979	1	6.08	.863
	2	3.65	.569
	3	2.60	.444
	4	2.03	.374
1980	1	6.14	.864
	2	5.70	.837
	3	5.19	.836
	4	4.76	.836
1981	1	6.24	.861
	2	5.64	.816
	3	4.76	.824
	4	4.76	.829
1982	1	6.32	.871
	2	5.05	.895
	3	4.99	.804
	4	4.20	.824

^aTreatment 1, 2, 3 and 4 were respectively, 100%, 75%, 50% and 25% of expected energy intake from concentrate.

Recordings

Calves were weighed at the first day of test and then every 14 d (i.e., at ages 28, 42, 56 d and so on). Feed intake was recorded daily and summed over the 2 week intervals between weighings. In production period 2, all calves were fed ad libitum and the animals were fed three to four times daily to ensure that they had feed available at all times. Weighbacks were performed twice weekly. The energy content of

the roughages used was determined both in vitro via chemical composition, and using in vivo experiments with sheep reared close to the maintenance level in order to obtain the digestibility of the diet. Energy intake was expressed as net energy intake computed according to the Danish feed evaluation system based on Scandinavian feed units (SFU) (Møller et al., 1983). That system expresses feed energy content as net energy for lactation at a certain level of production. Another measure of energy intake is metabolizable energy (ME). Since the Danish net energy system assumes a nearly constant net energy efficiency the net energy intake can be converted to ME by $ME = 4.16 + 1.17 NE$ which gave an R^2 of .96 based on information given by Van de Honing and Alderman, (1988). Since this simple linear relationship exists the genetic parameters to be estimated later are invariant to choice of feed evaluation system. Live weight and carcass weight were recorded at slaughter. Carcasses were graded for conformation and fat cover using a scale from one to 10 with 10 being the best for conformation, and a scale from one to five for fat cover with three the optimum grade and a grade of 4 or 5 indicates too fat animals. One side of the carcass was dissected into lean, fat and bone following anatomic lines at the Danish Meat Research Institute. Samples were taken to determine nitrogen and fat content of the lean meat and for determining palatability using test panels. However, only the dissection data will be used in this report. Procedures used for dissection of carcasses were described by Andersen et al. (1977). A total of 650 bulls completed the experiment, and their distribution over years and treatments is shown in Table 15. The number of bulls

per sire by treatment by slaughter weight subclass were 2 with a few exceptions of 1 due to death.

Table 15.
Distribution of Observations on Years and Treatments.

Year	Treatment ^a				Total
	1	2	3	4	
1978	28	34	35	31	128
1979	34	30	33	35	132
1980	31	33	36	30	130
1981	46	46	16	14	122
1982	35	33	35	35	138
Total	174	176	155	145	650

^aTreatment 1, 2, 3 and 4 were respectively, 100%, 75%, 50% and 25% of expected energy intake from concentrate.

Definition of Traits

Based on weights at start and end of each production period, total feed intake in each production period and carcass composition, the following 17 traits were defined as below:

In production period 1, P1(28 d to 200 kg liveweight):

WGT28	Weight in kg at 28 d.
DG	Average daily gain in g.
EI	Total energy intake in mJ.
FCR	Feed conversion ratio, EI/(Total weight gain), calculated using the Danish feed evaluation system.
DEI	Daily energy intake (appetite), EI/(Days on test).
DMI	Total dry matter intake in kg.

Similar traits except WGT28 were defined in production period 2 from 200 kg LW to slaughter. In all analysis measurements in different production periods were treated as different traits. In tables a

postscript of P1 or P2 is used where necessary to indicate production period.

At slaughter:

DRSPCT	Dressing percentage.
CARGRD	Carcass grade. Scale 1-10 with 10 being the best grade.
FATGRD	Fat grade. Scale 1-5 with 3 being the optimum value.
LEANPCT	Percent lean meat in carcass.
FATPCT	Percent fat in carcass.
EICG	(Total energy intake)/(Total carcass gain).

In computing total carcass gain it was assumed that the dressing percentage of 28 d of age was 50, following definitions given by Andersen (1977).

Estimation of genetic parameters

The 17 traits defined in the preceding paragraph were analyzed together with traits describing energy requirements to be reported in a companion paper. All traits were analyzed simultaneously by a multiple trait model with equal design matrices for each trait. The model for each trait was:

$$y_{ijklm} = t_i + g_j + (tg)_{ij} + p_k + s_{kl} + e_{ijklm} \quad [1]$$

where: y_{ijklm} is a record for the m^{th} bull of year-treatment subclass i slaughter weight group j and the progeny of sire l of breed k ; t_i is the fixed effect of the i^{th} year-treatment with $i=1,2,\dots,20$; g_j is the fixed effect of the j^{th} slaughter weight with $j=1,2,3$; $(tg)_{ij}$ is the interaction between i^{th} year-treatment and the j^{th} slaughter weight; p_k is the fixed effect of the k^{th} breed with $k=1,2$; s_{kl} is the random effect of the l^{th} sire within the k^{th} breed, where the total number of sires were 31; and e_{ijklm} is the random residual.

Preliminary single trait analysis based on a model including all

factors in [1] and all other two-way interactions were conducted. Since the results indicated that other interactions were insignificant, they were dropped from the model.

In matrix notation the multitrait model for all traits simultaneously was:

$$\mathbf{y} = (\mathbf{I} \cdot \mathbf{X})\mathbf{b} + (\mathbf{I} \cdot \mathbf{Z})\mathbf{u} + \mathbf{e} \quad [2]$$

where $\mathbf{y}$ was a vector of observations for all traits, $\mathbf{b}$ a vector of fixed effects, $\mathbf{u}$ a vector of random sire effects and $\mathbf{e}$ a vector of random residuals. $\mathbf{X}$ and $\mathbf{Z}$ were incidence matrices corresponding respectively to $\mathbf{b}$ and $\mathbf{u}$; $\mathbf{I}$ was an identity matrix of order equal to the total number of traits in the analysis

Assumptions on expectations and variances were:

$$E(\mathbf{y}) = (\mathbf{I} \cdot \mathbf{X})\mathbf{b}, E(\mathbf{u})=0, E(\mathbf{e})=0;$$

$$V(\mathbf{y}) = \mathbf{G}(\mathbf{Z}\mathbf{Z}') + \mathbf{R} \cdot \mathbf{I}_n. V(\mathbf{u}) = \mathbf{G} \cdot \mathbf{I}_q; \text{ and } V(\mathbf{e}) = \mathbf{R} \cdot \mathbf{I}_n;$$

where $\mathbf{G}$ and $\mathbf{R}$ were sire and residual (co)variance matrices, $\mathbf{I}_q$ and $\mathbf{I}_n$ are identity matrices, respectively, of order equal to the number of sires, $q=31$, and the number of observations, $n=650$ and "*" denotes the direct product operator. All sires were assumed unrelated. Since relationships existed among very few sires, taking additive genetic relationships into account would therefore be inconsequential to the results reported. The elements of $\mathbf{G}$ and $\mathbf{R}$ were estimated by use of restricted maximum likelihood (REML) in the multiple trait model including all traits simultaneously. An expectation maximization (EM) algorithm augmented with canonical and Householder transformations, as described by Jensen and Mao (1988) was used. No standard errors on genetic parameters are given, since no such statistics have yet been

developed for estimates from multitrait models.

Results and Discussion

Interactions

Preliminary single trait analysis were used to check for all two way interactions. Components of variance due to sire by treatment and sire by slaughter weight group interactions were estimated using a single trait REML algorithm. In all cases estimates of zero were obtained. Estimation of variance components usually requires considerable amounts of data in order to obtain estimates with reasonable accuracy. To investigate how small interaction components could be detected, data were simulated using exactly the same design as the real data. Magnitude of components of variance due to sire and the two interaction components were varied. Components as small as one percent of total phenotypic variance could be detected. In conclusion, therefore, no interaction existed between sire and treatment or sire and slaughter weight group in this experiment.

Andersen et al. (1981) expressed concerns about selecting bulls tested on concentrate diets when roughage is the main component in the diet of milk producing daughters of these bulls. Performance testing systems were therefore changed in several European countries from feeding mainly concentrates to feeding diets containing a large proportion of roughages. The lack of evidence in sire by treatment interaction from this study suggested such a change is not necessary.

Mean, Phenotypic Standard Deviation and Heritability

The means and phenotypic standard deviations in Table 16 show good

accordance with results from the literature, e.g., Andersen, 1977. Heritability estimates (Table 16) for average daily gain were .354 and .373 for production period 1 and 2, respectively. These estimates were somewhat lower than usually found for average daily gain from test station data. However several recent estimates were in the same range: Andersen et al. (1987) found estimates of .392, Hanset (1987) found .44 and Oldenbroek et al. gave estimates of .36 for veal calves and .59 for young bulls, both estimates from data on Dutch Red and White cattle. Dijkstra et al. (1987) gave estimates of .12 and .14 for veal calves and young bulls respectively in the Dutch Holstein breed.

The heritability estimates for total energy intake, feed conversion ratio, appetite and total dry matter intake were lower than the estimates for daily gain in the corresponding production periods, except for appetite in production period 2. Again the results were well in line with the recent literature estimates cited above.

For dressing percentage and carcass grading the heritability estimates were in the range from .31 to .39 which were slightly lower than those in the literature cited earlier. For percent lean and percent fat in the carcass, very high heritability estimates of .706 and .894, respectively were obtained, in comparison to estimates at .52 and .44 found by Andersen (1977).

Table 16.
Mean, Heritability and Phenotypic Standard Deviation for Production Traits.

Trait ^a	Mean	Heritability	Phenotypic standard deviation
WGT28	48.7	.394	6.58
DGP1	893	.354	63.5
EIP1	2932	.313	225
FCRP1	19.4	.195	1.35
DEIP1	17.2	.246	.711
DMIP1	393	.259	30.4
DGP2	1225	.373	133.0
EIP2	12231	.266	1116
FCRP2	42.3	.267	4.51
DEIP2	50.8	.412	2.48
DMIP2	1971	.264	214
DRSPCT	53.0	.333	1.45
CARGRD	6.08	.386	.961
FATGRD	2.87	.310	.354
LEANPCT	67.5	.706	1.985
FATPCT	15.3	.894	2.092
EICG	9.28	.315	.790

^aSee text in Materials and Methods for definition of traits.

Genetic and Phenotypic Correlations Among Traits Measured in Production Period 1

As shown in Table 17, weight at 28 d was positively correlated to daily gain but negatively to total energy intake and total dry matter intake both on the phenotypic and the genetic level. The reason for such negative relations was that a high starting weight leads to a lower need for weight gain in order to reach 200 kg live weight. Also it seems logical that the correlation between weight at 28 d and daily gain would tend to make the correlation between weight at 28 d and total energy intake negative. Daily gain and feed conversion ratio

were strongly negatively correlated as expected for animals fed restricted amounts of feed. Both genetic and phenotypic correlations between daily gain and appetite were positive with estimates of .707 and .325, respectively, which were partially due to the feeding system, because animals were fed restricted amounts according to weight. Efficient animals would grow faster, and thereby advance into the next weight class and thus receive more feed.

Table 17.

Genetic (Under Diagonal) and Phenotypic (Above Diagonal) Correlations Among Traits Measured in Production Period 1 (28 d to 200 kg LW).

Trait ^a	WGT28	DG	EI	FCR	DEI	DMI
WGT28	---	.174	-.442	.149	.558	-.369
DG	.435	---	-.850	-.830	.325	-.826
EI	-.698	-.916	---	.820	-.101	.989
FCR	-.093	-.889	.776	---	.240	.854
DEI	.746	.707	-.709	-.314	---	.000
DMI	-.661	-.900	.989	.794	-.639	---

^aSee text in Materials and Methods for definition of traits.

Genetic and Phenotypic Correlations Among Traits Measured in Production Period 2

Estimates are shown in Table 18. Total energy intake, total dry matter intake and feed conversion ratio were all very highly correlated both phenotypically and genetically. This was expected, since energy content of the feed and dry matter content are closely related. The close correlations between total energy intake and feed conversion

ratio were caused by the fact that intake was measured in a fixed weight interval. Both genetic and phenotypic correlations obtained in production period 2 between daily gain and feed intake traits were almost identical to the corresponding estimates obtained in production period 1. This is in contrast to an expectation of a lowered correlation when changing the feeding regimen from restricted feeding to ad libitum feeding. Andersen et al. (1987) found a genetic correlation of $-.72$ between daily gain and feed conversion ratio when bulls on performance test were fed ad libitum whereas their corresponding estimate for animals under restrictive feeding was $-.98$.

Table 18.

Genetic (Under Diagonal) and Phenotypic (Above Diagonal) Correlations Among Traits Measured in Production Period 2 (200 kg LW to Slaughter).

Trait ^a	DG	EI	FCR	DEI	DMI
DG	---	$-.725$	$-.862$	$.336$	$-.716$
EI	$-.876$	---	$.907$	$.143$	$.997$
FCR	$-.905$	$.979$	---	$.103$	$.902$
DEI	$.594$	$-.195$	$-.232$	---	$.146$
DMI	$-.885$	$.998$	$.979$	$-.218$	---

^aSee text in Materials and Methods for definition of traits.

The genetic correlation between average daily gain and appetite was estimated at $.594$ and between appetite and feed conversion ratio the estimate was $-.232$. Both estimates are comparable to those obtained by Andersen et al. (1987). Brown et al. (1986) obtained a genetic correlation of 0.84 and 0.59 between daily gain and appetite for Angus and Hereford bulls, respectively, on postweaning gain test

under an ad libitum feeding regimen. Their estimates of the genetic correlation between appetite and feed conversion ratio were .47 and .05 for the two breeds mentioned above, results that deviate substantially from the estimates obtained in this investigation. Reasons for this deviation might be due to the different breeds involved and the fact that they used cattle tested in fixed time interval instead of fixed weight interval.

The genetic correlation between appetite and total energy intake was $-.709$ in production period one, but only $-.195$ in period 2. The corresponding phenotypic correlations were $-.101$ and $.142$, for production period 1 and 2, respectively. The negative phenotypic correlation in period 1 was due to the restricted feeding according to weight over a fixed weight interval. Fast growing animals moved faster to the next weight class and thus received more feed. However, these fast growing animals would reach 200 kg live weight in a shorter time and therefore had a lower total energy intake. In production period 2 with ad libitum feeding a large appetite was not necessarily related to a high daily gain. The phenotypic correlation between appetite and total energy intake was therefore positive in production period 2.

Phenotypic and Genetic Correlations between Similar Traits Measured in the Production Periods Before and After 200 kg Live Weight

All phenotypic correlations (Table 19) were low, ranging from $.084$ to $.194$. This clearly shows that similar measures taken in the two production periods, which differed in age and weight of the animals as well as feeding should be regarded as different traits. For daily gain the estimate was $.189$, which is consistent with estimates obtained for

similar weight intervals by Jensen and Andersen (1982), Andersen (1977) and Hanset et al. (1987). The genetic correlation between average daily gain in the two production periods was .471. Oldenbroek et al. (1987) found estimates at .61, Dijkstra et al. (1987) found .53, Jensen and Andersen (1982) at .70 and Andersen (1977) found .85. The lower estimates found in this investigation might be due to the different feeding systems used in the two production periods. However, for total energy intake, total dry matter intake, and feed conversion ratio the genetic correlation between the two production periods was around .60. This is higher than Oldenbroek et al. (1987) who found an estimate of .49 for feed conversion ratio. The correlation for appetite was low .127, which is because average daily feed intake is influenced more than the other traits when changing the feeding regimen from restricted feeding to ad libitum feeding.

Table 19.

Genetic and Phenotypic Correlations Among Similar Traits Measured in Production Period 1 and 2.

Trait ^a	Genetic correlation	Phenotypic correlation
DG	.471	.189
EI	.559	.194
FCR	.577	.159
DEI	.127	.084
DMI	.626	.192

^aSee text in Materials and Methods for definition of traits.

Genetic and Phenotypic Correlations between Traits Measured at Slaughter

As shown in Table 20 the correlation between dressing percentage and carcass grading were estimated at .478 and .351, respectively, genetically and phenotypically. It is interesting to note that neither dressing percentage nor carcass grading were highly correlated to carcass composition, but there is a strong genetic correlation between fat grade and percent fat in the carcass with an estimate at .65. However the corresponding phenotypic correlation was low. Percent lean and percent fat in the carcass were highly correlated since they make up about 83% of total carcass weight and there is only limited variation in the proportion of bone in the carcass (Andersen, 1977). Total energy intake per unit of carcass gain is related to carcass composition such that selection for leaner carcasses would decrease the feed intake per kg carcass gain. Again the corresponding phenotypic correlation was low.

Table 20.
Genetic (Under Diagonal) and Phenotypic (Above Diagonal) Correlations Among Traits Measured at Slaughter.

Trait ^a	DRSPCT	CARGRD	FATGRD	LEANPCT	FATPCT	EICG
DRSPCT	---	.351	.094	.118	.032	-.143
CARGRD	.478	---	.112	.236	-.079	-.295
FATGRD	-.065	-.157	---	-.261	.343	-.085
LEANPCT	.043	.373	-.664	---	-.899	-.361
FATPCT	.011	-.189	.658	-.920	---	.226
EICG	-.220	-.290	.048	-.482	.465	---

^aSee text in Materials and Methods for definition of traits.

*Genetic and Phenotypic Correlations between Traits Measured in
Production Period 1 and 2 and Traits Measured at Slaughter*

As shown in Table 21, all traits measured in production period 1 had low genetic correlations to carcass traits, except net energy intake per kg carcass gain and this was probably due to the part-whole relationship. Daily gain in production period 2 was genetically correlated to dressing percentage and body composition such that selection for higher daily gain would tend to lower dressing percentage and increase the percentage of lean meat in the carcass at a given body weight. These results are similar to results obtained by Andersen (1977). Total net energy intake, total dry matter intake and feed conversion ratio all had positive genetic correlations to percent fat in the carcass. Thus selection for leaner animals would reduce total feed requirement. This is probably to some extent caused indirectly by daily gain, since fast growing animals are leaner at a given weight because they are less mature at that weight. Also fast growing animals reach a fixed weight in shorter time, thus reducing the accumulated maintenance requirement. Appetite is also related to carcass composition such that selection for higher daily feed intake will yield leaner animals with an estimate of the genetic correlation between appetite and percent fat in the carcass at $-.397$ when slaughter weight is held constant. All the corresponding phenotypic correlations are not shown, but were of same sign, although much lower in magnitude than, the corresponding genetic correlations. Exceptions were the correlations between daily feed intake and percent lean at $-.134$ and daily feed intake and percent fat at $.157$. The latter corresponded to

an environmental correlation between percent fat in the carcass and daily feed intake at .33. This implies that an animal who has a large daily feed intake due to environmental reasons tends to be fat, whereas if it is due to its genotype it will not be fat at a fixed weight and tend to grow faster.

Table 21.
Genetic Correlations Between Growth, Feed Conversion and Appetite in Production Period 1 and 2 and Traits Measured at Slaughter.

Trait ^a	DRSPCT	CARGRD	FATGRD	LEANPCT	FATPCT	EICG
WGT28	-.245	-.282	.214	-.143	-.073	-.156
DGP1	-.042	.129	.244	.175	-.205	-.524
EIP1	.071	.008	-.307	-.082	.172	.581
FCRP1	-.117	-.235	-.247	-.244	.178	.688
DEIP1	-.207	-.118	.130	-.041	-.140	-.033
DMIP1	.082	.000	-.297	-.119	.190	.649

DGP2	-.249	.144	-.263	.592	-.619	-.788
EIP2	.203	.005	.053	-.476	.523	.877
FCRP2	.189	-.084	.060	-.457	.484	.904
DEIP2	-.184	.290	-.391	.413	-.397	-.161
DMIP2	.195	-.017	.069	-.489	.528	.881

^aSee text in Materials and Methods for definition of traits.

Conclusions and Implications

No interaction between genotype represented by paternal halfsib groups and rations of differing proportion of roughages were found in this experiment. In several European countries the feeding of bulls on

performance test have been changed from diets based mainly on concentrates to diets with a large proportion of roughages. The reason for this change was concern about the roughage intake of daughters of bulls selected on a concentrate diet, (Andersen et al. 1981). The results of the present experiment did not support such concerns.

All the traits analyzed show additive genetic variances and heritabilities in a range that would allow for considerable response to genetic selection. Selection for daily gain would as a correlated effect improve feed conversion ratio and increase appetite. However, in ad libitum fed animals, the literature cited earlier indicates that the correlation between daily gain and feed conversion ratio might be lower in ad lib. fed animals than found in this investigation. The relatively low correlations between the same trait measured before and after 200 kg live weight and on different feeding systems, indicate that animals must be tested for these traits during age or weight intervals and feeding systems that are similar to normal practice in commercial production to ensure genetic progress in this environment.

Results indicate that selection on daily gain or appetite will decrease carcass fatness at a given weight, but there is a positive environmental correlation between appetite and carcass fatness.

CHAPTER 5

Performance Testing of Dual Purpose Bulls For Beef Traits.

Residual Intake and Energy Requirements For

Growth and Maintenance

Introduction

Supply of feed energy is a major cost factor in any cattle production system. Selection for more efficient use of energy may therefore be profitable. Genetic improvement of feed efficiency requires measures of feed intake. For dual purpose cattle, feed intake can in principle be measured on different groups of animals: (1) Progeny groups under field conditions; (2) Bull-dams either in commercial herds or on special testing stations, most probable in connection with breeding schemes using multiple ovulation and embryo transfer (MOET); (3) Future AI bulls while they are being performance tested for beef traits. In this paper we are concerned only with the third possibility.

The total utility of measuring feed intake on future AI bulls depends on the genetic correlation between efficiency traits measured on the growing bull and the same traits in other groups of animals, primarily lactating cows. Traditional measures of feed efficiency such as feed conversion ratio are closely correlated to the level of production as shown in Chapter 4. The total intake of metabolizable energy can be partitioned into productive (growth) and nonproductive (maintenance and efficiency of the digestive tract) use of energy. These parts are collectively called partial energy requirements. The nonproductive use of energy is a major part of the total use of feed energy (Andersen, 1978). Residual intake, defined as actual energy intake minus predicted energy intake, has been suggested as a measure of efficiency that is independent of level of production (Koch et al.,

1963. Brelin and Bränning, 1985). A lower residual intake would indicate a better efficiency. However, errors introduced by use of an inappropriate model in predicting intake would be included in this measure as would errors of measuring feed intake. The genetic nature of residual intake and partial energy requirements is not well understood.

The objective of the present paper therefore was to explore different measures of the young growing bulls' energy requirements for growth and main-tenance and their residual intake, and to estimate the genetic parameters of these traits. A necessary requirement for the use of such measures in performance testing of future AI bulls is that they can be obtained on the live animal. The previous chapter reported genetic parameters of traditional beef production characteristics of the same young bulls. In a following paper, we will report phenotypic and genetic correlations between residual intake and partial energy requirements defined in this paper, and traditional beef production characteristics. Genetic correlations to the milkfat production of female halfsibs also will be reported.

Materials and Methods

Animals and records

An experiment was carried out in Denmark at the experiment station "EGTVED" under the supervision of the National Institute of Animal Science. A total of 650 bull calves of 31 Holstein Freisian (HF) or Brown Swiss (BS) sires completed the experiment. The experiment was carried out in yearly batches, with a batch initiated in each of the

years from 1978 to 1982. All calves started in the experiment at the age of 28 d. In the production period from 28 d and until the animals reached a live weight of 200 kg (P1) feeding of calves was restricted, at a level of 75% of expected ad libitum intake. In production period 2 (P2), from 200 kg live weight to slaughter, the animals were placed at random on four treatments with ad libitum feeding. Treatments 1, 2, 3 and 4 were respectively, 0%, 25%, 50% and 75% of expected energy intake from roughages. The 0% treatment was concentrates fed from automatic feed hoppers, while the other treatments were fixed amounts of concentrates and roughages fed 3-4 times daily to ensure that feed was available at all times.

Live weights of the animals were recorded at the age of 28 d and thereafter biweekly throughout the experiment. Feed intake of a young bull was recorded as a sum of daily intakes in the weighing intervals. All feed given at each feeding was weighed. Weighbacks were taken twice a week. Feed intake was then recorded as the sum of all feed given in a two week period minus weighbacks. The periods when feed intake was recorded coincided with the intervals between body weight measures.

Energy intake was computed according to the Danish feed evaluation system based on Scandinavian feed units (SFU). That system expresses feed energy content as net energy for lactation (Møller et al., 1983). Since the Danish net energy system assumes a nearly constant net energy efficiency, the net energy intake (NE) can be converted to metabolizable energy (ME) by $ME = 4.16 + 1.17NE$ which gave an R^2 of .96. This equation assumes both ME and NE to be measured in mJ and is based

on information given by Van der Honing and Alderman (1988). Since this simple linear relationship exists the genetic parameters to be estimated later are invariant to the choice of feed evaluation system.

Records on a total of 18,111 weighing intervals were available. The number of intervals available for an individual animal ranged from 16 to 45 depending on the animal's growth rate and slaughter weight. Animals were slaughtered at 340, 470 or 600 kg live weight. At slaughter, live weight and cold slaughter weight was recorded and the left half of the carcass was dissected into lean, fat, and bone, following anatomic lines, at the Danish Meat Research Institute. A detailed description of the experiment and the procedures used were given in Chapter 4 and Bailey et al. (1985).

Estimation of partial energy requirements for individual bulls

The total energy intake (EI) of an animal can be partitioned into:

$$EI = NPE + PE,$$

where NPE is nonproductive use of energy and PE is productive use of energy. Both components can be further subdivided. The PE is energy used for growth, mainly in the form of fat or protein. Fat has a higher capacity for storing energy than protein, and 1 g of protein is accompanied by about 5 g of water (Webster, 1977). Therefore, storage of one g of lean meat should require much less energy than storing one g of fat. However the synthesis of protein is a very complex process that requires more energy than synthesis of the same amount of fat. This means that the partial energy requirement for growth might not be as highly dependent on the composition of the weight gain as the energy content of fat and lean would indicate (Pullar and Webster, 1977,

Kielanowski, 1976). Such association perhaps is different in ruminants as in single-stomach animals (Geay, 1984). The maintenance requirement might be dependent on the composition of the body weight maintained.

Based on the considerations mentioned above, simple models for estimating partial energy requirements were defined. The partitioning of energy intake into productive and nonproductive use of energy for each individual bull was based on the biweekly measures of energy intake and live weight. The following alternative multiple regression models were used to obtain estimates of partial energy requirements for individual young bulls within a production period:

$$EI_i = b_{I1} + b_{G1}(G_i) + b_{W1}(W_i^{3/4}) + e_i \quad [1]$$

$$EI_i = b_{I1} + b_{G2}(G_i) + b_{W2}(W_i^{3/4}) + b_{GW2}(G_i W_i^{3/4}) + e_i \quad [2]$$

where EI_i was the energy intake (MJ) in the i^{th} two week weighing interval for an individual bull; G_i was the total live weight gain in kg in the i^{th} weighing interval; W_i was the average weight in kg in the i^{th} weighing interval; b_{I1} , b_{G1} etc. were partial regression coefficients; and e_i was a random residual.

The intercept in each model, b_{I1} and b_{I2} , describes a baseline intake not associated with growth rate or metabolic weight. The regression on metabolic weight, b_{W1} and b_{W2} , denote the energy requirement for maintaining one kg of metabolic body weight in a weighing interval. The regression on growth, b_{G1} and b_{G2} , in a weighing interval expressed the energy requirement for one kg of body weight gain.

The intercept together with the regression on metabolic weight

estimates the nonproductive use of energy. The intercepts in the models indicate use of energy not associated with other factors in the model and is the part of nonproductive use of energy independent of body weight. Since the energy expenditure at zero metabolic weight and zero gain is expected to be zero, deviations of this intercept from zero might also indicate lack of fit of the model used. As the animal grows larger the composition of body weight gain changes (Geay, 1984). Interactions between productive and nonproductive use of energy can therefore be expected.

In model [2] an interaction between growth and metabolic weight was included with b_{GW2} as the corresponding partial regression coefficient. The reason for including the interaction in the model was to account for the changes in the composition of body weight gain and of the body weight maintained as metabolic weight changes. Instead of using the interaction term in model [2], it might have been desirable to use a regression on lean and fat depositing separately. However, this requires knowledge of body composition and change in body composition throughout the production period and under practical conditions such information is not available.

All estimates of baseline intake and weight dependent nonproductive use of energy were divided by 14, so that they were expressed as energy requirement per day, instead of per two weeks.

Since the feeding regime was different in production period 1 and 2, each of the models was applied within each period. For ease of reference in tables the coefficients were labeled BI1, BG1, and BW1 for model [1] requirements and BI2, BG2, BW2 and BGW2 for the requirements

estimated in model [2].

Several other, more complex, models were investigated. However, they did not provide enough additional information beyond the models above to warrant reporting.

Residual intake

The residual efficiency, here termed residual intake, is defined as the total energy intake minus predicted total energy requirement in a given production period (Brelín and Bränning, 1982). The total energy requirement can either be predicted from feeding standards or derived directly from analysis of the experimental data. Earlier analyses of residual intake of growing cattle have been presented by Brelín and Bränning (1982) and Brelín and Martinsson (1986). In this investigation, total energy requirement was estimated directly from the data, because this gave the possibility of taking carcass composition into account in the prediction. The residual intake was therefore estimated as the *residual* from the following two alternative models:

$$y_{ijk} = t_i + g_j + (tg)_{ij} + p_k + b_1(w_{ijk}^{3/4}) + b_2(G_{ijk}) + b_3(D_{ijk}) + e_{ijk} \quad [3]$$

$$y_{ijk} = t_i + g_j + (tg)_{ij} + p_k + b_4(w_{ijk}^{3/4}) + b_5(G_{ijk}) + b_6(D_{ijk}) + b_7j(K_{ijk}) + b_8j(F_{ijk}) + e_{ijk} \quad [4]$$

where: y_{ijk} was the total energy intake in production period 1 or 2 for a bull of the k^{th} breed in slaughter weight group j and year-treatment i ; t_i was the effect of i^{th} year-treatment; g_j was the effect of j^{th} slaughter weight group; $(tg)_{ij}$ was the interaction between t_i and g_j ;

p_k was the effect of k^{th} breed; W_{ijk} was the average weight in the production period; G_{ijk} was the total live weight gain in the production period; D_{jk} was the number of days in the production period; and b_1 through b_6 were corresponding regression coefficients. In model [4], carcass measures were considered, where K_{ijk} was the dressing percentage; F_{ijk} was the percent fat in the carcass; and b_{7j} and b_{8j} were corresponding heterogeneous regression coefficients within slaughter weight group. In [3] and [4], e_{ijk} was a random residual and was defined as alternative measures of residual intake in each production period.

The residual intake from [3] is hereafter denoted as RES, while that from [4] is RESC with post letter "C" indicating the consideration of carcass composition in the prediction of energy requirement. Other more complex models were fitted in order to estimate residual efficiency. However, estimates from those models were very highly correlated with those from the simple models presented and hence only the simple models were reported in this paper.

Estimation of genetic parameters

Nine traits were defined by parameter estimates from models [1] through [4] for each of the 650 bulls in each production period. Since there were two production periods, a total of 18 traits were analyzed.

These traits were analyzed together with traditional beef production characteristics which were reported in Chapter 4. All traits were analyzed simultaneously using a multiple trait model with equal design matrices for each trait.

The model for each trait was:

$$y_{ijklm} = t_i + g_j + (tg)_{ij} + p_k + s_{kl} + e_{ijklm} \quad [5]$$

where y_{ijklm} was the record of a trait for a bull in year-treatment i , in slaughter weight group j , of breed k and of sire l ; t_i was the fixed effect of the i^{th} year-treatment; g_j was the fixed effect of the j^{th} slaughter weight group; $(tg)_{ij}$ was the interaction between t_i and g_j ; p_k was fixed effect of k^{th} breed; s_{kl} was the random effect of l^{th} sire within the k^{th} breed and e_{ijklm} was a random residual. Note that for the four residual intake traits from [3] and [4], the fixed effects needed to be repeated in [5] so that degrees of freedom would be accounted for properly. Precise description of assumptions for the model were given in Chapter 4.

Variance-covariance matrices corresponding to sire and residual effects were estimated by restricted maximum likelihood (REML) utilizing the expectation maximization (EM) algorithm augmented with canonical and Householder transformations, as described in Chapter 1. No standard errors on genetic parameters are given, since such statistics have not yet been developed for estimates from multitrait models.

Results and Discussion

Table 22 shows simple means, heritability estimates and phenotypic standard deviations for partial energy requirements from model [1] and [2] for both production periods 1 and 2.

Table 22.
Mean Heritability and Phenotypic Standard Deviation For Estimates of
Energy Requirements.

Traits ^a	Production period					
	28d to 200 kg live weight			200 kg LW to slaughter		
	Mean	h^2	σ_p	Mean	h^2	σ_p
Model [1]						
BI1	-4.01	.252	1.49	-3.31	.185	15.3
BG1	9.26	.106	22.1	23.0	.188	51.4
BW1	.604	.067	.062	.684	.208	.199
Model [2]						
BI2	1.90	.258	4.86	1.45	.154	75.9
BG2	-27.1	.258	75.5	-21.5	.161	712
BW2	.539	.199	.154	.626	.142	1.07
BGW2	1.03	.248	2.03	.560	.142	10.3
Model [3]						
RES	0	.077	96.5	0	.275	619.7
Model [4]						
RESC	0	.082	96.4	0	.363	600.8

^aSee text in Materials and Methods for definition of traits.

Baseline intake

Average model [1] energy requirements showed a slightly negative baseline intake in both production periods. The baseline intake reflects energy intake corrected for weight-dependent nonproductive use of energy and productive use of energy (weight gain) and might therefore be said to reflect a baseline metabolism. The use of energy cannot be negative, but the estimates were expressed at zero production and zero metabolic weight, a state that no animal can, of course, attain. For selection purposes, variation among animals is more important than the actual level of the estimates obtained, since ranking of animals might be a primary goal. The standard deviation of

15.3 MJ/d in production period 2 showed that there were considerable variation in energy requirement at constant production and at constant metabolic weight. The heritability was estimated at approximately .2 which is the same level as the traditional feed conversion ratio obtained in Chapter 4.

Partial energy requirement for growth

The average model [1] energy requirement for one kg of body weight gain were 9.26 and 23.0 MJ in production periods 1 and 2, respectively. The partial energy requirement for growth is generally thought to be dependent on the composition of the body weight gain (Webster, 1980). In older animals, a larger proportion of the body weight gain consists of fat (Andersen et al., 1984 and Geay, 1984), but in this experiment the composition of the gain is not known for each animal in each individual weighing interval. However the partial efficiency for fat and protein gain is very different. In a literature review, Geay (1984) gave preferred values of .20 and .75 for protein and fat accretion on an energy basis, respectively, based on pooled data from 52 experiments. The large differences in the partial efficiencies of protein and fat accretion tend to diminish the relation between body composition and energy requirement for growth. This might especially be true in the present experiment since bulls of dairy breeds have relatively small amounts of fat deposition.

The feeding level and production in production period 2 was much higher than in period 1, with average daily gains of 1225 g vs. 893 g, respectively. The efficiency of energy utilization is dependent on the production level (Milligan and Summers, 1986, Andersen, 1980). This

might be a reason for the big difference in the partial energy requirement for growth in the two production periods. Also the composition of the body weight gain can be of importance.

A detailed analysis of the genetic and phenotypic correlations between partial energy requirements and carcass composition at slaughter will be reported in a subsequent paper. The heritability of model [1] energy requirement for body weight gain was estimated at .106 and .188 for production period 1 and 2, respectively. These estimates together with the phenotypic standard deviations of 22.1 and 51.4 mJ/kg shows considerable variation among animals in partial energy requirement for growth and also that a significant proportion of this variance is due to additive genetic effects.

Weight dependent nonproductive use of energy

The average model [1] requirements for weight-dependent nonproductive use of energy were .604 in production period 1 and .684 in period 2, both expressed in mJ per kg metabolic weight per day. These values correspond to predicted maintenance requirements, and are almost twice the values assumed in most systems of estimating energy requirements, e.g., NRC, (1978). However, the weight-dependent nonproductive use of energy is very dependent on production level, and the values used in several energy systems were estimated in fasting animals or in animals close to weight equilibrium. Andersen (1980) found estimates at .541, .468 and .355 mJ/kg^{3/4}/d for ad libitum feeding, 85% and 70% of ad libitum intake, respectively, based on data from a crossbreeding experiment.

The nonproductive use of energy is dependent on weight or age of the animals. Van Es (1980) estimated the maintenance requirement in ME of bulls that were crosses between Hereford and Freisian to be .607 mJ/kg^{3/4}/d at 250 kg live weight and .573 at 450 kg live weight. Milligan and Summers (1986) stated that the maintenance requirement decreases with increasing weight or age. However, this decreasing effect might have been counteracted in the present experiment by the change in the feeding strategy before and after 200 kg liveweight. Thorbek (1980) estimated the maintenance requirement of calves weighing from 100 to 275 kg liveweight using respiration chambers and found estimates varying from .377 to .486 mJ/d, but found no relation to liveweight. Larsen (1979) cf. Andersen, (1980) using a similar approach as in the present investigation found estimates at .688 mJ/kg^{3/4}/d on bull calves fed concentrates ad libitum, a result very similar to the results obtained in this study. The considerable variation among different estimates of weight-dependent nonproductive use of energy found in the literature might well be ascribed to differences in level of intake in the different experiments.

The heritability estimates for weight-dependent nonproductive use of energy were .067 and .208 for production period 1 and 2 respectively. In comparison Larsen (1979) cf. Andersen (1980) obtained a figure of .31 from a small experiment. Andersen (1980) demonstrated differences among different crosses between beef breeds and dual purpose breeds for weight-dependent nonproductive use of energy. Also, Ferrell and Jenkins (1985) based on an extensive literature review concluded that there are considerable differences among cattle types in

energy requirements for maintenance and growth. The heritability estimates, together with the phenotypic standard deviations, show considerable variation among animals for the weight dependent non-productive use of energy, and also show that the nonproductive use of energy can be altered through genetic selection.

Interaction of energy requirements

The baseline intake for this model was slightly above zero in both production periods (Table 22). The interpretation of the partial requirements for growth and weight-dependent nonproductive use of energy was difficult, due to the interaction between the two factors. However, the results indicated that this interaction was important. The standard deviation of model [2] requirements were all larger than corresponding model [1] requirements, a feature that may render model [2] more useful in distinguishing among animals.

The heritability of model [2] partial energy requirements were higher than corresponding model [1] requirements in production period 1, whereas the opposite were the case in period 2. The interaction term showed heritability estimates at a level similar to the heritability of conventional measures of feed efficiency reported for the same animals in Chapter 4.

Residual intake

The last two rows of Table 22 shows means, heritability estimates and phenotypic standard deviations for the two alternative expressions for residual intake. The average is zero due to the method used in determining residual intake. The phenotypic standard deviation of

residual intake is smaller in production period 1 than in period 2, which is partly due to the fact that intake was obviously easier to predict in production period 1, where the animals were fed restricted amounts according to live weight. The phenotypic standard deviation for residual intake was slightly less than 100 mJ in period 1 and slightly more than 600 mJ in period 2, or 3.3% and 5.1% of total energy intake in the respective production periods. These percentages correspond very well to the 4.3% found by both Brelín and Bränning (1982) and Brelín and Martinsson (1986) working with intake on an ME basis.

Residual intake is, by definition, independent of daily gain. Therefore, intake also can be expected to have a low correlation with feed conversion ratio, since the feed conversion ratio is closely correlated to daily gain. Thus, there is considerable variation in feed intake that is unrelated to production level in terms of average daily gain.

Correction for carcass composition in predicting residual intake only reduced the phenotypic standard deviation by 3% in production period 2 and did not reduce the standard deviation in period 1 at all. However, the correction increased the heritability estimate from .275 to .363 in production period 2. This increase might be an effect of a very high heritability of percent lean and percent fat in the carcass found in this experiment (Chapter 4). Brelín and Bränning (1982) found a heritability estimate for residual intake at .27, a result well in line with the results in this study.

Table 23.
Genetic (Below Diagonal) and Phenotypic (Above Diagonal) Correlations
Among Partial Energy Requirements and Residual Intake in Production
Period 1 (28 d to 200 kg BW).

Trait ^a	Model [1]			Model [2]				Model [3]	Model [4]
	BI1	BG1	BW1	BI2	BG2	BW2	BGW2	RES	RESC
Model [1]									
BI1	---	-.087	-.643	.306	-.039	-.277	.033	-.139	-.142
BG1	-.605	---	-.668	-.021	.277	-.252	-.005	-.072	-.072
BW1	-.760	.019	---	-.176	-.205	.379	.012	.242	.252
Model [2]									
BI2	.473	-.433	-.099	---	-.907	-.942	.949	-.122	-.123
BG2	-.273	.400	-.140	-.957	---	.759	-.947	.041	.043
BW2	-.435	.341	.141	-.985	.942	---	-.903	.190	.189
BGW2	.230	-.285	.110	.957	-.987	-.949	---	-.075	-.075
Model [3]									
RES	.063	-.040	-.101	-.137	.132	.098	-.104	---	.988
Model [4]									
RESC	.067	-.038	-.099	-.171	.174	.133	-.145	.981	---

^aSee text in Materials and Methods for definition of traits.

Correlations among traits in production period 1

Genetic and phenotypic correlations among traits measured in production period 1 are shown in Table 23. For model [1] energy requirements, the phenotypic correlation between baseline intake and requirement for growth was close to zero, whereas baseline intake and weight-dependent nonproductive use of energy were negatively correlated with an estimate at $-.643$. Genetically, baseline intake and requirement for growth and weight-dependent nonproductive use of energy were strongly negatively correlated.

The model [2] partial energy requirements were all very highly intercorrelated. With only one exception, all phenotypic and genetic

correlations had absolute values above .95. This means that they varied together as a unit, since knowledge of any one of the partial energy requirements could lead to a precise prediction of the remaining requirements. This may make model [2] easier to use in comparing energetic efficiency of different animals.

Partial energy requirement from model [1] were generally much less correlated to model [2] requirements than were requirements estimated within the same model. Even coefficients with similar biological definitions, but estimated in different models were generally not very highly correlated, which implies that the biological interpretation of a partial energy requirement was very dependent on the model used in its estimation. This dependency have probably contributed to the large variation in estimates of partial energy requirements found in the literature.

The two expressions of residual intake in production period 1 were very highly correlated. Consideration of carcass composition in calculating residual intake added very little information. Residual intake in production period 1 had low correlations to all estimates of partial energy requirements both phenotypically and genetically.

Correlations among traits in production period 2

The genetic and phenotypic correlations among partial energy requirements and residual intake in production period 2 (Table 24) were in most cases in reasonably good agreement with the corresponding estimates from production period 1. There were a few exceptions, for example the phenotypic correlation between model [1] requirements for growth and weight-dependent nonproductive use of energy was $-.668$ in

production period 1 but .141 in period 2. As in period 1, partial energy requirements from the same model were more closely correlated to each other than were similar requirements from different models.

Results involving residual intake in production period 2 also were similar to those in period 1. Again, consideration of body composition in computing residual intake did not add significant information. The phenotypic correlations between residual intake and the partial energy requirements were low. However, there were relatively strong genetic correlations between residual intake and model [1] partial energy requirements.

Table 24.

Genetic (Below Diagonal) and Phenotypic (Above Diagonal) Correlations Among Partial Energy Requirements and Residual Intake in Production Period 2 (200 LW to Slaughter).

Trait ^a	Model [1]			Model [2]				Model [3]	Model [4]
	BI1	BG1	BW1	BI2	BG2	BW2	BGW2	RES	RESC
Model [1]									
BI1	---	-.453	-.932	.349	-.187	-.317	.156	-.032	-.026
BG1	-.298	---	.141	-.179	.176	.112	-.104	.027	.012
BW1	-.901	-.110	---	-.327	.150	.322	-.141	.139	.134
Model [2]									
BI2	.550	-.340	.420	---	-.970	-.993	.965	.019	.016
BG2	-.439	.440	.258	-.977	---	.963	-.994	-.039	-.034
BW2	-.536	.263	.449	-.993	.956	---	-.970	.012	.014
BGW2	.440	-.387	-.284	.983	-.996	-.971	---	.028	.022
Model [3]									
RES	.196	-.556	.165	.232	-.337	-.133	.282	---	.970
Model [4]									
RESC	.080	-.467	.245	.048	-.152	.042	.102	.939	---

^aSee text in Materials and Methods for definition of traits.

Correlations between production periods 1 and 2

Phenotypic correlations between partial energy requirements or residual intake measured in production period 1 and the corresponding measures in period 2 were all low (Table 25). The genetic correlations were also relatively low and even negative for model [1] weight dependent nonproductive use of energy. Only model [2] energy requirements showed significant correlations at approximately .4 between the two periods. In comparison, Jensen et al. (1989) found genetic correlations between the two production periods at .56 and .58 for energy intake and feed conversion ratio, respectively.

Table 25.

Genetic and Phenotypic Correlations Among Partial Energy Requirements and Residual Intake in Production Period 1 and 2.

Trait ^a	Genetic correlation	Phenotypic correlation
Model [1]		
BI1	.076	.047
BG1	.284	.002
BW1	-.239	.045
Model [2]		
BI2	.395	.061
BG2	.404	.081
BW2	.397	.043
BGW2	.437	.072
Model [3]		
RES	.190	.098
Model [4]		
RESC	.248	.093

^aSee text in Materials and Methods for definition of traits.

Conclusions and Implications

It is well known that growth rate shows good responses to genetic selection and as a correlated effect the feed conversion ratio is reduced. As noted by Webster (1977), this reduction is mostly achieved by shortening the production period so that the accumulated maintenance requirement is reduced if animals are slaughtered at a constant weight. He also noted that selection for increased growth rate probably would have limited effect on the partial requirements for growth and maintenance. This study showed that it is possible to measure partial energy requirements for growth and nonproductive use of energy based on live animals. Hence it is possible to include selection for partial energy requirements in large scale programs for genetic improvement.

The partitioning of energy intake into productive and nonproductive use, by the relatively simple models used in this study, yielded three or four coefficients for each animal. Coefficients from the same model were highly correlated. Also, vectors of coefficients instead of single values must be used as comparison criteria. Choice of model for computing the partial energy requirements is important because coefficients with similar biological interpretation, but from different models, were not as highly correlated as were different coefficients within a given model. The reason for the high correlations between partial requirements within a model might be due to the arbitrary statistical partitioning of energy intake into productive and nonproductive use. This partitioning does not necessarily reflect specific physiological events but merely different aspects of the animal's energy conversion system.

Residual intake as a criterion of energetic efficiency is easier to use than the partial energy requirements in comparing animals. The heritability estimates for residual intake when the animals were fed ad libitum were slightly larger than those of partial energy requirements. Results indicate that residual intake can be calculated without correction for carcass composition. Another advantage of residual intake is that it did not require the biweekly body weights that were needed in the calculation of partial energy requirements, but only the total energy intake and weight at start and end of the production period.

Results obtained in the present investigation using simple models clearly showed considerable variation among young bulls in partial energy requirements and in residual intake. A significant proportion of this variance was due to additive genetic effects. More research is needed to find better models of energy conversion for individual animals in ways that are suitable for inclusion in selection programs. Such modeling work will require input from both physiologists and geneticists.

The utility of measuring partial energy requirements and residual intake of the young growing bulls on performance test is dependent on their genetic correlations to the total merit of the animals in the cattle production system. Total merit includes energy requirements of the young bulls themselves, but also the energy requirement of other groups of animals in the production system such as their female relatives used as replacement heifers and lactating cows. This is an area where much further research is needed. Some of this research

already is ongoing at several institutes. It is also unknown to what extent the parameters estimated for each animal in the approach used in the present investigation corresponds to energy chamber results.

CHAPTER 6

Performance Testing of Dual Purpose Bulls for Beef Traits.

Genetic and Phenotypic Correlations Between Partial
Energy Requirements and Beef Traits of Young Bulls and
The Milk Yield on Their Female Halfsibs

Introduction

Future selection programs for total merit in dual purpose cattle might need to include selection for a more efficient use of energy from feeds, which is a major cost factor in cattle production systems. Measuring feed intake on each of the animals in the population might be prohibitively expensive. However, feed intake measures can be obtained with relative ease during performance testing of future AI bulls for beef traits. Such performance tests are carried out in many European countries. The total utility of measuring feed intake during the performance test depends on the magnitude of the genetic correlation between feed intake measured on the growing bull and overall merit of cattle in the production system. Conventional measures of feed efficiency of growing animals, such as total feed intake or feed conversion ratio, are usually closely correlated to the level of production in terms of growth rate, because increasing growth rate reduces the time needed to reach a given slaughter weight, and therefore reduces the accumulated maintenance requirement. Feed conversion ratio or total feed intake are not necessarily related to the partial energy requirements for productive and nonproductive use of energy. An experiment, comprising 650 young bulls by 31 Holstein Friesian or Brown Swiss sires was conducted at the experiment station "EGTVED" in Denmark. The first group of traits measured on the young bulls included growth rate, total feed intake, feed conversion ratio, appetite, dressing percentage, carcass grading and carcass composition. The second group of traits measured on the young bulls included residual intake and estimates of partial requirements for productive

and nonproductive use of energy. Conventional beef production traits measured in this experiment were studied in Chapter 4 and residual intake and partial requirements for productive and nonproductive use of energy were studied in Chapter 5.

Milk yield is economically the most important trait in selection programs in most dual purpose cattle populations. The first objective of this chapter was to investigate genetic and phenotypic correlations between the two groups of traits measured in the experiment with young bulls. A second objective was to investigate the relationships between traits measured on the young bulls and the milkfat production of their female halfsibs.

Materials and Methods

Animals and data

Data on 650 bull calves, the progeny of 31 Holstein Friesian or Brown Swiss sires, were analyzed. The experiment consisted of two consecutive production periods for each young bull. Production period 1 was from initiation of experiment at the age of 28 d and until the animal reached 200 kg liveweight (LW), all animals were fed restricted at approximately 75% of expected ad libitum intake. In production period 2, from 200 kg LW and until slaughter, the animals were placed on four different treatments. The treatments were ad libitum feeding of rations differing in energy concentration by varying the proportion of roughage in the ration. Body weight was measured biweekly, feed intake was recorded as the sum of biweekly intakes and carcass composition and carcass grading were obtained at slaughter. A detailed

description of the experimental procedures was given in Chapters 4 and 5.

Energy intake was an important variable in our studies and needs to be defined clearly: Energy intake was expressed as net energy intake computed according to the Danish feed evaluation system based on Scandinavian feed units (SFU) (Møller et al., 1983). That system expresses feed energy content as net energy for lactation at a certain level of production. Another measure of energy intake is metabolizable energy (ME). Since the Danish net energy system assumes a nearly constant net energy efficiency the net energy intake can be converted to ME by $ME = 4.16 + 1.17 NE$ which gave an R^2 of .96 based on information given by Van de Honing and Alderman, (1988). Since this simple linear relationship exists the genetic parameters estimated were invariant to choice of feed evaluation system. Live weight and carcass weight were recorded at slaughter.

The following production traits were defined (Jensen et al. 1989a). In production period 1 (28 d to 200 kg LW):

WGT28	LW in kg at 28 d.
DG	Average daily gain in g.
EI	Total energy intake in mJ.
FCR	Feed conversion ratio, $EI/(\text{Total weight gain})$.
DEI	Daily energy intake (appetite), $EI/(\text{Days on test})$.
DMI	Total dry matter intake in kg.

Similar traits except WGT28 were defined in production period 2 from 200 kg LW to slaughter. At slaughter the following traits were obtained:

DRSPCT	Dressing percentage.
CARGRD	Carcass grade. Scale 1-10 with 10 being the best grade.
FATGRD	Fat grade. Scale 1-5 with 3 being the optimum value.
LEANPCT	Percent lean meat in carcass.
FATPCT	Percent fat in carcass.

EICG (Total energy intake)/(Total carcass gain).

Partial energy requirements for productive and nonproductive purposes were estimated for each individual animal in each production of the two periods separately (Jensen et al. 1989b). This was accomplished by a statistical partitioning of energy intake using two different models. The partial energy requirements estimated in the first model were:

- BI1 Baseline energy intake in mJ/d at zero metabolic weight and at zero growth rate.
- BG1 Partial energy requirement in mJ for one kg of body weight gain.
- BW1 Partial energy requirement in mJ/kg^{3/4}/d for weight dependent nonproductive use of energy.

The corresponding partial energy requirements estimated in the second model were defined similarly to the estimates from the first model and are denoted as BI2, BG2 and BW2. The second model also contained an interaction between partial energy requirements for growth and weight dependent nonproductive use of energy. This interaction component was denoted as BGW2. The second model was called the interaction model and the first model was called the no interaction model.

Residual intake was defined as total energy intake in a production period minus predicted intake in the same period. Two different estimates of residual intake were obtained for each young bull and were denoted as:

- RES Residual intake.
- RESC Residual intake corrected for carcass composition.

Since the feeding regime were different in the two production

periods, partial energy requirements and residual intake were estimated within production period for each animal and the estimates for each production period was treated as different traits. In tables a postscript P1 or P2 in the abbreviations for traits identifies production period.

Estimation of genetic parameters and breeding values

The genetic and phenotypic (co)variances were estimated for all traits by use of restricted maximum likelihood (REML) in a multitrait model including all traits simultaneously (Chapter 4).

Predicted breeding values for milkfat production of the 31 sires used in the experiment were obtained from the national sire evaluation program in Denmark. These predicted breeding values were correlated to the sire solutions of various traits from the multitrait model used on the experimental data. Such correlations are approximations to the genetic correlations between traits measured on young bulls in the experiment and milkfat production of their female halfsibs, and tend to be biased toward zero. However, no correction was made for this bias. The sires breeding value for milk fat production were denoted MILKFAT in tables.

Analysis of estimated (co)variance matrices

Estimation of genetic and phenotypic (co)variance matrices for many traits yield a plethora of variances and covariances. In order to draw inferences from such a mass of parameters the information needs to be further summarized, especially in this case where the traits analyzed were to be highly intercorrelated. To gain more insight into

the covariance structure of the traits analyzed, the estimated covariance matrices were subjected to a factor analysis.

The factor analysis extracted principal components followed by an orthogonal VARIMAX rotation for easy interpretation (SAS Institute Inc., 1985). The objective of the factor analysis is to identify a small number of uncorrelated and unobservable underlying variables called factors, such that the traits observed can be represented as linear combinations of the underlying factors. The decision on how many factors to extract is arbitrary. The rule followed was to include as many factors as necessary to account for at least 95% of total variance, which is the sum of the variances of the individual traits. The results were presented as factor loadings for each underlying factor. A factor loading is a correlation between the underlying factor and the observed trait in question. Only loadings with a numerical value greater than .3 were presented. A group of traits that all have large loadings on the same factor vary largely together as a group and are said to be controlled by the same underlying factor. The factors were ordered such that the first factor explained the largest proportion of total variance, the second factor the second largest proportion of total variance and so on. The theory behind factor analysis can be found in several texts on multivariate analysis, e.g., Morrison (1976). Application to animal breeding problems is scarce, but has recently been used by Sieber et al. (1988), Sieber et al. (1987) and Graf (1987).

Results and Discussion

Phenotypic factor analysis

The factor analysis was applied to the estimated phenotypic and genetic covariance matrices separately. The phenotypic factor loadings with a numerical value greater than .3 are shown in Table 26. A total of 14 phenotypic factors were necessary to explain 95% of the total phenotypic variance. This means that the 35 recorded traits can be expressed as linear combinations of 14 uncorrelated variables or factors. The most important phenotypic factor described average daily gain, feed conversion ratio, total energy intake, total dry matter intake, all measured in period 2, and energy intake per kg carcass gain. The second factor described interaction model energy requirements in production period 2. The energy requirements in production period 1 were similarly described by factor 3. These results indicate that the interaction model was superior to the no interaction model in describing variation among animals in partial energy requirements. Factor 4 described the production level in production period 1 similarly to factor 1 for production level in period 2. Factor 5 and 6 described appetite and residual intake in production period 1 and 2, respectively. The same factor described residual intake, whether or not carcass composition was used in estimating residual intake. This shows that appetite and residual intake was closely correlated and that there was variation in those traits that could not be explained by variation in either partial energy requirements or level of production in terms of growth rate.

Table 26.
Factor Loadings for Phenotypic Factors.

Trait ^a	Factors													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
WGT28	-	-	-.30	-	-	-	-	-	-	-.37	-	.80	-	-
DGP1	-	-	-	.96	-	-	-	-	-	-	-	-	-	-
EIP1	-	-	-	.93	-	-	-	-	-	-	-	-	-	-
FCRP1	-	-	-	.90	-	-	-	-	-	-	-	-	-	-
DEIP1	-	-	-	-	.86	-	-	-	-	-	-	.35	-	-
DMIP1	-	-	-	.92	-	-	-	-	-	-	-	-	-	-
DGP2	-.89	-	-	-	-	.30	-	-	-	-	-	-	-	-
EIP2	.93	-	-	-	-	-	-	-	-	-	-	-	-	-
FCRP2	.96	-	-	-	-	-	-	-	-	-	-	-	-	-
DEIP2	-	-	-	-	-	.92	-	-	-	-	-	-	-	-
DMIP2	.93	-	-	-	-	-	-	-	-	-	-	-	-	-
DRSPCT	-	-	-	-	-	-	-	-	-	-	.75	-.31	-	-
CARGRD	-	-	-	-	-	-	-	-	-	-	.86	-	-	-
FATGRD	-	-	-	-	-	-	-	-	-	-	-	-	-	.95
LEANPCT	-	-	-	-	-	-	-	-.93	-	-	-	-	-	-
FATPCT	-	-	-	-	-	-	-	.94	-	-	-	-	-	-
EICG	.87	-	-	-	-	-	-	-	-	-	-	-	-	-
BI1P1	-	-	-	-	-	-	-	-	-	.95	-	-	-	-
BG1P1	-	-	-	-	-	-	-	-	.99	-	-	-	-	-
BW1P1	-	-	-	-	-	-	-	-	-.72	-.64	-	-	-	-
BI2P1	-	-	.97	-	-	-	-	-	-	-	-	-	-	-
BG2P1	-	-	.95	-	-	-	-	-	-	-	-	-	-	-
BW2P1	-	-	.92	-	-	-	-	-	-	-	-	-	-	-
BGW2P1	-	-	.99	-	-	-	-	-	-	-	-	-	-	-
BI1P2	-	-	-	-	-	-	-.93	-	-	-	-	-	-	-
BG1P2	-	-	-	-	-	-	-	-	-	-	-	-	.97	-
BW1P2	-	-	-	-	-	-	.96	-	-	-	-	-	-	-
BI2P2	-	.98	-	-	-	-	-	-	-	-	-	-	-	-
BG2P2	-	.99	-	-	-	-	-	-	-	-	-	-	-	-
BW2P2	-	.98	-	-	-	-	-	-	-	-	-	-	-	-
BGW2P2	-	.99	-	-	-	-	-	-	-	-	-	-	-	-
RESP1	-	-	-	-	.96	-	-	-	-	-	-	-	-	-
RESCP1	-	-	-	-	.96	-	-	-	-	-	-	-	-	-
RESP2	-	-	-	-	-	.93	-	-	-	-	-	-	-	-
RESCP2	-	-	-	-	-	.93	-	-	-	-	-	-	-	-

^aSee text in Materials and Methods for definition of traits.

Factor 7 described baseline intake from the no interaction model in production period 2 and factor 13 described the partial energy requirement for growth also estimated in the no interaction model in period 2. Baseline intake and weight dependent nonproductive use of energy were strongly correlated, since they had loadings of similar absolute value but with opposite signs. Similarly, factor 9 and 10 combined described the no interaction model partial requirements in production period 1.

Factor 8 described carcass composition in terms of percent lean and percent fat in the carcass. It's interesting to note that carcass composition traits were not grouped together with either production traits or energy requirements, illustrating the low correlation between carcass composition and feed conversion ratio or partial energy requirements.

Factor 11 described carcass grading and dressing percentage and factor 12 and 14 described weight at 28 d and fat grading, respectively.

The factors describing partial energy requirements grouped traits according to model used in the estimation of requirements and the production period where requirements were measured. That was opposed to a prior expectation of grouping according to a "biological" interpretation, by grouping together say measures describing weight dependent nonproductive use of energy.

Genetic factor analysis

For the genetic covariance matrix a total of 10 factors were needed to describe 95% of total variance (Table 27). The genetic

factor analysis did not separate the traits analyzed into groups as clearly as did the phenotypic analysis. Instead, several traits were described by two or more factors.

Factor 1 on the genetic level described interaction model partial energy requirements in production period 2, but was also correlated to production level in terms of the growth rate in the same period and to carcass composition. Factor 2 described mainly production level in period 1, but was also correlated to production level in period 2. The third factor mainly described interaction model requirements in production period 1 but was also correlated to the appetite in the same period.

The genetic factors 4 and 5 described residual intake and appetite in production period 1 and 2 similarly to factor 5 and 6 on the phenotypic level. Factor 6 on the genetic level mainly described the carcass composition and fat grading. However, carcass grading was described by factor 9 and 10. Factor 7 mainly described model the no interaction model, partial energy requirements in production period 2, but were also correlated to the level of production in this period. Factor 8 and 9 mainly described no interaction model requirements in production period 1 and was also correlated to the carcass grade. Factor 10 described dressing percentage and was correlated to carcass grade.

Table 27.
Factor Loadings for Genetic Factors.

Trait ^a	Factors									
	1	2	3	4	5	6	7	8	9	10
WGT28	-	-.41	.68	-	-	-	-	.44	-	-
DGP1	-	-.95	-	-	-	-	-	-	-	-
EIP1	-	.92	-	-	-	-	-	-	-	-
FCRP1	-	.90	-	-	-	-	-	-	-	-
DEIP1	-	-.58	.58	-	.39	-	-	-	-	-
DMIP1	-	.92	-	-	-	-	-	-	-	-
DGP2	-.50	-.51	-	.41	-	-.32	-.38	-	-	-
EIP2	.65	.49	-	-	-	-	.37	-	-	-
FCRP2	.58	.57	-	-	-	-	.43	-	-	-
DEIP2	-	-	-	.92	-	-	-	-	-	-
DMIP2	.65	.48	-	-	.31	-	.38	-	-	-
DRSPCT	-	-	-	-	-	-	-	-	-	.92
CARGRD	-	-	-	-	-	-	-	-	.67	.49
FATGRD	-	-	-	-	-	.88	-	-	-	-
LEANPCT	-.47	-	-	-	-	-.75	-	-	-	-
FATPCT	.52	-	-	-	-	.71	-	-	-	-
EICG	.64	.59	-	-	-	-	-	-	-	-
BI1P1	-	-	-.34	-	-	-	-	-.76	-.42	-
BG1P1	-	-	-	-	-	-	-	-	.94	-
BW1P1	-	-	-	-	-	-	-	.89	-	-
BI2P1	-	-	-.91	-	-	-	-	-	-	-
BG2P1	-.32	-	.88	-	-	-	-	-	-	-
BW2P1	-	-	.92	-	-	-	-	-	-	-
BGW2P1	.31	-	-.91	-	-	-	-	-	-	-
BI1P2	.33	-	-	-	-	-	.83	-	-	-
BG1P2	-	-.33	-	-.58	-	-.35	-	-	-	.38
BW1P2	-	-	-	-	-	-	-.87	-	-	-
BI2P2	.93	-	-	-	-	-	-	-	-	-
BG2P2	-.92	-	-	-	-	-	-	-	-	-
BW2P2	-.92	-	-	-	-	-	-	-	-	-
BGW2P2	.93	-	-	-	-	-	-	-	-	-
RESP1	.36	-	-	-	.87	-	-	-	-	-
RESCP2	-	-	-	-	.89	-	-	-	-	-
RESP2	-	-	-	.93	-	-	-	-	-	-
RESCP2	-	-	-	.90	-	-.34	-	-	-	-
MILKFAT	-.39	-	-	-	.41	-	-	.61	-	-

^aSee text in Materials and Methods for definition of traits.

Production level was controlled by a combination of several factors, namely, factor 1, which mainly controlled the interaction model energy requirements in period 2; factor 2, which mainly controlled production level in period 1; and factor 7, which mainly controlled the nonproductive use of energy in production period 2.

The sires breeding value for milkfat production was also controlled by a combination of several factors: Factor 1, which controlled interaction model requirements in production period 2; factor 5, which controlled residual intake and appetite in period 1; and factor 8, which controlled the nonproductive use of energy in period 1. The fact that the sires breeding value for milkfat production was controlled by a combination of factors which mainly controlled different traits on the young bull might lead to a way of developing indirect selection criteria for milk yield based on a combination of traits measured on the growing bull during the performance test. It also shows that the genetic correlation between milk and beef production traits is complex.

Genetic correlations between production traits and partial energy requirements in production period 1

Genetic correlations between selected production traits and partial energy requirements from both models are shown in Table 28. The genetic correlations between production traits and no interaction model partial energy requirements were generally low. Most pronounced was an estimate at $-.365$ between daily feed intake and baseline intake. The interaction model partial energy requirements in production period 1 were much more closely correlated to the production traits than the

no interaction model requirements, except for feed conversion ratio which was essentially uncorrelated to interaction model energy requirements in period 1. The interaction model energy requirements in period 1 were genetically correlated to daily gain and appetite such that higher daily gain or higher appetite tends to be associated with higher requirements for growth and weight dependent nonproductive use of energy, but to a lower baseline intake and also a smaller interaction component. The interaction model energy requirement in period 1 were also genetically related to body composition in terms of dressing percentage and percent fat in the carcass, where the corresponding phenotypic correlations (not tabled) were essentially zero.

Table 28.

Genetic Correlations Between Selected Production Traits and Partial Energy Requirements in Production Period 1.

Trait ^a	DGP1	FCRP1	DEIP1	DRSPCT	FATPCT
BI1P1	-.128	-.032	-.365	-.013	.010
BG1P1	-.023	.021	.033	-.172	-.002
BW1P1	-.088	.214	.177	.213	.008
BI2P1	-.225	-.046	-.549	.140	.415
BG2P1	.224	-.003	.467	-.139	-.445
BW2P1	.154	.124	.515	-.149	-.422
BGW2P1	-.204	-.038	-.480	.160	.448

^aSee text in Materials and Methods for definition of traits.

Genetic correlations between production traits and partial energy requirement in production period 2

The estimates are shown in Table 29. The no interaction model energy requirements were genetically correlated to daily gain and feed

conversion ratio, such that selection for higher daily gain yields a lower baseline intake and a higher energy requirement for gain and weight dependent nonproductive use of energy. Results presented in Chapter 4 showed that selection on daily gain would improve feed conversion ratio. This is not contradictory to the results obtained here because the increased growth rate decreases the time needed to produce a young bull of a given weight so the accumulated maintenance requirement is reduced. The correlations between interaction model requirements and feed conversion ratio were similar to those between interaction model requirements and daily gain, but of opposite sign due to the definition of feed conversion ratio. The no interaction model energy requirements were genetically correlated to dressing percentage such that higher dressing percentage is associated with a higher baseline intake and a higher energy requirement for growth, but a lower weight dependent nonproductive use of energy. However, the interaction model requirements were not related to dressing percentage. The interaction model requirements in production period 2 were genetically correlated to daily gain, feed conversion ratio and percent fat in the carcass with absolute values of estimates in the range .5 to .6. The corresponding phenotypic correlations (not tabled) were all close to zero.

Table 29.

Genetic Correlations Between Selected Production Traits and Partial Energy Requirements in Production Period 2.

Trait ^a	DGP2	FCRP2	DEIP2	DRSPCT	FATPCT
BI1P2	-.605	.729	-.072	.190	.353
BG1P2	.156	-.384	-.434	.450	-.172
BW1P2	.641	-.616	.396	-.354	-.339
BI2P2	-.576	.696	-.072	.080	.535
BG2P2	.516	-.663	-.039	.137	-.503
BW2P2	.601	-.684	.165	.054	-.542
BCW2P2	-.533	.659	-.014	-.112	.506

^aSee text in Materials and Methods for definition of traits.

Correlations between production traits and residual intake

Table 30 and 31 shows phenotypic and genetic correlations between selected production traits and residual intake in production period 1 and 2, respectively. Even though residual intake in production period 1 and 2 were almost uncorrelated (Chapter 5), their relation to the production traits were similar in the two production periods.

Phenotypically, residual intake were not correlated to daily gain as expected due to the definition of residual intake. However, the genetic correlation were estimated at approximately .3. This was in accordance with the genetic correlation between daily gain and energy requirements, where high daily gain were associated with high energy requirements for growth and for weight dependent nonproductive use of energy. Residual intake and feed conversion ratio were positively correlated phenotypically, with estimates around .4, but the corresponding genetic correlation were close to zero. Appetite and residual intake were highly positively correlated, which seems to indicate that animals with a high appetite tends to use energy less

efficient than the average animal. This conclusion was supported by the correlation between daily intake and energy requirements. Phenotypic correlations between residual intake and body composition were low. If body composition was taken into account when calculating residual intake, the phenotypic correlation between residual intake and body composition was expected to be zero. The estimates of the corresponding genetic correlations were negative such that high breeding value for dressing percentage and percent fat in the carcass was associated with a low residual intake. This is in accordance with the results of the factor analysis showing that residual intake and appetite were controlled by the same underlying factor.

Table 30.

Phenotypic and Genetic Correlations Between Selected Production Traits and Residual Intake in Period 1.

Production trait ^a	Phenotypic correlation		Genetic correlation	
	RESP1	RESCP1	RESP1	RESCP1
DGP1	.003	.004	.319	.326
FCRP1	.465	.462	-.044	-.062
DEIP1	.783	.781	.598	.581
DRSPCT	-.034	.029	-.129	-.127
FATPCT	-.048	-.004	-.058	-.240

^aSee text in Materials and Methods for definition of traits.

Table 31.
Phenotypic and Genetic Correlations Between Selected Production Traits
and Residual Intake in Period 2.

Production trait ^a	Phenotypic correlation		Genetic correlation	
	RESP2	RESCP2	RESP2	RESCP2
DGP2	.015	.029	.234	.329
FCRP2	.396	.374	.160	.009
DEIP2	.808	.778	.886	.913
DRSPCT	.025	-.017	-.175	-.192
FATPCT	.221	.000	-.129	-.457

^aSee text in Materials and Methods for definition of traits.

*Correlations between breeding values of traits measured on male progeny
and breeding value for milkfat production*

Correlations between sires' breeding values for beef and energy requirement traits measured in the experiment and breeding values for milkfat production from the National population is shown in Table 32. As mentioned in the section Materials and Methods in this Chapter, these correlations were not true genetic correlations but only approximations. The correlation between daily gain and milk fat production was .36 and .18 for daily gain in production period 1 and 2, respectively. These results are in line with recent literature estimates of the genetic correlation between daily gain of a bull and the milk yield of his daughters, e.g. Van der Werf et al. (1987) who found an estimate at .21. Breeding values for milkfat production were uncorrelated to those for dressing percentage but highly negatively correlated to those for percent fat in the carcass with a correlation estimated at -.47. Also total energy intake and feed conversion ratio were negatively related to milk fat production. Note that in this

case a negative correlation is advantageous. Appetite had a positive correlation to milkfat production in production period 1 but a negative although nonsignificant correlation in period 2. This latter result is contradictory to the expectation of a positive correlation between appetite of the ad libitum fed bull and the milkfat production of female halfsibs, since intake might be a main limiting factor for milk production of the dairy cow during first lactation. The correlations between partial energy requirements in production period 1 and milkfat production were similar to those obtained for the partial energy requirements in period 2. High breeding value for milkfat production were associated with high energy requirements for growth and weight dependent nonproductive use of energy. This unfavorable relation is offset in correlations between milkfat production and feed conversion ratio or total energy intake because of the advantageous correlation to daily gain. Milkfat production and residual intake were positively correlated in production period 1 but negatively in period 2. However, none of these correlations were significantly different from zero.

Table 32.

Correlations Between Predicted Breeding Values of Sires for Milkfat Production and Predicted Breeding Values for Traits Measured on Male Progeny.

Trait ^a	Correlation ^b	Trait ^a	Correlation ^b
WGT28	.42	BI191	-.45
DGP1	.36	BG1P1	.21
EIP1	-.43	BW1P1	.33
FCRP1	-.28		
DEIP1	.33	BI2P1	-.37
DMIP1	-.40	BG2P1	-.31
		BW2P1	.33
DGP2	.18	BGW2P1	.28
EIP2	-.30		
FCRP2	-.26	BI1P2	-.14
DEIP2	-.16	BG1P2	.15
DMIP2	.12	BW1P2	.02
SLP	-.02	BI2P1	-.27
CARGRD	-.03	BG2P1	.28
FATGRD	.05	BW2P1	.24
LEANPCT	.33	BGW2P1	-.28
FATPCT	-.47		
EICG	-.27	RESP1	.15
		RESCP1	.22
		RESP2	-.34
		RESCP2	-.17

^aSee text in Materials and Methods for definition of traits.

^bIf the correlations, $|r| > .3$, then $P(r=0) < .10$.

Conclusions and Implications

The factor analysis proved to be a valuable tool in analyzing large correlation matrices to locate groups of traits that vary together as units. The results of this analysis showed that the partial energy requirements of individual bulls could best be estimated in a model that included requirements for baseline intake, weight dependent nonproductive use of energy, productive use of energy and an interaction between productive and nonproductive energy use. The partial energy requirements from this model were very strongly

intercorrelated and essentially controlled by a single underlying factor.

The results also indicated that there was no strong relation between carcass composition and partial energy requirements when observed within a relatively homogeneous population. This is opposed to a common assumption of a close relation between net energy requirements of growing cattle and the proportion of fat in the carcass (Robelin and Daenicke, 1980). The phenotypic correlations between daily gain and partial energy requirements were very low. However, there were genetic correlations, especially in production period 2, such that selection for increased daily gain would increase the partial energy requirement for growth and for weight dependent nonproductive use of energy, but decrease the baseline intake. Increased growth rate would also reduce the time needed for a young bull to reach a given weight and thus reduce the accumulated maintenance requirement.

Residual intake was closely related to appetite. Selection for increased appetite would increase residual intake and thus lead to less efficient animals. The results reported in Chapter 4 indicated that selection for increased appetite would lead to leaner animals at a constant weight.

The genetic correlations between daily gain and milk production in terms of milkfat were positive, with the highest correlation when daily gain was measured in production period 1. This correlation was carried over to total energy intake and feed conversion ratio due to the close relation between these traits and daily gain.

The genetic correlation between milkfat production and appetite

was positive for appetite in production period 1, but negative in period 2. This was in contrast to prior expectations, since feed intake is a major limiting factor for milk yield in the lactating cow.

Correlations were also found between milkfat production and partial energy requirements such that selection for increased milk production would tend to increase the energy requirement for weight gain and weight dependent nonproductive use of energy, but decrease the baseline feed intake.

The factor analysis showed that the sires' breeding values for milkfat production can partly be described by a combination of several factors measured on young bulls. It might lead to a way of developing indirect selection criteria for milk yield based on a performance test of potential AI bulls.

CHAPTER 7

Additive and Heterotic Effects of Immigration of Brown Swiss Genes Into the Red Dane Cattle Population on Production and Calving Traits

Introduction

Although crossbreeding programs are common in swine, broilers, and beef cattle such programs are rare in dairy or dual purpose cattle. However, experiments have shown significant heterosis effects in production traits (E.g. Christensen and Pedersen, 1988, Robison et al. 1981).

Many dual purpose or dairy populations throughout the world have initiated immigration programs especially with germ-plasm from North America. Import of genes to the Red Dane breed was initiated during the seventies, first with imports in a planned experiment reported by Christensen and Pedersen (1988), and then in a field study (Kim et al., 1984). Later large scale imports of genes primarily from American Brown Swiss have been made.

Immigration of genes can give rise to effects similar to what can be expected in a crossbreeding program. These effects are due to additive genetic differences between the breeds involved and heterosis. Heterosis is defined as the deviation of the performance of crosses from the expected performance based on the additive breeding value of the breeds involved. These deviations are mainly caused by intralocus interactions (Dominance) and interlocus interactions (Epistasis). Of epistatic effects, additive by additive interactions is generally thought to be the most important (Christensen and Pedersen, 1988, Kinghorn, 1980, Rendel 1953). Additive by additive epistatic effects are often expected to be negative. The reason being that selection in the parent breeds have favored gene complexes together instead of single genes. Such gene complexes are then broken down in crossbreeding

programs (Kinghorn, 1983). Such effects are therefore often termed recombination loss (Dickerson, 1969) or F_2 breakdown (Hill, 1982).

Crossbreeding programs or immigration programs in cattle almost invariably includes many types of crosses so that recombination effects might become important in predicting responses to such programs.

The main objective of the present investigation was to obtain crossbreeding effects between the Red Danish and the Brown Swiss breed for production and calving traits and to investigate whether recombination effects were of importance between the breeds involved. These effects are between breed genetic effects. Within breed effects, in terms of genetic parameters will be reported in a companion paper.

Materials and Methods

Definition of traits

Three production traits and three traits related to calving were analyzed. The production traits were 305-d milk production in kg (MLK), 305 d butterfat production in kg (FAT) and 305 d protein production in kg (PRT). All three traits were recorded during first lactation. The calving traits were calving difficulty (DIF), calf survival (SURV) and calf size (SIZE). The calving traits were recorded by individual farmers on all calvings reported after October 1984. Farmers were required to record SURV on all calvings while DIF and SIZE were optional. DIF was recorded on a scale from 1 to 4; with 1 being easy without help, 2 being easy with help, 3 being difficult but without veterinary assistance, and 4 being difficult with veterinary assistance. SURV was coded as 1 for stillborn, 2 born alive but dead

within 24 h, 3 born alive but dead after 24 h but before the first milk test day and, 4 was born alive and still alive on first test day after calving. SIZE was recorded as; 1 little, 2 somewhat below average, 3 somewhat above average, and 4 large.

Records

Pedigree information on 593,585 females born in the period from 1978 to 1988 inclusive was obtained from the Danish Dairy Records Processing Center. Production and calving records on cows freshening in the period 1980 to 1988 was obtained. Only records with known calving/lactation number was included. This yielded a total of 1,034,156 records. The production and calving records were merged with the pedigree file and all animals without production/calving records or with parity number greater than 3 were deleted. This procedure left a total of 858,464 records.

Three more steps of editing was done. In the first step, production records with MLK, FAT or PRT outside the intervals [1,500;12,500], [70;425] and [50;375] kg, respectively, were deleted. Other reasons for deletion were; days in milk less than 100-d, previous calving interval outside the interval [280;500] d, age at first calving outside the interval [19;42] months, sire of cow or sire of calf not registered. The editing steps mentioned above reduced the dataset to 565,090 records. In the next editing step, second and third parity records were deleted if one or more of the previous records were missing. In other words all previous records were required to be present for second and third lactation records. This rule reduced the dataset to 504,065 records. In the third step, every herd-year group,

sire of cow group, and sire of calf group was required to be represented with at least 5 records on first lactations/calvings. This rule was applied iteratively until all three rules were satisfied simultaneously. This finally left 308,382 records on 170,166 cows available for analysis. In this investigation, however, only records on first lactation/calving records were used. The amount of information on each animal varied. The number of records for each trait together with average and phenotypic SD are shown in Table 33.

Table 33.
No. of observations, mean, and phenotypic SD for traits analyzed.

Trait	Abbreviation	N	Mean	SD
Milk production, kg	MLK	146179	5370	737
Fat production, kg	FAT	146179	222.5	30.2
Protein production, kg	PRT	110331	186.7	26.2
Calving difficulty	DIF	74297	1.71	.73
Calf survival	SURV	103830	3.75	.77
Calf size	SIZE	80363	2.45	.72

For each record, the proportion of genes originating from different populations were known from pedigree information. Genes from a total of 10 different populations were present in data. However only native Red Dane (R) and Brown Swiss (B) had gene proportions of more than two percent. Therefore, all other breeds were combined into one group called Other (O). For each record gene proportions on five individuals were known; the calf born, the cow, the sire of calf, the sire of cow (Maternal grandsire of calf), and the dam of cow (Maternal granddam of calf).

Based on information on gene proportions, the expected amount of

heterozygosity in cow and offspring were computed, together with proportion of pairwise non-allelic genes that were of different breed origin. Examples of such coefficients involving R and B are shown for different types of crosses in Table 34.

Table 34.

Coefficients of crossbreeding parameters for cows and progeny in various crossbreeding systems.

Mating (Cow) x (Sire)	Cow				Progeny			
	P(R)	P(B)	$h_{R,B}^C$	$a_{R,B}^C$	P(R)	P(B)	$h_{R,B}^O$	$a_{R,B}^O$
RxR	1	0	0	0	1	0	0	0
BxB	0	1	0	0	0	1	0	0
<u>Change of breed from R to B</u>								
RxB	1	0	0	0	.5	.5	1.0	.5
[RxB]xB	.5	.5	1.0	.5	.25	.75	.5	.375
[(RxB)xB]xB	.25	.75	.5	.375	.125	.875	.25	.2188
[[(RxB)xB]xB]xB	.125	.875	.25	.2188	.0625	.9375	.125	.1172
<u>Change of breed from B to R</u>								
BxR	0	1	0	0	.5	.5	1.0	.5
[BxR]xR	.5	.5	1.0	.5	.75	.25	.5	.375
[(BxR)xR]xR	.75	.25	.5	.375	.875	.125	.25	.2188
[[(BxR)xR]xR]xR	.875	.125	.25	.2188	.9375	.0625	.125	.1172
<u>Continued breeding of crosses (Synthetic)</u>								
[RxB][RxB]	.5	.5	1.0	.5	.5	.5	.5	.5
[(RxB)(RxB)] ²	.5	.5	.5	.5	.5	.5	.5	.5
<u>Rotational crossing</u>								
RxB	1	0	0	0	.5	.5	1.0	.5
[RxB]xR	.5	.5	1.0	.5	.75	.25	.5	.375
[(RxB)xR]xB	.75	.25	.5	.375	.375	.625	.75	.4688
[[(RxB)xR]xB]xR	.375	.625	.75	.4688	.6875	.3125	.625	.4297

Models

Crossbreeding parameters have traditionally been estimated by least squares procedures. However, as shown by Kommender and Hoeschele (1989), the use of mixed models reduces the true SE of the estimates

obtained. Use of mixed models also should reduce biases resulting from using data from populations undergoing selection. The crossbreeding parameters to be estimated were between breed additive genetic differences, dominance effects and additive by additive epistatic effects. These effects were estimated both as effects of the cows genotype and of the offspring (calf) genotype.

The model for calving traits were:

$$\begin{aligned}
 y_{ijklmnopqr} = & \mu + \Sigma p_i^C A_i^C + \Sigma h_{ij}^C D_{ij}^C + \Sigma a_{ij}^C (AXA)_{ij}^C \\
 & + \Sigma p_i^O A_i^O + \Sigma h_{ij}^O D_{ij}^O + \Sigma a_{ij}^O (AXA)_{ij}^O \\
 & + hy_k + m_l + t_m + k_n \\
 & + g_o + s_{p(o)}^C + 1/2 s_{p(o)}^O + s_{r(o)}^O + e_{ijklmnopqr} \quad [1]
 \end{aligned}$$

Elements in the model with a superscript C (Cow) were considered an effect of cow genotype and similar effects with superscript O (Offspring) were considered and effect of the offspring genotype.

Definitions for the model are:

μ is an overall mean;

p_i^C is the proportion of genes in the cow from the i^{th} breed (R,B,O); A_i^C is the additive genetic effects of the i^{th} breed on the cow performance;

h_{ij}^C is the proportion of loci with one gene from breed i and one gene from breed j. Together the h_{ij}^C describes the degree of heterozygosity of the cow due to breed origin;

D_{ij}^C is the dominance effect on the cow due to within locus interactions of genes from breed i and j;

a_{ij}^C is the proportion of pairwise non-allelic genes in the cow that were of different breed origin;

$(AXA)_{ij}^C$ is the additive by additive recombination effects between breed i and j ;

Similar crossbreeding effects were defined for the progeny genotype, all denoted with superscript 0.

hy_k is the effect of the k^{th} herd-year;

m_1 is the effect of the 1^{th} month of calving;

t_m is the effect of the m^{th} age group at first calving, with ages grouped in one month intervals;

k_n is the effect of the n^{th} sex of calf.

g_o is the effect of the o^{th} sire group;

$s_{p(o)}^C$ is the effect of the p^{th} sire of cow nested within the o^{th} sire group;

$s_{p(o)}^O$ is the effect of the p^{th} maternal grandsire of offspring nested within the o^{th} sire group.

$s_{q(o)}^O$ is the effect of the q^{th} sire of calf nested within the o^{th} sire group.

$e_{ijklmnopqr}$ was a residual.

All effects except $s_{p(o)}^C$, $1/2s_{p(o)}^O$, $s_{q(o)}^O$, and $e_{ijklmnopqr}$ were considered fixed. Model [1] was similar for production traits except that k_n was replaced with d_n , where d_n was the effect of the n^{th} group of days in milk, grouped in 10 d intervals. Also, $1/2s_{p(o)}^O$ and $s_{q(o)}^O$ were dropped from the model. The proportion of R genes in cows and offspring was not included in the model. The reason was that all gene proportions sum to 1.0 and thus creating a linear dependence. The proportion of R genes were therefore dropped from the model as a constraint. This means that all effects are expressed relative to

native Red Dane genes.

Reduced models were also run. In model [2] all recombination effects were left out. Model [3] and [4] were run only on production traits and did not include effects of calf genotype. Model [3] included recombination effects, whereas these effects were left out in model [4]. The reasons for running models without recombination effects were that several authors (e.g. Cunningham, 1987) maintains that crossbreeding effects can be sufficiently described using models including only additive and dominance effects.

The models took additive genetic relationships due to sires and maternal grandsires into account. Genetic parameters used to obtain variances of s^C , s^O and e , and the covariance between s^C and s^O , where applicable, were estimated from the same data and will be reported in Chapter 8.

The models lead to systems of equations of order from 10,614 to 16,661 to be solved, so these systems had to be solved iteratively. SE of estimates are functions of diagonal elements of the inverse of the coefficient matrix and could therefore not be obtained. Tests of various hypothesis were therefore instead obtained from least square analysis with similar models, but with effects of sires ignored.

Results and Discussion

Gene and Loci Fractions

The average proportion of genes immigrated into R from B and O are shown in Table 35 for genes in both cows and offspring. The average proportion of B genes in cows were .101, which increased to .137 in the progeny, a reflection of a continuing immigration of genes from B over

time since offspring of course were born later than cows. The proportion of genes other than R and $B_1(O)_1$ were 2-3% in both cows and progeny. In order to estimate crossbreeding effects, there must be variation in the different gene proportions. That such variation indeed were present is illustrated by the SD of the gene proportion and is also shown in Table 35.

Table 35.

Average and SD of various proportions of genes and loci in cows and progeny and correlation between cow and progeny proportions.

	Average	SD	Corr. Cow/ Progeny
Proportion in cows			
Genes from B	.101	.145	.979
Genes from O	.021	.071	.961
Loci with genes from both R & B	.184	.258	.513
Loci with genes from both R & O	.038	.132	.363
Loci with genes from both B & O	.004	.025	.282
Pairwise nonallelic genes from R & B	.138	.182	.967
Pairwise nonallelic genes from R & O	.030	.096	.963
Pairwise nonallelic genes from B & O	.002	.013	.972
Proportions in progeny			
Genes from B	.137	.203	
Genes from O	.027	.198	
Loci with genes from both R & B	.220	.234	
Loci with genes from both R & O	.053	.139	
Loci with genes from both B & O	.011	.040	
Pairwise nonallelic genes from R & B	.153	.208	
Pairwise nonallelic genes from R & O	.031	.108	
Pairwise nonallelic genes from B & O	.002	.010	

The amount of dominance effects expressed by an individual is proportional to the fraction of loci with genes from two breeds. In cows, this proportion for (R,B) dominance interactions was on average .184 for cows and .220 for progeny with SD .258 and .203, respectively.

This means that .184 and .220 of total dominance effects were expected to be present in the overall average. The SD shows that there were considerable variation among animals, both cows and progeny, in the expected degree of dominance expressions. Finally, the degree of additive by additive recombination effects is expected to be proportional to the fraction of pairwise non-allelic genes descending from two breeds. For R and B recombination effects this fraction was on average .138 for cows and .153 for offspring with SD .182 and .208, respectively. The fraction of loci with genes descending from two breeds or the fraction of pairwise nonallelic genes from two breeds were all small if not both of the R and B breeds were involved.

The 16 proportions of genes and loci computed for each cow/calf pair, with averages shown in Table 35, were not independent of each other. An optimum design for estimating crossbreeding effects would have these effects orthogonal to each other. Such designs usually cannot be obtained, even in planned experiments (Robison, 1981) and certainly not when field data are used. The lack of orthogonality is illustrated in Table 35 by the correlation between gene/loci proportions for similar effects in cows and offspring. It is seen that in many cases these proportions were highly correlated as were also several other fractions. These correlations mean that the partial effect of including/excluding a particular crossbreeding effect in the model might be expected to be small even though interpretation of an estimate might be dependent of what other effects that were included in the model simultaneously. Biases in various estimates of crossbreeding parameters were shown for various designs by Hill (1982).

Significance of Crossbreeding Effects

Levels of significance for partial F-tests in model [1] associated with contrasts for various crossbreeding effects are shown in Table 36. For production traits, all contrasts except effects of dominance in progeny were highly significant. That the effect of progeny genotype on subsequent production was significant was somewhat surprising. The results in Table 36 also shows that both cow and progeny recombination effects were highly significant. That the genotype of offspring might influence subsequent production has been indicated on a within breed basis in investigations by Skjervold and Fimland (1975).

For calving traits, the only significant individual effect were effect of dominance in progeny for DIF and SIZE. However, the combined tests shows significant additive, dominance and recombination effects for both DIF and SIZE. The reason is that the different effect are highly correlated as explained in the previous section. For SURV the overall cow effect was significant even though none of the individual effects were significant.

Most models used to estimate crossbreeding effects only include additive and dominance effects (Cunningham, 1987). The models were therefore run without recombination effects included. As can be seen in Table 36 R^2 -values were hardly reduced by leaving out the recombination effects even though results from model [1] showed that these effects were highly significant. Similar effects were seen for production traits when leaving out effect of progeny genotype. One reason for this is that the various effects are highly correlated, so that estimates of remaining effects may change considerably when some effects are left

out of the model.

Table 36.

Levels of significance for crossbreeding effects in LS-model [1].

Effect	MLK	FAT	PRT	DIF	SURV	SIZE
Cow Additive	.0001	.1308	.0038	.4255	.5647	.2832
Cow Dominance	.0001	.0001	.0001	.3132	.7815	.2377
Cow A x A	.0001	.0474	.0010	.4649	.6727	.1696
Progeny Additive	.0001	.0001	.0002	.5806	.4940	.3342
Progeny Dominance	.3497	.8484	.0031	.0001	.9941	.0001
Progeny A x A	.0001	.0001	.0001	.6490	.6980	.1433

Overall Additive	.0001	.0001	.0006	.1224	.1502	.0087
Overall Dominance	.0001	.0003	.0001	.0001	.9789	.0001
Overall A x A	.0001	.0001	.0001	.0001	.7899	.0179
Overall Cow	.0001	.0001	.0001	.0005	.0002	.2621
Overall Progeny	.0001	.0001	.0001	.0001	.6059	.0001

R2 - Model [1]	.651	.663	.677	.219	.098	.213
R2 - Model [2]	.650	.663	.677	.218	.098	.212
R2 - Model [3]	.650	.662	.677			
R2 - Model [4]	.650	.662	.676			

Crossbreeding Effects

The estimates of crossbreeding effects from model [1] are shown in Table 37. Of particular interest in this model is the recombination effects. For production traits the effect of recombination in the cows own genotype were large and negative, with estimates of -1328, -32.8 and -53.6 kg, for MLK, FAT and PRT, respectively. This, however was to some degree counteracted by a positive effect of recombination in the genotype of calves, with estimates of 611, 17.3 and 22.5 kg MLK, FAT and PRT, respectively. In general, most estimates for production traits was surprisingly large, and similar effects of cow and progeny genotype were generally opposite in sign. Whether these effects have an underlying physiological explanation or are merely an artifact of the

model cannot be determined from the present data.

For calving traits, positive recombination effects for cow genotype were found for DIF and SURV, but negative effects were found for SIZE. The recombination effects of cow genotype were small for SURV and SIZE, but for DIF the recombination effects of cow and offspring genotype were of the same magnitude although opposite in sign.

Table 37.
Crossbreeding parameters estimated in Model [1].

Effect	MLK	FAT	PRT	DIF	SURV	SIZE
A_B^C	1065	14.3	40.5	-.44	.08	.22
A_O^C	-815	-18.3	1.2	-.62	-.42	.90
$D_{R,B}^C$	848	26.1	32.0	.02	-.06	.09
$D_{R,O}^C$	46	9.2	2.2	-.53	.21	.27
$D_{B,O}^C$	1369	85.9	40.2	-.62	-.30	1.36
$AxAR_{R,B}^C$	-1328	-32.8	-53.6	.09	.19	-.16
$AxAR_{R,O}^C$	1289	19.0	10.4	1.19	-.09	-.67
$AxAB_{B,O}^C$	350	-11.2	12.5	1.11	.82	-4.37
A_B^O	-850	-20.1	-29.0	.11	.04	-.11
A_O^O	1238	23.0	-14.8	.41	.20	-.63
$D_{R,B}^O$	-2	.0	.0	.06	.10	.13
$D_{R,O}^O$	20	.3	2.7	.08	.01	.09
$D_{B,O}^O$	-67	-3.0	-.9	.01	.07	.19
$AxAR_{R,B}^O$	611	17.3	22.5	-.10	.03	.0
$AxAR_{R,O}^O$	-1150	-23.6	2.9	-.29	-.11	.38
$AxAB_{B,O}^O$	-3063	-173.7	-91.7	-.04	-.20	2.10

The estimates of crossbreeding parameters from model [2] with recombination effects dropped are shown in Table 38. For production traits, estimates of remaining crossbreeding parameters changed dramatically when recombination effects were deleted from the model. The effects of offspring genotype is now relatively small and do not counteract effects of cow genotype. The model indicates that B is inferior to R in production. A direct comparison of breeds and various crosses will be discussed in a later section.

For calving traits results shows that B has considerable less calving difficulty than R with an estimate of $-.37$ units in additive genetic difference in maternal calving ability. For direct effects (calf genotype) the effect is $.06$, e.g. an increase in calving difficulty. That means that B cows calve easily, but B calves tend to have difficult births.

Similar trends can be seen in SURV. B cows give birth to calves with a higher survival rate, but B calves tend to have a lower survival rate. Both cow and calf dominance effects tended to improve survival. For SIZE, B cows give birth to larger calves, whereas there were no direct additive effect on calf size. There were no maternal dominance effects on calf size, but a positive effect on calf size from dominance in the calf (Direct effect).

Table 38.
Crossbreeding parameters estimated in Model [2].

Effect	MLK	FAT	PRT	DIF	SURV	SIZE
A_B^C	-60	-13.6	-4.1	-.37	.26	.07
A_O^C	304	.7	8.9	.33	-.44	.24
$D_{R,B}^C$	409	16.2	13.6	.02	.05	.01
$D_{R,O}^C$	242	9.8	7.8	-.04	.12	.09
$D_{B,O}^C$	419	15.5	11.7	-.07	.04	-.03
A_B^O	-83	-.2	.2	.06	-.07	-.01
A_O^O	112	-1.0	-15.2	-.06	.11	-.14
$D_{R,B}^O$	-3	.0	.0	.06	.10	.13
$D_{B,O}^O$	19	.3	2.7	.08	.01	.09
$D_{B,O}^O$	-60	-3.1	-.9	.01	.06	.19

Crossbreeding effects on production traits estimated in model [3] and model [4] with effects of calf genotype dropped in shown in Table 39. Again results show that B are inferior to R in production traits, with an estimate of the additive genetic difference between R and B of 12-14 kg butterfat in favor of R. Recombination effects in this model was negative, as expected, and with estimates of -135, -2.6 and -14.5 for MLK, FAT and PRT respectively. Results from model [3] and [4] also showed estimates of dominance effects on production traits ranging from 7.2% to 10.9%.

Table 39.

Crossbreeding parameters for production traits estimated in Model [3] and Model [4].

Effect	Model [3]			Model [4]		
	MLK	FAT	PRT	MLK	FAT	PRT
A_B^C	-28	-12.0	4.6	-114	-13.8	-4.1
A_O^C	45	-2.3	-6.7	359	-.4	1.8
$D_{R,B}^C$	461	17.3	20.4	398	16.1	13.6
$D_{R,O}^C$	-19	7.5	1.2	256	9.9	7.4
$D_{B,O}^C$	1010	79.2	28.3	407	15.3	12.1
$A \times A_{R,B}^C$	-135	-2.6	-14.5	---	----	----
$A \times A_{R,O}^C$	577	4.6	13.2	---	----	----
$A \times A_{B,O}^C$	-1246	-128.1	-32.5	---	----	----

Heterosis Effects

Heterosis expressed as the expected performance of F_1 crosses deviated from the average of the R and B purebreds is equal to the dominance effects between R and B plus half the recombination effects between the two breeds. The heterosis expected in F_1 animals is summarized in Table 40 for estimates from all models.

For production traits estimates from models [2], [3] and [4] are all in very close agreement. Results from model [2] indicates that effects of calf dominance on subsequent production of the cow seems to be small. Estimates of F_1 heterosis, expressed in percent of the overall average, range from 7.1 to 7.6% when estimates from model [2], [3] and [4] are considered. Individual estimates from model [1] are lower, but the effect of heterosis in cow and calf are to some degree

additive and of the same sign. The exact degree of F_1 heterosis estimated in model [1] then depends on both the cow and the calf genotype, and will be discussed in a later section where various breeding systems are compared.

Estimates of heterosis estimates of 7.1 to 7.6% are in good agreement with several literature estimates. E.g. Robison et al. (1981), who found estimates of 5.1%, Rincon et al. (1982) with estimates of 5.9% , Hollon et al. (1969) who found an estimate of 8.7% and Christensen and Pedersen, (1988) who found and estimate of 6.7%. All the above results were estimated in models that ignored recombination effects.

Both models show that calving difficulty increases in F_1 animals, both as a function of cow genotype and of offspring genotype. This is in contrast to most literature reports that shows increased calving difficulty when the offspring is crossbred, but a decrease in calving difficulty when the cow is crossbred. E.g. Vesely et al. (1986), Kim and Petersen (1985), and Christensen and Pedersen, (1988).

For calf survival estimates from model [1] and [2] are in good agreement. (Table 40). Heterosis in both cow and calf have a positive effect on calf survival. This again is in contrast to the literature cited above, where most authors found that crossbreed offspring had lower survival but that but that crossbreed cows increased the survival rate of the offspring.

Calf size were not influenced by heterosis in the cow, but crossbreed progeny were larger. The agreement between model [1] and model [2] was very good for calf size.

Table 40.
Estimates of F_1 Heterosis from different models.

	MLK	FAT	PRT	DIF	SURV	SIZE
Model [1]						
Cow Genotype	185	9.7	5.2	.07	.04	.01
Calf Genotype	304	8.7	11.3	.01	.12	.13
Model [2]						
Cow Genotype	409	16.2	13.6	.02	.05	.01
Calf Genotype	-3	.0	.0	.06	.10	.13
Model [3]						
Cow Genotype	394	16.0	13.2	---	---	---
Model [4]						
Cow Genotype	398	16.1	13.6	---	---	---

Response to Various Breeding Systems

As discussed in the previous section, parameters estimated in different models vary considerably. To gain a better understanding of various effects, responses to different breeding systems were estimated. The systems compared were: purebred R, purebred B, change of breed from R to B by continued use of B bulls, change of breed from B to R by continued use of R bulls. A synthetic breed consisting of 50% genes from each of R and B and created by mating F_1 animals and so on, and finally a system using rotational crossing by using purebred B and R bulls alternately in each generation starting out from R cows. The coefficients needed for each program in the initial generations are shown in Table 34.

The only production trait discussed is FAT, whereas all calving traits are discussed. Estimated responses in FAT estimated in all four models is shown in Table 41. All results are shown relative to purebred R which always are zero. Estimated responses from models [2], [3] and

[4] all show good agreement, whereas model [1] differs in several instances. All models predict lower performance of purebred B cows with estimates of a 12-14 kg lower butterfat production of B cows estimated in models [2], [3] and [4]. Model [1] only estimates a 6 kg genetic inferiority of the B breed in comparison with R. The reason for this can be seen in the system of change of breed from B to R. In generation 0, when the cow is purebred B, but carries an F_1 offspring, model [1] estimates a large positive effect on subsequent production when a cow with B genes carry an F_1 calf. On the other hand as seen in generation 0 of the system of changing breed from R to B, model [1] predicts a slight decrease in production when an R cow carries F_1 progeny. Change of breed from R to B would increase production in generation 1 with 8-10 kg FAT in first lactation. In subsequent generations production would gradually regress back to the B purebred level, as dominance effects are lost and additive genetic effects of B becomes more important.

Change of breed from B to R would yield even larger increases in the production of F_1 cows as compared to generation 0 cows. Model [2], [3] and [4] estimates increases of 22-23 kg FAT. Model [1] estimates much smaller increases due to the large positive effect of B cows carrying F_1 progeny. I.e. B cows would show a large increase already in generation 0. In later generations production gradually approaches the level of purebred R performance.

The use of a synthetic breed with 50% genes from each breed shows a large positive effect of 10-16 kg FAT of the F_1 cows. In generation 2 and all subsequent generations production regresses back to a level

slightly above that of purebred R cows.

The last crossbreeding system investigated was a two-breed rotational system with alternate use of purebred bulls. Again estimates from model [2], [3] and [4] are very similar, with large positive effects in early generations, similar to the effects seen when changing breed. In later generations production declines to a level 3.4 kg FAT above that of purebred R cows, but 16-17 kg FAT above that of purebred B cows. Estimates of effects of rotational crossing in model [1] differs again considerable from the other models, due to the large positive effect when a cow with a large proportion of B genes is mated to an R bull.

Responses in calving traits, estimated in models [1] and [2] in the same breeding systems are shown in Table 42. For DIF both models predict a genetic difference between R and B of .31 to .33 units in favor of B. This corresponds to .42 to .45 phenotypic standard deviations.

In the system of change of breed from R to B the estimate in generation 0 shows that when an R cow carries an F_1 offspring DIF is increased by .07 to .09 and then reduces in subsequent generations when the cow either becomes crossbreed or carries a large proportion of B genes. In the reciprocal system of changing breed from B to R it is seen that B cows carrying F_1 offspring do not experience increased DIF. Model [1] even predicts an improvement in DIF, -.38 versus -.33 for the purebred B cow carrying B offspring.

Table 41.
Response in FAT from various crossbreeding systems.

Mating		Model			
(Cow) x (Sire)	Gen	[1]	[2]	[3]	[4]
Purebred R	---	0	0	0	0
Purebred B	---	-5.8	-13.8	-12.0	-13.8
<u>Change of breed from R to B</u>					
RxB	0	-1.4	-.1	0.0	0.0
[RxB]xB	1	8.3	9.3	10.0	9.2
[(RxB)xB]xB	2	-2.3	-2.3	-1.3	-2.3
[((RxB)xB)xB]xB	3	-5.0	-8.3	-6.7	-8.1
<u>Change of breed from B to R</u>					
BxR	0	12.9	-13.7	-12.0	-13.8
[BxR]xR	1	18.3	9.4	10.0	9.2
[(BxR)xR]xR	2	5.6	4.7	4.6	4.6
[((BxR)xR)xR]xR	3	1.9	2.3	2.3	2.3
<u>Continued breeding of crosses (Synthetic)</u>					
RxB	0	-1.4	-.1	0.0	0.0
[RxB][RxB]	1	15.5	9.3	10.0	9.2
[(RxB)(RxB)] ²	2	2.4	1.2	1.4	1.2
<u>Rotational crossing</u>					
RxB	0	-1.4	-.1	0.0	0.0
[RxB]xR	1	18.3	9.4	10.0	9.2
[(RxB)xR]xB	2	-.1	4.6	4.7	4.6
[((RxB)xR)xB]xR	3	14.3	3.6	4.3	3.5

Estimated effects on SURV from the various breeding programs is also shown in Table 9 for both models [1] and [2]. Results shows that B has a higher survival rate than R with a difference of .12 to .19 corresponding to .16 to .25 phenotypic SD. All crossbreeding programs shows positive responses in early generations. Of course the system of changing breed from B to R will eventually revert back to the purebred R level. The largest discrepancies between estimated responses from model [1] and [2] is in the rotational system. This indicates that recombination effects might be of some importance for SURV.

Finally, effects of the breeding systems in SIZE is shown in Table 10. Purebred B calves are .06 to .11 units larger than R calves, corresponding to .08 to .15 phenotypic standard deviation units. From the systems of change of breed it is seen that if a cow carries a crossbreed progeny SIZE is increased considerably, whereas effects in later generations are smaller.

Table 42.

Response in calving traits from various crossbreeding systems depending on estimation model.

Mating		DIF, Model		SURV, Model		SIZE, Model	
(Cow) x (Sire)	Gen	[1]	[2]	[1]	[2]	[1]	[2]
Purebred R	---	.00	.00	.00	.00	.00	.00
Purebred B	---	-.33	-.31	.12	.19	.11	.06
<u>Change of breed from R to B</u>							
RxB	0	.07	.09	.14	.07	.08	.13
[RxB]xB	1	-.08	-.09	.17	.18	.10	.10
[(RxB)xB]xB	2	-.20	-.20	.17	.18	.09	.08
[((RxB)xB)xB]xB	3	-.26	-.26	.15	.19	.09	.07
<u>Change of breed from B to R</u>							
BxR	0	-.38	-.28	.22	.33	.30	.20
[BxR]xR	1	-.14	-.12	.15	.21	.16	.11
[(BxR)xR]xR	2	-.06	-.06	.10	.11	.06	.05
[((BxR)xR)xR]xR	3	-.03	-.03	.06	.05	.02	.03
<u>Continued breeding of crosses (Synthetic)</u>							
RxB	0	.07	.09	.14	.07	.08	.13
[RxB][RxB]	1	-.12	-.11	.16	.20	.13	.11
[(RxB)(RxB)] ²	2	-.13	-.12	.19	.17	.09	.10
<u>Rotational crossing</u>							
RxB	0	.07	.09	.14	.07	.08	.13
[RxB]xR	1	-.14	-.12	.15	.21	.16	.11
[(RxB)xR]xB	2	.00	.00	.18	.12	.07	.11
[((RxB)xR)xB]xR	3	-.19	-.16	.18	.24	.18	.13

Conclusions

For production traits, analysis indicate some effects on calf genotype on the subsequent production of the cow. This was especially so if recombination effects was included in the model. Whether these effects was due to underlying physiological interactions or was an artifact of the model could not be determined from the present data. If recombination effects were removed from the model there were no effects of calf genotype on the subsequent production of the cow. Models without effects of offspring genotype indicated recombination effects from -1.1% to -7.7% with small effects on MLK and FAT but relatively large effect on PRT.

Most of the models used on production traits yielded F_1 heterosis of 7.1 to 7.7%. Such an effect should therefore be beneficial in crossbreeding programs. Positive heterosis, however, was to some degree counteracted by a large genetic difference between R and B in favor of R, with R being 2.6 to 6.2% superior to R in FAT. The benefits to R breeders in production traits is therefore minimal after the initial generations where the cow expresses large levels of heterosis. For B breeders, however there seems to be a large advantage in production traits to be gained from introducing R genes into their population.

For calving traits results showed a large genetic difference in favor of B for DIF and SURV. Heterosis effects tend to increase DIF, both when the cow is crossbred and when the calf is crossbred. However for calf survival both these effects were positive. Heterosis effects on DIF and SURV were small compared to the additive genetic difference between R and B.

The overall advantage of crossbreeding to R breeders is small. The easiest breeding system for R breeders to implement seems to be the creation of a synthetic based on R and B genes, which is also what happens in practice (Table 35). This system would also reduce calving difficulty and improve calf survival.

For B breeders there would be a large advantage in production by introducing R genes into their population. However, this would have some negative effects on calving difficulty and calf survival.

CHAPTER 8

Genetic Parameters of Dairy Production and Calving Traits in Danish Red Cattle

Introduction

Simultaneous selection for several characteristics requires knowledge of genetic parameters in terms of SD, heritabilities and phenotypic and genetic correlations. In most cattle populations the major selection emphasis has been on milk production traits. However, several other traits are of economic importance, for example dystocia and stillbirth. Philipsson (1976) assessed the cost related to the dystocia-stillbirth complex. He found costs associated with increased dystocia and stillbirth amounting to more than 50% of calf value per case of dystocia. These costs, however, are very dependent on calf price so it is difficult to translate such calculations into other economic conditions. Nevertheless, his results indicated that selection for decreased dystocia and stillbirth might be worthwhile. Result of evaluating sires for dystocia and stillbirth maybe more important from another standpoint, that is to find sires suitable for heifer matings, where the dystocia and stillbirth problems are most prevalent. Meijering (1984) gave an excellent review of current knowledge about the dystocia and stillbirth complex in cattle.

Genetic variation in dystocia and stillbirth stems from both the genotype of the cow (maternal effects) and the genotype of the calf (direct effects) and there may exist a genetic correlation between these effects (Van Vleck, 1978). This complicates the estimation of genetic parameters of maternal and direct effects on calving traits. In order to separate these effects, models that simultaneously include effects of both dam and progeny genotype must be used.

The objective of this study was to obtain genetic parameters of production and calving traits in Danish Red Cattle and to study the genetic and phenotypic relationships between these traits.

Materials and Methods

Definition of traits

Three production traits and three traits related to calving were analyzed. The production traits were 305 d milk production in kg (MLK), 305 d butterfat production in kg (FAT) and 305 d protein production in kg (PRT). All three traits were lactation totals in the first parity. The calving traits were calving difficulty (DIF), calf survival (SURV) and calf size (SIZE). The calving traits were recorded by individual farmers on all calvings. SURV must be recorded on all calvings while DIF and SIZE were optional. DIF was recorded on a scale from 1 to 4; with 1 being easy without help, 2 being easy with help, 3 being difficult but without veterinary assistance, and 4 being difficult with veterinary assistance. SURV was coded as 1 for stillborn, 2 for born alive but dead within 24 h, 3 for born alive but dead after 24 h but before the first milk test day and, 4 for born alive and still alive on first test day after calving. SIZE was recorded as; 1 for little, 2 for somewhat below average, 3 for somewhat above average, and 4 for large.

Records

A total of 170,166 cow-calf pairs were available for analysis. A complete description of editing procedures was given in Chapter 7. The number of observations on each individual trait or combination of two

traits are given in Table 43.

Table 43.

Number of observations for each trait (on diagonal) and combination of two traits (off diagonal).

	MLK	FAT	PRT	DIF	SURV	SIZE
Milk prod. (MLK)	146,179					
Fat prod. (FAT)	146,179	149,179				
Protein prod. (PRT)	110,331	110,331	110,331			
Calf diff. (DIF)	55,829	55,829	55,589	74,297		
Calf survival (SURV)	80,456	80,456	79,525	73,968	103,830	
Calve size (SIZE)	61,121	61,121	60,595	70,374	80,160	80,363

Pre correction of data

As reported in chapter 7, the Danish Red Cattle population contains a large proportion of genes originating from American Brown Swiss. Therefore, genetic effects of both additive genetic differences between the breeds involved and heterosis are important. For calving traits these effects were of importance in the genotype of the cow (maternal effects) as well as that in the genotype of the calf (direct effects). Other effects of importance was herd-year, month of calving, age at calving, days in milk, sex of calf, and random effects due to sire of cow and sire of calf. Thus, a total of 14 factors were included in the model.

In the estimation of (co)variance components for multiple traits, the mixed model equations needs to be constructed many times when iterative estimation procedures are used. For models with many factors this became prohibitively expensive. Data were therefore precorrected for all fixed effects, with the exception of herd-year effects, which had by far the largest number of levels. Additive correction factors

estimated from model [1] of Chapter 7 were used.

Models and sampling of data

The dataset included 1650 bulls that were either sire of cow or sire of calf. All traits and all sires could not be included in the analysis simultaneously due to computer constraints. Samples of data were therefore taken. Each sample was constructed by first choosing 300 bulls at random and then selecting those records with both sire of cow and sire of calf appearing in the sample of 300 bulls. This sampling process was repeated eight times, and each sample was analyzed separately. To further reduce computational cost, only two or three traits were analyzed simultaneously. A total of seven analyses were performed on each sample. FAT was included in each of the trait combinations, while MLK and PRT was only analyzed together with FAT but not together with any of the calving traits. Analyses were run for all possible 2-traits-combinations of FAT, DIF, SURV and SIZE.

The model for the precorrected production traits was:

$$y_{ijkl} = h_i + g_j + s_{k(j)}^C + e_{ijkl} \quad [1]$$

where:

h_i was the effect of the i^{th} herd-year;

g_j was the effect of the j^{th} group of sires grouped according to year of birth;

$s_{k(j)}^C$ was the random effect of sire of cow nested within the j^{th} genetic group; and

e_{ijkl} was a random residual.

For calving traits the model was:

$$y_{ijklm} = h_i + g_j + s_{k(j)}^C + (1/2)s_{k(j)}^0 + s_{l(j)}^0 + e_{ijklm} \quad [2]$$

where effects not previously defined were:

$(1/2)s_{k(j)}^0$ was the random effect of the k^{th} maternal grandsire of offspring (sire of cow) nested within the j^{th} genetic group.

$s_{l(j)}^0$ was the random effect of sire of offspring nested within the j^{th} genetic group.

The model [1] and [2] are now combined in matrix notation and illustrated below for an analysis including one production trait and one calving trait:

$$\begin{bmatrix} y_P \\ y_C \end{bmatrix} = \begin{bmatrix} X_P & 0 \\ 0 & X_C \end{bmatrix} \begin{bmatrix} b_P \\ b_C \end{bmatrix} + \begin{bmatrix} Z_P & 0 & 0 \\ 0 & Z_M & (1/2Z_M + Z_D) \end{bmatrix} \begin{bmatrix} u_P \\ u_C^M \\ u_C^D \end{bmatrix} + \begin{bmatrix} e_P \\ e_C \end{bmatrix} \quad [3]$$

where:

y_P was a vector of production records;

y_C was a vector of calving records;

X_P and X_C were incidence matrices for fixed effects;

b_P and b_C were vectors of fixed effects on the production and calving trait, respectively;

Z_P , Z_M and Z_D were known incidence matrices of random effects;

u_P was a random vector of sire effects the on the production trait;

u_C^M was a random vector of sire effects on maternal effects on the calving trait;

u_C^D was a random vector of sire effects on direct effects on the calving trait;

Thus, the model was a sire model for production traits and

maternal effects on calving traits, but for direct effects on calving traits the model was a sire and maternal grandsire model.

Expected first and second moments of random vectors in model [3] were:

$$E \begin{bmatrix} y_P \\ y_C \end{bmatrix} = \begin{bmatrix} X_P & 0 \\ 0 & X_C \end{bmatrix} \begin{bmatrix} b_P \\ b_C \end{bmatrix} \quad \text{and}$$

$$\text{Var} \begin{bmatrix} u_P \\ u_C^M \\ u_C^D \end{bmatrix} = A * S_0 = A * \begin{bmatrix} \sigma_P^2 & \sigma_{P,MC} & \sigma_{P,DC} \\ & \sigma_{MC}^2 & \sigma_{MC,DC} \\ & \text{Symmetric} & \sigma_{DC}^2 \end{bmatrix}$$

where A was the additive genetic relationship matrix accounting for relationships due to sires and maternal grandsires, and S_0 was 1/4 of the additive genetic (co)variance matrix.

The residual (co)variance matrix,

$$\text{Var} \begin{bmatrix} e_P \\ e_C \end{bmatrix} = R$$

was a block diagonal matrix with one block $\{R_i\}$ for each cow calf pair with data. There were three types of blocks: If both traits were recorded for the i^{th} cow-calf pair, then $\{R_i\} = R_0$ the 2X2 matrix of residual (co)variances. If only one of the two traits was recorded then $\{R_i\}$ was a scalar of the residual variance for that trait.

Note that S_0 was a 3X3 matrix, whereas R_0 was a 2X2 matrix for the model indicated. The phenotypic variance for the traits analyzed was then:

$$\sigma_{PP}^2 = \sigma_P^2 + \sigma_{eP}^2$$

$$\sigma^2_{pC} = \sigma^2_{MC} + (5/4)\sigma^2_{DC} + \sigma_{MC,DC} + \sigma^2_{eC}$$

where σ^2_{eP} and σ^2_{eC} was the residual variances for production and calving traits, respectively. The coefficient 5/4 stems from the fact that the submodel for direct effects on calving traits was a sire and maternal grandsire model.

The (co)variance matrices S_0 and R_0 was estimated by a derivative free REML algorithm for multiple traits using a computing strategy similar to the one outlined by Meyer (1989). The restricted likelihood function was maximized using a quasi-Newton method given by Dennis et al. (1983) and using code from IMSL (1987).

Several parameters were estimated more than once from analyses of the same data sample because only two or three traits were included at a time in a given analysis. These estimates were then averaged to obtain a single estimate of each parameter per sample. The estimates from the eight samples were then averaged and the variance of the eight estimates was used to obtain SE of estimates.

Results and Discussion

Production Traits

The genetic parameters estimated for production traits are shown in Table 44. The heritability estimates for MLK and FAT were lower than found in several recent reports in the literature, e.g., Cue et al. (1987), Wade and Van Vleck (1989), Van Vleck et al. (1988) and Van Vleck and Dong (1988). These authors found estimates ranging from .315 to .382. However, Meyer (1984) found estimates at .283 for MLK and .268 for FAT. For PRT, the heritability estimate was considerably higher

than those for MLK and FAT. Cue et al. (1987) found an estimate of the heritability for PRT of .254, a value considerably lower than their estimates for MLK and FAT. Van Vleck and Dong (1988) found an estimate of .36, a value similar to those for MLK and FAT.

Genetic and phenotypic correlations between production traits are also shown in Table 44. Phenotypic correlations were always higher than the corresponding genetic correlations which are in agreement with most literature results cited earlier. The phenotypic correlation between MLK and FAT were estimated at .707 which is higher than the .57 by Meinert et al., (1989) and deJager and Kennedy (1987). The genetic correlation between MLK and PRT were estimated at .599. Most investigators, however, have found that PRT are closer related to MLK than FAT, e.g., deJager and Kennedy (1987) and Meinert et al. (1989). The estimate of the genetic correlation between FAT and PRT of .628 are well in line with the aforementioned literature estimates.

Table 44.

Genetic parameters of production traits and their SE (in parenthesis).

Trait	Heritability	Phenotypic SD	Correlations ^a		
			MLK	FAT	PRT
Milk yield (MLK)	.259 (.030)	736.6 (6.33)	---	.857 (.004)	.821 (.013)
Fat yield (FAT)	.262 (.026)	30.2 (.166)	.707 (.067)	---	.779 (.010)
Protein yield (PRT)	.396 (.040)	26.2 (.339)	.599 (.082)	.628 (.057)	---

^aPhenotypic correlations are above the diagonal, and additive genetic correlations are below the diagonals.

Calving Traits

Direct Effects. Genetic parameters for FAT and direct effects on calving traits are shown in Table 45. Heritability estimates for FAT are repeated for easy reference. The heritability estimates for direct effects on calving traits were well within the ranges given by Philipsson et al., (1979). These ranges were based on a literature review of work published before 1977. Weller et al., (1988), however, obtained lower estimates of heritability for DIF of .031 and .027 for SURV.

The residual correlations between FAT and calving traits were all estimated to be essentially zero. Genetic correlation estimates between FAT and direct effects on calving traits were small to moderate, but were antagonistic. Selection for FAT would tend to increase direct effects on DIF and decrease direct effects on SURV and SIZE, but none of these correlations were very strong. It should be noted that the estimates of genetic correlations between FAT and the calving traits had relatively large SE. Philipsson (1976) concluded that milk production were unaffected by dystocia and stillbirth, but he considered only phenotypic relationships. Thompson (1980) found that calving difficulty and production were uncorrelated when calving difficulty was measured as a direct effect.

The residual correlations between calving traits (Table 45) showed that larger calves experienced more difficulty at birth than smaller calves. Calves with a more difficult calving had a reduced survival, however, calf size and survival were essentially uncorrelated.

The genetic correlation estimates between direct effects on

calving traits were all greater than the corresponding residual correlations, but were of the same sign. Selection for reduced direct effects on calving difficulty would also improve survival but decrease size. Again the genetic correlation between calf size and survival were relatively low with an estimate of $-.178$.

Table 45.

Genetic parameters for milkfat production and direct effects on calving traits and their SE in parenthesis.

Trait	h^2	σ_p	Correlations ^a			
			FAT	DIF	SURV	SIZE
Milkfat prod. (FAT)	.262 (.026)	30.2 (.166)	---	-.007 (.027)	.034 (.010)	.023 (.022)
Calving diff. (DIF)	.155 (.036)	.734 (.011)	.345 (.220)	---	-.274 (.006)	.343 (.007)
Calf survival (SURV)	.068 (.012)	.768 (.019)	-.131 (.201)	-.631 (.067)	---	-.081 (.009)
Calf size (SIZE)	.199 (.031)	.721 (.006)	-.240 (.205)	.692 (.032)	-.178 (.029)	---

^aResidual above the diagonal and genetic below the diagonal.

Maternal Effects. Genetic parameters for FAT and maternal effects on calving traits are shown in Table 46. The estimates for DIF and SIZE were considerably lower than the corresponding direct effects with estimates of .087 and .044, respectively. For SURV the estimate were approximately the same as the estimate for heritability of direct effects. All estimates agree reasonably well with normal ranges given by Philipsson et al., (1979).

The genetic correlation between FAT and maternal DIF was estimated at $-.079$, whereas the genetic correlation between FAT and direct DIF

was .345. For maternal SURV the genetic correlation with FAT was -.147, a value similar to the genetic correlation between FAT and direct SURV. The genetic correlation between FAT and maternal SIZE was .271, whereas the corresponding correlation between FAT and direct SIZE was -.240. Thus, selection for FAT would tend to produce cows that give birth to larger calves, but the cows themselves would be smaller at birth. The genetic correlations between the maternal effects on calving traits was similar to the correlations between the direct effects although lower in absolute value.

Table 46.

Genetic parameters for milkfat production and maternal effects on calving traits and their SE in parenthesis.

Trait	h^2	σ_p	Correlations ^a			
			FAT	DIF	SURV	SIZE
Milkfat (FAT)	.262 (.026)	30.2 (.166)	---	-.007 (.027)	.034 (.010)	.023 (.022)
Calving difficulty (DIF)	.087 (.016)	.734 (.011)	-.079 (.119)	---	-.274 (.006)	.343 (.007)
Calf survival (SURV)	.086 (.021)	.798 (.019)	-.147 (.185)	-.464 (.061)	---	-.081 (.009)
Calf size (SIZE)	.044 (.011)	.721 (.006)	.271 (.213)	.219 (.021)	-.051 (.070)	---

^aResidual above the diagonal and genetic below the diagonal.

Genetic Correlations between Direct and Maternal Effects

Estimates of genetic correlations between direct and maternal effects are shown in Table 47. Genetic correlations between direct and maternal effects were all negative with estimates of -.474, -.366 and -.560 for DIF, SURV and SIZE, respectively. Based on a relatively small

set of data, Philipsson (1976) found estimates at -.19 and -.53 for DIF and SIZE, respectively, whereas his estimate for SURV was .07, a result deviating considerable from our result. For DIF, Thompson (1980) (Cf. Balcerzak et al., 1989) found estimates of -.38.

Table 47.

Genetic correlations between maternal and direct effects for calving traits and their SE in parenthesis.

Maternal	Direct		
	DIF	SURV	SIZE
Calving difficulty (DIF)	-.474 (.080)	.100 (.052)	.110 (.057)
Calf survival (SURV)	.299 (.116)	-.366 (.071)	.046 (.051)
Calf size (SIZE)	-.397 (.037)	.007 (.039)	-.560 (.029)

The correlations between direct and maternal effects when different traits were considered were all smaller in absolute value than when the same trait were considered. The most notable correlations were the genetic correlation between direct DIF and maternal SURV with an estimate of .299 and between direct DIF and maternal SIZE with an estimate of -.397. This means that selection for decreased direct DIF would yield cows that gives birth to calves with decreased SURV and increased SIZE.

SUMMARY AND CONCLUSIONS

The ultimate goal of this series of work is the construction of total merit indices to be used as selection criterion in dairy and dual purpose cattle populations. Parts of the series are included in this thesis. These total merit indices will consider dairy and beef production, calving characteristics, management or type traits and fertility as well as biological efficiency traits. In order to construct an index, genetic parameters involving all traits must be known, but many especially genetic covariances are not known. To estimate these parameters, however, strategies need to be developed to alleviate computational difficulties and to avoid biases due to selection. Selective mating for genetic improvement has been and will continue to be conducted on a within breed basis. However, utilization of between breed genetic effects which involves crossbreeding needs to be explored.

Therefore, this series of studies covered three main topics. The first topic is computation algorithms and data sampling in alleviating computational difficulties in the estimation of genetic parameters. The second topic relates to beef production and its biological efficiency, of young bulls of dual purpose breeds, and the genetic relationships between traits measured on the growing young bulls and the dairy production of female relatives. The third topic deals with estimation of crossbreeding effects and genetic parameters on dairy production and calving performance in a population importing genetic material.

CHAPTER 1. Transformation Algorithms in Analysis of Single Trait and of Multitrait Models with Equal design Matrices and One Random Factor per Trait: A review.

Transformation algorithms for models with two variance components per trait are reviewed and illustrated with a numerical example. The emphasis is on multiple trait models with equal design matrices. Algorithms of canonical, "Cholesky", and Householder transformations are discussed. The series of transformations offers an alternative that drastically reduces the amount of computation per round of the iterative expectation maximization algorithm for estimating (co)variance components by the restricted maximum likelihood method. After all the transformations are carried out, no matrices need to be inverted and the computations in each round of the iteration process can be evaluated in linear time. Thus, in practice, once the initial computing work is done, any number of iterations can be performed with ease. This allows the use of conservative stopping criteria. The stopping criteria often need to be conservative because considerable changes in parameter estimates can occur during later rounds of the iteration process, even though the change per round is very small.

CHAPTER 2. A Stochastic Model of Breeding Schemes in Cattle Populations.

A stochastic model of breeding events in a dual purpose or in a dairy cattle population was constructed. It was aggregated such that year could be the unit of time.

The model primarily simulates performance testing of young bulls

for growth in a central testing facility and milk production of cows in commercial herds. In dairy populations only milk production in commercial herds is simulated. Primary use of the model is to study the effects of population size, breeding structure, magnitude of underlying genetic parameters and economic conditions on the genetic response from a genetic improvement program. The build-up of inbreeding, the reduction of genetic variance due to both inbreeding and Bulmer effect, and random variation in response due to genetic drift can also be studied. The model can generate data from simulated populations which has been either undergoing selection for one or more traits or is mating at random.

As illustration, the model was used to study the effect of population size and number of tested bulls used per year.

CHAPTER 3. Estimation of Genetic Parameters Using Sampled Data from Populations Undergoing Selection.

In populations undergoing selection, genetic variances and covariances are altered in amounts dependent on selection intensity among parents and the mating structure. In order to estimate the genetic parameters of the unselected population using data from populations undergoing selection all data that led to the current population must be included in the analysis. This is often not possible due to missing information or computer limitations. Therefore, often only subsamples of data are analyzed and/or simplified operational models are used. A simulation study was conducted to investigate different sampling strategies and different operational models in dual purpose populations selecting for beef and milk and in single purpose

dairy populations. Genetic parameters estimated by REML were unbiased if all data and all relationships were included in analysis even though selection was not within fixed effects. Use of a model including only additive effects of males, where bulls had own record on growth and daughter records on milk also seemed to yield unbiased estimates of genetic parameters. Sire models used in dairy populations gave biased estimates of genetic parameters, even when all data were included in the analysis. Treating sire effects on second crop daughters as fixed did not alleviate any selection bias in the populations investigated.

CHAPTER 4. Performance Testing of Dual Purpose Bulls for Beef Traits.

Genetic Parameters of Growth, Feed Intake, Appetite and Carcass Composition.

Genetic parameters for growth, energy intake, feed conversion ratio, average daily energy intake and carcass composition were estimated in an experiment with 650 bull calves from 31 halfsib groups of Holstein Friesian or Brown Swiss sires. All traits analyzed showed an amount of additive genetic variance that allows for considerable response to selection. No interaction between genotype (sire group) and proportion of roughage in the diet was found. Daily gain was strongly negatively correlated with feed conversion ratio but positively correlated with daily feed intake or appetite. Results indicate that selection for either daily gain or average daily energy intake would decrease carcass fatness at a constant slaughter weight.

CHAPTER 5. Performance testing of Dual Purpose Bulls for Beef Traits.

Residual Intake and Energy Requirements for Growth and Maintenance.

The residual feed intake and the partial requirement for productive and nonproductive use of feed energy was estimated for each of 650 bull calves of 31 Holstein Friesian or Brown Swiss sires. The partial requirements for nonproductive use of energy, or more conventionally the maintenance requirement, was further partitioned into a part dependent on metabolic body weight and a part independent of metabolic body weight. The partial energy requirements were obtained for each individual bull based on biweekly measures of body weights and energy intake. Two different models were used in partitioning energy intake in the production period before 200 kg live weight with animals fed restricted amounts, and again in the production period after 200 kg live weight where the animals were fed ad libitum. Genetic analysis of the partial energy requirements showed considerable variation among bulls in requirements for both productive and nonproductive use of energy, and also showed that these traits were heritable to approximately the same degree as conventional measures of feed efficiency.

Results indicated that it is possible to obtain individual estimates of partial requirements for productive and nonproductive use of energy from frequent measures of body weight and energy intake. Biological interpretation of the partial energy requirements was very dependent on the model used in the partitioning of energy intake, because different partial requirements estimated in the same model were

more closely correlated than were similar coefficients from different models.

Residual intake, defined as actual minus predicted energy intake, was also computed for each bull in each production period. Residual intake showed a larger degree of additive genetic variance than the partial energy requirements when the animals were fed ad libitum, whereas the opposite was the case when the animals were on a restricted feeding regime. Residual intake estimates with and without correction for carcass composition were very closely correlated. Thus residual intake can be calculated without the knowledge of carcass composition.

CHAPTER 6. Performance Testing of Dual Purpose Bulls for Beef Traits.

Genetic and Phenotypic Correlations Between Partial Energy Requirements and Beef Traits of Young Bulls and the Milk Yield of their Female halfsibs.

Genetic and phenotypic correlations between growth, feed intake, feed conversion ratio, appetite, carcass composition, residual intake and partial energy requirement for growth and maintenance were studied in an experiment on 650 bull calves of 31 Holstein Friesian or Brown Swiss sires. The correlations between these traits and the sires breeding value for milkfat production were also studied. The phenotypic and genetic (co)variance matrices were analyzed by factor analysis and accordingly interpreted. Energy requirements for growth and maintenance were unrelated to growth rate phenotypically. However, genetic selection for higher daily gain would increase the energy requirement for growth and weight dependent nonproductive use of energy, but decrease intake at constant growth rate and constant

metabolic weight. Feed conversion ratio and partial energy requirements for growth and maintenance were all phenotypically unrelated to carcass composition. However, selection for leaner animals would increase the partial energy requirement for growth and the weight dependent nonproductive use of energy, but decrease baseline intake. The sires' breeding values for milkfat production and daily gain of his male progeny bulls were positively correlated, especially when daily gain were measured before 200 kg live weight. Appetite of the ad libitum fed young bull was not correlated with the sires' breeding values for milkfat production. Sires' breeding values for milkfat production was negatively correlated to percent fat in the carcass of the growing young bull.

CHAPTER 7. Additive and Heterotic Effects of Immigration of Brown Swiss Genes into the Red Dane Cattle Population on Dairy Production and Calving Traits.

Data on 170,166 cows were analyzed in order to estimate the effects of immigration of genes into the Red Dane Cattle population. Most foreign genes originated from American Brown Swiss. Effects on first lactation production and calving traits were estimated. Relatively small but negative recombination effects were found for production traits. A model including both additive, dominance and recombination effects indicated large effects of progeny genotype on the cows subsequent production. If effects of progeny genotype were ignored, however, recombination effects were small for milk and fat production but still large and negative for protein production.

Heterosis for production traits, expressed as F_1 heterosis was 4.4 to 7.7% depending on model used in estimation. Models without recombination effects estimated heterosis effects for production traits in the range 7.1 to 7.7%. The large positive heterosis for production was to some extent counteracted by a large genetic difference between Red Dane and Brown Swiss, with Brown Swiss being 2.6 to 6.2% inferior to Red Dane in production.

For calving traits small recombination effects were found. Heterosis for calving difficulty and calf survival tended to improve calf survival, but also increased the level of calving difficulty. Heterosis effects for calving traits were small, however, in comparison to additive genetic differences between Red Dane and Brown Swiss, the latter having considerable less calving difficulty and better calf survival.

The advantages of crossbreeding to Red Dane breeders seems to lie in the use of a synthetic breed consisting of genes from both breeds. For Brown Swiss breeders, however, there seems to be a large advantage in production traits, by introducing Red Dane genes into their population. Such immigration, however, will increase calving difficulty and yield a slight decrease in calf survival.

CHAPTER 8. Genetic Parameters of Dairy Production and Calving Traits in Danish Red Cattle.

Data on 170,166 cow-calf pairs of Danish Red Cattle were analyzed in order to estimate genetic parameters of first lactation production and of calving traits recorded at first calving. The traits analyzed were 305 days milk, fat, and protein production and calving difficulty,

calf survival and calf size. For calving traits effects due to both genotype of cow (maternal effects) and genotype of calf (direct effects) were considered. Genetic parameters were estimated using a multivariate derivative free REML algorithm. Heritability estimates for milk, fat, and protein production were .259, .262 and .396, respectively. Heritability estimates for direct effects on calving difficulty, calf survival, and calf size were .155, .068 and .199, respectively, and the corresponding estimates for maternal effects were .087, .086, and .044. Fat production had positive genetic correlations to direct calving difficulty and a negative genetic correlation to direct calf size. Fat production was not correlated with maternal effects on calving difficulty and calf survival, but had a positive genetic correlation with maternal effects on calf size. Genetic correlations between direct and maternal effects were all negative with estimates of -.475, -.366 and -.560 for calving difficulty, calf survival and calf size respectively.

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