**INFLUENCE OF POPULATION STRUCTURE ON ESTIMATES OF
DIRECT AND MATERNAL PARAMETERS**

A Thesis

Presented to

The Faculty of Graduate Studies

of

The University of Guelph

by

MAHYAR HEYDARPOUR

In partial fulfilment of requirements

for the degree of

Doctor of Philosophy

September, 2006

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ISBN: 978-0-494-24568-2

Our file Notre référence

ISBN: 978-0-494-24568-2

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ABSTRACT

INFLUENCE OF POPULATION STRUCTURE ON ESTIMATES OF DIRECT AND MATERNAL PARAMETERS

Mahyar Heydarpour
University of Guelph, 2006

Advisor:
Professor L. R. Schaeffer

The impact of population structure on the estimation of (co)variance components for traits affected by maternal effects was investigated through stochastic simulation. Two traits in a closed breeding herd of 400 cows and 50 sires with overlapping generations and random mating was simulated over nine generations. Simulations considered five different population structures on the basis of different proportions of dams with performance records ($mis = 0, 0.1, 0.5, 0.8, \text{ and } 0.9$); three genetic correlations ($r = -0.5, 0.0, +0.5$) between direct and maternal effects; and three different values of genetic correlations ($t = 0, 0.3, 0.8$) between two traits. Three different parameter sets based on the ratio between direct and maternal genetic variances ($par = 1:3, 1:1, \text{ and } 3:1$) for each trait of interest were also considered. Variance components were estimated by restricted maximum likelihood (REML) through DMU (a package for analyzing multivariate mixed models). The mis had no influence on SE of estimates of maternal, direct, and permanent environmental variances, but for direct-maternal covariance estimates, larger SE were obtained when mis was high (0.8 or 0.9) and r was negative. The influence of the parameter sets on the SE of the estimates was greater than that of the population structure. The t had no major influence on the SE of the estimates. The mis and r had

greater effects on bias of estimates than the ρ and t . Bias was obtained when m was high and r was positive. The largest biases were detected when the direct variance was greater than the maternal variance, as would be the situation of most growth traits in livestock, particularly in beef cattle. Total bias (%) of the whole set of parameters were large when m was 0.9, r was positive, and the variance ratio between direct and maternal was equal (1:1). In general, results of this study showed that the ρ and r had more influence on the SE of the (co)variance estimates than m and t . However, m and r had greater effect on bias of the estimates. Complete data sets with more links of dam-offspring are required for accurate estimation of maternal genetic parameters in the single and multiple trait situations.

ACKNOWLEDGEMENTS

I would like to express my deepest sense of gratitude to my advisor, Dr. L. R. Schaeffer, for providing me with the opportunity to pursue my study in PhD program at the University of Guelph, supporting me with his encouragement, guidance, and friendship during my graduate program and also for allowing me to conduct an independent research project. I would like to extend sincere thanks to the other members of my advisory committee, Dr. Ian McMillan, Dr. Andy Robinson, and Dr. Brian Allen for their time, advice, and recommendations.

I am deeply indebted to Dr. H. Yazdi who tutored me on how to write a simulation program and helped me to complete the simulation program for my PhD research project. I often discussed animal breeding and statistics matters with him during my graduate program and these discussions have always been fruitful, for which I am thankful.

I would like to acknowledge Dr. Isobel Heathcote, the Dean of Graduate Studies at the University of Guelph, for her understanding, kindness, financial support, and also for her thoughts which helped me in during difficult times. Thanks for giving me a hand.

I am very thankful to Mr. Jalal Fatehi for his friendships, guidance and particularly for teaching me the SAS program, and also for his time spent revising some chapters of my thesis.

I would like to thank the members of the Center for Genetic Improvement of Livestock (CGIL) for their help, kindness, and support. I would especially like to thank Mr. Bill Szkotnicki who provided me with a program to implement my simulation program very quickly and efficiently and to Dr. Flavio Schenkel for his guidance and suggestions.

I would like to acknowledge the Chair, faculty, staff and graduate students of the Animal and Poultry Science Department at the University of Guelph for their help and support.

I would like to thank the Ministry of Science, Research, and Technology of Iran and also Ferdowsi University of Mashad - Iran for their financial support.

Mr. Benny Quay, International student advisor, helped in some moments of financial need, for which I am thankful.

I would like to acknowledge the members of the Office of Open Learning of the University of Guelph who gave me this opportunity to improve my English ability during my PhD program, particularly Mr. Bill Hodges, Mrs. Kristy Foss, Mrs. Eve Mazereeuw, Mr. Michael Kinsey, and Mrs. Peggy Nagle for their encouragement and support.

A special thanks to my friends Vicente, Gabriela, Hossein, Shahin, Dave and Sandra, who made me and my family feel at home during our stay in Guelph and also for their kindness and support.

I would like to acknowledge the love and support of my whole family. I am particularly grateful to my wife, Leila, for her constant love, understanding and support during these years which made all my achievements possible. I am also thankful to my son, Mohamad-Ali and my daughter, Assal, for their love and patience. I would like to give special thanks to my parents for their continuous support and love and also for their encouragement to pursue graduate studies. I am thankful to all my brothers and sisters for their kindness and support. I also acknowledge my father-in-law and mother-in-law for their constant love and continuous support, morally and financially.

Finally, I thank God for opening new windows in my life which really lifted my spirits and also for all the good things that my family and I have received from Him.

I would like to finish my words with a quote from a renowned Iranian scientist, Abo-Ali Sina (Avicenna), who said (in Persian) “Ta Bedanja Resid Danesh Man, Keh Bedanam Hami Keh Nadanam”.

تا بدانجا رسید دانش من که بد انم همی که نا دانم (ابوعلی سینا)

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Chapter 1

General Introduction

Maternal influences on early growth of offspring are of great importance in livestock that are reared naturally. Weaning weight is a classical example of a maternally influenced trait. In most species of livestock (cattle, sheep, goat, etc) the female supplies an atmosphere for its progeny to survive and develop. There are some genetic and environmental sources of variation in a female's ability to provide a suitable environment for her progeny. This trait is called "maternal ability" and is genetically transmitted from both parents, but expressed only in females when female offspring have progeny of their own. Maternal genetic sources of variation can be partitioned into additive, dominance and epistatic effects. The additive genetic variance component is associated with an individual's genetic makeup and is usually termed the direct genetic effect. The additive genetic ability of the dam which provides a suitable environment for her progeny is usually termed the indirect or maternal genetic effect of the progeny.

Maternal effects in mammals can be classified into prenatal (i.e. cytoplasmic and uterine components) and postnatal (i.e. lactation, behavior, and other postnatal maternal components). In postnatal growth, the dam's milk production and mothering ability are mainly involved, while effects of uterine environment and extra chromosomal inheritance may also contribute. For instance, selection programs in beef cattle focus on birth weight and weight gained during the later stages of the life of an animal up to slaughter time. Therefore, in analyzing data, not only is a differentiation of the genetic and

environmental proportions of phenotypic variation needed but the genetic part also has to be separated into direct and maternal effects (Swalve, 1993). The separation of direct and maternal effects is particularly problematic because these effects are normally confounded when the biological dam is also providing the maternal environment. For data obtained under embryo-transfer or cross-fostering schemes, this separation would easily be possible because the biological dam is different from the dam providing the maternal environment (Meyer, 1992a). The relationship between direct and maternal effects is also important. The existence of an antagonistic relationship between direct and maternal genetic effects would have an adverse effect on a breeding program. With all of these potential challenges, the estimation of maternal effects and the associated genetic parameters is inherently problematic.

Biological mechanisms that explain maternal effects include cytoplasmic inheritance, intrauterine and postpartum nutrition provided by the dam, antibodies and pathogens transmitted from dam to offspring, and maternal behavior (Hohenboken & Brinks, 1971). Maternal ability is transmitted by both parents but is expressed only when the female has progeny of her own. Maternal genetic effects can have an influence on genetic improvement of litter size, even when maternal heritability is low relative to direct heritability, depending on the genetic correlation between maternal and direct genetic effects (Roche & Kennedy, 1993b). Although maternal effects are strictly environmental with respect to offspring, these effects can have both environmental and genetic components for the dam (Willham, 1963). Direct and maternal effects are generally

confounded (except in embryo transfer cases), but the expression of maternal effects occurs late in the life of female and lags by one generation (Willham, 1972).

In many studies, particularly in growth traits of livestock, a negative correlation has been found between direct and maternal genetic effects, often as strong as -0.5 or larger in magnitude. In the presence of such an antagonistic correlation, both direct and maternal components should be taken into account simultaneously in a selection program to achieve optimum genetic progress. Ignoring the maternal genetic effect in models can produce a severe problem for selection strategies (Eler et al. 1995). The negative correlation between direct and maternal genetic effects may be explained as the negative influence of dams on the maternal ability of their female offspring through overfeeding (Koch, 1972). For example a mother with high maternal ability may over-feed her daughter and thereby may have a negative influence on her daughter's maternal ability by inhibiting development of udder tissue, which is called "fatty udder syndrome" (Totusek *et al.*, 1971).

Selection based on genetic evaluations requires accurate estimates of genetic and environmental parameters. A negative correlation between direct and maternal genetic effects has a considerable effect on response to selection for litter size (Southwood and Kennedy, 1990). When maternal effects are included in the evaluation model, a complete pedigree is important to obtain the greatest separation between estimated maternal and direct breeding values (Roehe and Kennedy, 1993a).

One possible reason for large negative estimates of the direct and maternal genetic correlation is the structure of the data (Meyer, 1992a). The direct additive genetic component is estimated from a single observation per animal, whereas estimates of maternal effects depend on the number of progeny per dam, the number of dams with recorded performance, and the number of generations of recorded data (Gerstmayr, 1992). Gerstmayr (1992) showed that the reliability of estimating maternal and direct genetic variances and their covariances was influenced by the magnitude of the true genetic parameters and data structure of the population. Reliability was significantly reduced when the genetic correlation was highly negative and the maternal genetic variance was equal to or less than the direct genetic variance. The estimation of maternal heritability and genetic correlation between direct-maternal had the largest standard deviation (SD) when none of the dams had records. Consequently, data structure was important for accurate estimation of maternal effects. Only a few studies have investigated the influence of data structure on parameter estimates when maternal effects are included in the model (e.g., Baker, 1980; Gerstmayr, 1992; Meyer, 1992a; Roehe and Kennedy, 1993a; Clement *et al.*, 2001; Maniatis and Pollott, 2003). These studies were usually based on univariate models and field data sets.

Because the influence of data structure and the underlying magnitude of maternal genetic effects on the estimation of direct and maternal genetic variances has not been examined utilizing multiple trait animal models in previous studies, this area of research was in need of investigation.

The objective of this project is to study the impact of population structure on the estimation of genetic parameters for traits influenced by direct and maternal effects using multiple-trait animal models through stochastic simulation.

In order to address this overall objective, several specific aspects of the population, the trait and the data will be explored:

- 1) The impact of population structure (includes the items listed below) on estimation, in terms of bias and accuracy of estimation, of variance components and genetic parameters (e.g. direct and maternal variance, direct and maternal heritability, and genetic correlation between direct and maternal) for traits that are affected by maternal effects.
- 2) Influence of the proportion of dams without records on variance and covariance estimates.
- 3) Influence of the sign of genetic correlation between direct and maternal on variance and covariance estimates.
- 4) Magnitude of the genetic correlation between two traits on variance and covariance estimates.
- 5) Influence of different ratios of direct to maternal variances on variance and covariance estimates.

Chapter 2

2) Literature Review

2.1. Maternal effects

Maternal effects are known to influence quantitative traits in many species. Maternal effects can be defined as any environmental influences a mother confers on the phenotype of her offspring (Willham, 1972). Maternal effects indicate that the dam has an influence on the performance of her offspring over and above that of her direct additive genetic contribution (Southwood & Kennedy, 1990). The maternal effect of a female is a function of her genotype and environment, the additive genetic part being inherited from both her sire and dam. Therefore, genotypic differences among females are expressed as phenotypic differences of their offspring. Maternal components are the environmental influence of the mother on her offspring and the transmission of maternal effects are partially under nuclear genetic control (Eisen, 1967). This situation is often found for mammalian quantitative traits, such as weaning weight in cattle, which may be affected by such maternal factors as lactation or behavior during progeny rearing. The phenotype of weaning weight is influenced by a direct genetic effect on growth of the progeny and a maternal genetic effect associated with lactation of the mother. Growth in body size is highly influenced by maternal effects which explain more than 80% of total phenotypic variation (Maurer et al., 1990). Litter size and parturition date are heritable and largely correlated with maternal effects. Dickerson (1947) first discussed maternal genetic effects in the context of animal breeding and quantitative genetics and defined maternal effects as arising when the phenotype of a mother or the environment she experiences has a phenotypic impact on her offspring. Dickerson (1947) expanded a

simple definition of heritability to include not only direct genetic effects but also indirect genetic effects and the direct-indirect genetic covariance as a proportion of total phenotypic variation in the offspring traits. Koch and Clark (1955) extended Wright's method of path coefficient analysis to include maternal effects in beef cattle evaluations. Kempthorne (1957) derived a single gene model, an extension of Fisher's original model of genetic effects, to include maternal genetic effects. Falconer (1965) considered maternal effects on litter size as a special case and found that artificial selection on litter size in mice resulted in a temporarily reversed evolutionary response. In the first generation of his experiment, selection on litter size resulted in smaller offspring, while selection for decreased litter size produced larger offspring. Falconer inferred that this was the consequence of maternal effects acting through the body size of mothers. As a result of such experimentation, animal breeders have been interested in maternal inheritance because of the substantial effects on the outcome of artificial selection. This interest has led to creation of models for the evaluation of a single trait that is maternally affected (Falconer, 1965), and for the evaluation of two traits one of which maternally affects the other (Van Vleck et al., 1977; Cheverud, 1983). A two-character model was extended by Willham (1972) to cases in which the maternal character affects its own expression as well as that of the offspring character.

Large differences in maternal effects have been demonstrated by differences between reciprocal crosses for growth traits in beef cattle and lactation yields in dairy cattle (Gregory et al., 1978; Robison, 1981).

Numerous estimates of genetic parameters for maternal effects on growth traits of beef cattle populations can be found in the literature (e.g. Burfening et al. 1981; Graser and Hammond, 1985; Quaas et al., 1985; Wright et al., 1987; Trus and Wilton, 1988; Garrick et al, 1989; Mrode and Thompson, 1990). Literature estimates for maternal effects on growth traits vary widely across authors, years, methods and breeds (Table 2.1).

Figure1. Path coefficient diagram showing Willham's model (1963) of maternal effects on an offspring's phenotype P_x .

- **A** and **M** indicate direct and maternal genetic effects
- **x** and **w** indicate offspring and mother respectively.
- r_{AM} is the correlation between direct and maternal breeding values.

$$P_x = G_{Ax} + E_x + G_{Mw} + E_{Mw}$$

- P_x = Phenotypic value of offspring
- G_{Ax} = Offspring's direct breeding value
- G_{Aw} = Mother's direct breeding value
- E_x = Non-maternal environmental effect of offspring
- G_{Mw} = Mother's breeding value of maternal effects
- E_{Mw} = Maternal Environmental effect

In this study, Willham's model was investigated, because it is simple and widely used to estimate genetic (co)variances. An important feature of Willham's model is that the traits

related to the mother's ability need not be specifically identified and the mother's ability is treated as an unspecified combination of traits. In Willham's model, the predicted response was proportional to the selection differential applied with a proportional constant h^2_T which referred to the total heritability, and is expressed as a function of the direct heritability (h^2_d), the maternal heritability (h^2_m) and direct-maternal genetic correlation (r_{dm}). $h^2_T = h^2_d + 0.5 h^2_m + 1.5 r_{dm}h_dh_m$

2.2. Estimation of maternal effects

Several approaches have been used to estimate maternal effects. One has been to define the expectation of covariances among a set of relatives to obtain direct estimates of the variance components (Ahlschwede & Robison, 1971b; Cantet et al., 1988; Meyer, 1992a). Willham (1972) described the biometrical relationships with direct and maternal effects acting on the genetic expression of a trait. The contribution of the dam's relationship in the pedigree may also be important. This approach has been well described by Eisen (1967) and theoretically can provide reasonable estimates for many of the genetic and environmental components. However, this approach is not well-suited to field data, because certain relationships may not be present and components may also be confounded. The main problem with field data sets is that often the types of covariances between relatives available in the data do not have sufficient potential to allow accurate partitioning of the phenotypic variance into all maternal (co)variance components.

Cross-fostering can separate prenatal and postnatal genetic effects and provide an estimate of the genetic covariance between additive direct and additive maternal genetic effects (El Oksh et al., 1967; Ahlschwede and Robison, 1971a). Again, this procedure is

only applicable to experimental data. Another method, which has been used on field data, involves the estimation of sire, dam, and maternal grandsire variances using mixed model methodology and equating the estimates to their genetic expectations (Bertrand and Benyshek, 1987). As with other approaches, estimates of variances may be biased if genetic drift and selection are not considered. The direction of the bias on the variance component estimates depends partly on the size of the additive maternal variance as well as the size and sign of the direct-maternal genetic covariance (Southwood & Kennedy, 1990). A negative genetic correlation between the direct and maternal effects can lead to conflict in the improvement of a trait. Estimates of these effects will also be required if selection for productivity traits is to be effective (Southwood & Kennedy, 1990). The maternal environmental component may be removed by appropriate management, such as cross-fostering, or by statistical methods such as adjustment of the data, while the genetic part may not be accounted for (Southwood & Kennedy, 1990).

The relationship between family structure and sampling (co)variances was investigated by Meyer (1992a) based on a list of covariances (obtained by Thompson, 1976) between relatives that have information available on direct and maternal components. Coefficients for the different components of variance and covariance which contributed to the phenotypic covariances between several types of relatives are summarized in Table 2.2.

Methods to estimate (co)variances relevant to maternal effects have been reviewed by Foulley and Lefort (1978). Their work relied on estimating covariances between relatives separately, equating them to their expectations and solving the constructed linear

equations. However, this ignored the fact that the same animal might contribute to different types of covariances and different observational components might have different sampling variances. Thompson (1976) presented a procedure (REML) which overcame these problems and showed how it could be applied to designs for animal breeding programs. Recently, in analyses under animal models, fitting a random effect for the additive genetic value of each animal has become a standard procedure. To a large extent, this was facilitated by the availability of different kinds of REML algorithms (e.g. DF, EM, AS, AI-REML) which made analysis involving thousands of animals feasible.

Maternal effects, both genetic and environmental, can be accommodated in animal model analyses by fitting appropriate random effects for each animal or each dam with progeny in the data. Conceptually, this simplifies the estimation of genetic parameters for maternal effects. Maternal (co)variance components can also be estimated in the same way as additive genetic (co)variances with the animal model. Special experimental designs for estimating (co)variances of maternal effects have been described by Eisen (1967) and Bondari et al. (1978). Thompson (1976) applied his REML procedure to these designs using Bondari's data, and found that the estimates of maternal components not only had large standard errors but also high sampling correlations. Thompson (1976) suggested that with presence of maternal effects, sampling variances of the direct heritability estimates would increase three to five fold over those obtained if only direct additive genetic effects existed.

In the estimation of maternal effects using data from livestock improvement schemes, non-additive genetic effects and direct-maternal environmental covariances have largely been ignored (Meyer, 1992a). In part, this has been due to the fact that often the types of covariances between relatives available in the data did not have sufficient potential to allow all components in the model to be estimated accurately. In field data, the contrasts between available relatives are likely to be fewer, thus limiting the scope to separate the various maternal components.

Thompson (1976) and Meyer (1992a) described the difficulties of estimating all parameters in Willham's model. The assumption of a dam-offspring environmental covariance of zero may result in a more accurate estimate for the remaining variance components. The failure to account for a non-zero environmental covariance between dam and offspring may bias the estimate of the correlations between the direct and the maternal genetic effects (Koerhuis and Thompson, 1997). This correlation, which often happened to be negative, may be biased downward due to a negative influence of dams on their daughters' maternal ability through overfeeding (Koch, 1972; Willham, 1972; Baker, 1980; Cantet et al., 1988). A potential source of negative direct-maternal environmental covariance can be explained by the level of nutrition available to the dam during early growth (Meyer, 1997). This is commonly referred to as 'fatty udder syndrome'. This causes daughters of dams with high maternal ability to provide a poorer maternal environment for their offspring than dictated by their maternal genetic potential, and gives rise to a negative environmental covariance between dams and their offspring over several generations (Meyer, 1997).

As a result, estimates of the correlation between direct and maternal genetic effects might be biased as noted in “National Cattle Evaluation Programs” (Dodenhoff et al. 1999).

Today, advanced methods of analysis along with the availability of high speed computers and efficient software effectively facilitate the estimation of genetic parameters relevant to maternal effects. But there are still some problems in estimating maternal effects which are briefly discussed below:

a) The maternal effect is confounded with the contribution of the dam to the direct effect. To obtain a rough idea of the importance of the maternal effect often the covariance between paternal half sibs is often subtracted from the covariance between maternal half sibs. By definition, a maternal effect is expressed by a female through the phenotypic values of her offspring. This is not the same as a trait of the female such as ovulation rate or birth weight. Repeatability from the same dam utilizes the covariance between maternal half sibs while repeatability of successive measures on the same dam involves the genotypic variance (Willham, 1972). In some species of livestock such as dairy cattle, the maternal effect is eliminated after the birth of the offspring by management systems that rear them without their dams.

b) There is the possibility that a genetic correlation between direct and maternal effects exists. This possibility is the most critical problem in estimating maternal effects particularly when this correlation is negative. The possibility of an antagonistic correlation between direct and maternal effects is real but this negative value will have serious effects on the prediction of breeding values for a selection scheme.

c) The maternal effect is a generation behind the direct effect in its expression. For example to adequately evaluate maternal effects in cross bred animals, crossbreeding experiments must be continued over more generations. Sometimes the maternal effects are influenced by previous maternal effects. In such situations, the lag will span more than one generation (Willham, 1972).

d) Maternal effects are sex limited and occur late in the life of the female. Therefore, estimation of maternal effects for males requires that female relatives' ancestors, collateral relatives or progeny be evaluated on the males. Crossbreeding studies can evaluate maternal effects after the F1 generation on half of the resources which are the females.

2.3. Models of estimation maternal effects

The animal models commonly fitted when estimating maternal effects include, in addition to the direct genetic effect of the animal, maternal genetic and permanent environmental effects, and are the models suggested by Willham (1963) (omitting dominance effects). While it is conceptually easy to extend these models to obtain direct-maternal and permanent environmental covariances, this might result in computational problems, especially for large and unstructured field data sets (Meyer, 1997). Consider the usual mixed linear model:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Zu} + \mathbf{e} \quad (1)$$

with $\mathbf{y}$ the vector of observations, $\mathbf{b}$ the vector of fixed effects, $\mathbf{u}$ the vector of random effects in the model, $\mathbf{e}$ the vector of residuals, and $\mathbf{X}$ and $\mathbf{Z}$ the incidence matrices pertaining to $\mathbf{b}$ and $\mathbf{u}$, respectively. Under an animal model, $\mathbf{u}$ always contains the vector

of the animal's direct additive genetic effects (**a**). If the traits under analysis are subject to maternal effects, this is usually taken into account by fitting vectors of the maternal additive genetic effects (**m**) and maternal permanent environmental effects (**c**) in addition with corresponding partitioning of $\mathbf{Z} = (\mathbf{Z}_A|\mathbf{Z}_M|\mathbf{Z}_C)$, and

$$\mathbf{u} = \begin{bmatrix} \mathbf{a} \\ \mathbf{m} \\ \mathbf{c} \end{bmatrix} \quad (2)$$

This is a reduced version of the model formulated by Willham (1963) to describe the mode of inheritance of maternal effects.

Further, let **A** denote the numerator relationship matrix between animals. While maternal genetic effects are assumed to have the same correlation structure as direct additive genetic effects, maternal permanent environmental effects are usually assumed to be independently distributed. So in the univariate case, the structure of the (co)variance matrix is as follows:

$$\mathbf{G} = \mathbf{V} \begin{bmatrix} a \\ m \\ c \end{bmatrix} = \begin{bmatrix} A\sigma_a^2 & A\sigma_{am} & 0 \\ A\sigma_{am} & A\sigma_m^2 & 0 \\ 0 & 0 & \mathbf{I}\sigma_c^2 \end{bmatrix} \quad (3)$$

where **I** denotes an identity matrix. Similarly, under Eq. (1) residuals are assumed to be independent. $\mathbf{R} = \mathbf{V}(\mathbf{e}) = \mathbf{I}\sigma_e^2$ (4)

Thus the phenotypic variance of an individual observation can be expressed as:

$$\sigma_p^2 = \sigma_a^2 + \sigma_m^2 + \sigma_{am} + \sigma_c^2 + \sigma_e^2 \quad (5)$$

Falconer's model (1965) is an alternative approach where maternal effects are estimated by a linear regression of the phenotype of the individual on the phenotype of the dam. The Falconer model (ignoring dominance effects) can be written as follows:

$$y = Xb + Zu + \beta(y_M - X_M b) + e \quad (6)$$

where β denotes the linear regression on maternal phenotype. Let y_M denote the vector of the dam's records pertaining to y . For animal i with dam j , the i^{th} element of y_M is y_j , the record for animal j , or 0 if a record of j is not available or the animal's dam is unknown. Correspondingly, let X_M be the incidence matrix for fixed effects pertaining to y_M . The i^{th} row of X_M is equal to the j^{th} row of X , or 0 for unknown dams or missing dam's records. The formulation of Falconer (1965) did not include a separate maternal genetic effect.

Koerhuis and Thompson (1997) extended the Falconer model by including m in u , as above mentioned and referred to an 'Integrated Falconer-Willham' model (IFW). In the IFW model the β is not a regression coefficient in the usual sense (i.e. a fixed or random effect in the linear model), but a ratio of variance components, namely the direct-maternal environmental covariance expressed as a proportion of the phenotypic variance. While it has an interpretation as the regression on maternal phenotype, it is a parameter to be estimated, in addition to σ_a^2 , σ_m^2 , σ_{am} , σ_c^2 , and σ_e^2 , which affects the log likelihood. The IFW model thus provides an alternative to the extended Willham model that allows for non-zero direct-maternal environmental covariances (Koerhuis and Thompson, 1997). As shown by Koerhuis and Thompson (1997), under Eq.(6) the covariances between an animal's direct and maternal genetic effects and their dam's phenotypes are given by geometric series in the genetic (co)variance components with a common ratio of $1/2\beta$, and can be summarized as $4\frac{\beta}{2-\beta}(\frac{1}{2}\sigma_a^2 + \frac{1}{4}\sigma_{am})$ and $4\frac{\beta}{2-\beta}(\frac{1}{2}\sigma_m^2 + \sigma_{am})$, respectively. Thus the phenotypic variance of individuals can be expressed as:

$$\sigma_p^2 = \left[\sigma_a^2 + \sigma_m^2 + \sigma_{am} + \sigma_c^2 + 4 \frac{\beta}{2 - \beta} \left(\frac{1}{2} \sigma_a^2 + \frac{5}{4} \sigma_{am} + \frac{1}{2} \sigma_m^2 \right) + \sigma_e^2 \right] / (1 - \beta^2)$$

The term $\left(\frac{1}{2} \sigma_a^2 + \frac{5}{4} \sigma_{am} + \frac{1}{2} \sigma_m^2 \right)$ is the dam-offspring covariance under the Willham model.

Robinson (1996b) suggested a model including a regression on maternal phenotype to account for environmental covariances between dam and offspring records. Based on Robinson's model, the phenotypic value for the i^{th} offspring of sire s and dam d in season y was as follows:

$$P_{sdyi} = \mu + a_i + m_d + f_s + g_{sy} + \beta(P_d - \mu) + e_{sdyi}$$

Where μ represents the mean phenotypic value of the base population, a_i is the direct additive genetic effect of animal i , m_d is the maternal genetic effect of the animal's dam, f_s is a random term representing additional variation between sires, g_{sy} is a random sire by mating season effect, β is the dam-offspring regression coefficient, P_d is the phenotypic value of the animal's dam and e_{sdyi} is a random error term.

Robinson's model has shown that estimates of direct-maternal correlations may be negative not only because of genetic antagonisms, but also because of additional sire or sire $\times$ year variation or negative dam-offspring covariances. However, Robinson (1996b) and Koerhuis and Thompson (1997) observed that such models still yielded biased estimates.

Quintanilla et al. (1999) proposed a maternal animal model which takes into account the correlation between maternal permanent environmental effects of dams and their

daughters as a reasonable approach to the non-genetic relationship between maternal effects of two generations. The model assumed that:

$$V \begin{bmatrix} u_d \\ u_m \\ u_{pe} \\ e \end{bmatrix} = \begin{bmatrix} A\sigma_d^2 & A\sigma_{dm} & 0 & 0 \\ A\sigma_{dm} & A\sigma_m^2 & 0 & 0 \\ 0 & 0 & E\sigma_{pe}^2 & 0 \\ 0 & 0 & 0 & I\sigma_e^2 \end{bmatrix}$$

where **A** was the additive relationship matrix among all animals. The **E** matrix was expressed as **E** = {g(λ)}, where λ was the correlation between maternal permanent environmental effects of dams and their daughters, assuming that the dam-daughter environmental relationship was constant across generations. As pointed out by Quintanilla et al. (1999), including the correlation matrix **E** provides a computationally feasible method to account for the non-genetic relationship that may exist between the maternal effects of dams and their daughters.

2.4. Effects of data structure on estimates

One of the problems in the analysis of maternally influenced traits is the large number of effects that influence a unique phenotype. The relationship between these effects leads to high sampling errors and strong sampling correlations between the estimates, and often the quantity and quality of data available are insufficient to separate them adequately (Meyer, 1992a).

The data structure for the direct additive genetic component is one observation per animal in the single trait animal model without repeated records. The design can be described by an identity matrix. The structure of the maternal effect depends on the number of

offspring per dam. The direct-maternal covariance component estimate is affected by the size of the dam's progeny group, and by the number of dams providing their own record of performance. If none of the dams is recorded, the genetic covariance can only be estimated by using the relationships amongst animals (Gerstmayr, 1992).

Gerstmayr (1992) investigated the impact of the data structure on the reliability of the estimated genetic parameters in an animal model with maternal effects. The effect of the number of offspring per dam on the maternal heritability and the influence of the number of dams with recorded performance on the correlation using several sets of genetic parameters were of particular interest in her study. The approximated standard deviation (SD) of the genetic parameter estimates was used as a criterion for the reliability of the estimates. No indication of bias was found from the results in any of the populations. The effect of population structure was found to be independent of the genetic parameters. With a true strong negative correlation, the differences between the populations were more pronounced. The SD of all estimated parameters was smallest when most of the dams had their own performance record. There was a strong increase in the SD of the maternal heritability when 80 to 100 percent of dams were without a record. The SD of all parameters was increased by a negative covariance between direct and maternal genetic effects. The correlation between direct and maternal effects along with the proportion of the direct and maternal variances had a stronger influence on the reliability of the estimates than aspects of the population structure. The most inaccurate estimates were obtained when the genetic correlation was high and negative, and also the maternal variance was the same or smaller than the direct variances. One progeny per dam led to

decreased accuracy of all estimates compared with larger progeny groups. Gerstmayr (1992) concluded that to obtain accurate maternal effect variance estimation, larger data sets with a better structure (e.g. more dams with records, and more progeny per dam) are required if the parameters are not known.

Lee & Pollak (1997a) investigated the influence of sire mis-identification on Sire $\times$ Year interaction (SY) variance and direct-maternal genetic covariance for weaning weight in beef cattle. Biased estimates of the genetic correlation between direct and maternal effects may occur when Sire $\times$ Year interaction (SY) effects are ignored in analytical models used to estimate (co)variance components for weaning weight in beef cattle. Estimates of (co)variance components in their study were obtained using multiple-trait DFREML. Results from analyses of data simulated with a negative covariance and a zero covariance were consistent with respect to the estimate of the covariance. In both cases, bias in the estimate of the covariance due to mis-identification of sires made the estimate more positive and including the SY effect in the analysis increased this effect. Mis-identification biased all parameters typically used for weaning weight genetic evaluation in beef cattle. Mis-identification was shown to be a source of bias in estimation of the direct and maternal covariance and the covariance became less negative with mis-identification of sires.

Clement et al. (2001) used a simulation analysis to test the influence of model adequacy and data structure on the estimation of genetic parameters for traits with direct and maternal effects. He found that data structure can affect the precision of variance

component estimation. Insufficient paternal information increased the standard deviations between replicates of the estimates, whereas insufficient genetic connectedness did not act on the precision of the estimates.

Maniatis & Pollott (2003) investigated the impact of data structure on genetic (co)variance components of early growth in sheep estimated using an animal model with maternal effects. The objectives of their work were to study the effect of particular genetic relationships, the number of offspring per dam and the influence of the proportion of dams with recorded performance on parameter estimates using farm records. Data used for the analysis came from the “Suffolk Sire Reference Scheme Ltd.” in UK. The study was based on an analysis of 8-week birth weight of sheep. With 50% of dams having records, the direct-maternal correlations decreased in magnitude compared with those obtained from families that had only 10% of dams with records. The magnitude of negative correlation estimates between direct and maternal effects declined with increasing number of progeny records. Both the number of progeny per dam and the proportion of mothers with recorded performance considerably influenced the parameter estimates. With a small progeny group per dam and limited information from recorded dams, the direct-maternal correlation had the highest negative value. Keeping progeny group size constant but increasing the number of dams with recorded performance produced a considerably lower negative correlation. A high proportion of both dams and maternal grand-dams with their own records were essential for estimating maternal effects and the covariance between direct and maternal genetic effects.

Roso (2004) studied pre-weaning weight gain in a typical multi-breed population of beef cattle in Ontario (Canada). He estimated variance components, direct and maternal breed additive, dominance, and epistatic loss effects, and breed additive genetic changes. He obtained a large negative correlation ($r_{dm} = -0.63$) between direct and maternal genetic effects for pre-weaning weight gain and concluded that a possible cause contributing to the strong negative genetic correlation was the small proportion of female calves with records having their own progeny. He obtained this large negative correlation when only 10% of female calves later became a cow and had records in the database. Roso (2004) concluded that the large estimated negative genetic correlation between direct and maternal effects seems to be more likely a consequence of a lack of enough information in the dataset to separate these effects than an indication of a true negative relationship.

2.5. Correlation of direct-maternal effects

From an evolutionary standpoint, it seems logical that some negative relationships providing checks and balances between direct and maternal effects for growth would be involved to prevent species from becoming increasingly larger or producing more and more milk (Cundiff, 1972). Such a system could be controlled by genetic or environmental relationships.

In cattle, where litter size is not a complicating factor, the direct-maternal genetic correlation appears to be negative but small in magnitude (Koch, 1972). This is consistent with genetic diversity observed between breeds. The genetic correlation cannot have been strongly positive or negative for large and small breeds with both high and low lactation

potential. However, evidence in cattle indicates that the genetic relationship is augmented when the maternal environment for gain from birth to weaning is negatively influenced by maternal environment from the previous generation (Koch, 1972). In beef cattle for instance, estimates of genetic correlations between additive direct and maternal genetic effects vary widely (Table 2.1). For weaning weight, estimates have ranged from -0.72 (Baker, 1980) to highly positive values. However, most estimates using field data have tended to be negative (Robinson, 1996b). For some breeds, estimates may be influenced by a negative dam-offspring environmental correlation (Baker, 1980), often known as fatty udder syndrome (Totusek et al., 1971 and Griggs, 1986). Hohenboken and Brinks (1971), for example, obtained estimates of -0.79 and -0.28 for r_{dm} from the same dataset depending on whether or not the estimating equations made use of the dam-offspring relationship.

In swine, the genetic correlation appears positive up to four weeks of age and then shifts to a negative value, possibly due to an interaction with postnatal environmental or management effects (Robison, 1972). It appears that postnatal environmental influences associated with compensatory consumption of creep feed contribute to a negative covariance between growth of the young and maternal ability of their dam. Robison (1972) also reported that the genetic correlation between direct and maternal effects was negative for fatness but positive for leanness. Southwood & Kennedy (1990) reported a high negative correlation between direct and maternal effect for litter size in Canadian Yorkshire and Landrace swine. The large negative covariance between direct and maternal genetic effects indicates that improvements in one effect will lead to reductions

in the second. This correlation increased between birth and weaning weight in the Yorkshire but remained high for all measures in the Landrace.

Bradford (1972) referred to results of a selection experiment in sheep in which about half of the response to selection for weaning weight was due to milk yield. This suggests that the genetic correlation between direct and maternal effects for growth is positive, or negative but small in magnitude in sheep. Some literature estimates of direct and maternal genetic parameters are presented in Table 2.1.

2.6. Solutions to negative estimates of direct-maternal correlation

The inclusion of sire $\times$ year (SY) interaction in the model was investigated by Robinson (1996b) as a cause of the negative correlation estimate between additive direct and maternal genetic effects observed in Simmental breed data. Negative values for the direct and maternal genetic correlation are used in the genetic evaluations of many beef cattle breeds (Lee & Pollak, 1997b). Accurate evaluations require accurate parameter estimates. For some breeds such as Simmental, this correlation may not be as negative as is currently used in national cattle evaluation system. The estimate currently being used may be inflated by the presence of a small SY interaction (Lee & Pollak, 1997b). The SY variance represented only 3% of phenotypic variance but explained 62% of the covariance between direct and maternal genetic effects estimated ignoring SY. Lee and Pollak (1997b) found that the model using both SY and correlation between direct and maternal (r_{dm}) fit the data better ($P < 0.01$) and halved the negative estimate of direct-maternal correlation compared to interactions being ignored in the model. Negative

genetic correlation estimates between direct and maternal effects were inflated when the SY interaction was not included in the model. Negative genetic correlations currently employed in animal evaluations might be more negative than true values due to ignoring SY interactions.

Negative correlation between dam and offspring due to environmental effects is due to management effects not accounted for in the most models. The importance of the management system has been demonstrated in dairy cattle. Jensen et al. (1991) estimated, amongst other correlations, the genetic correlation between daily gain in young bulls and milk production of cows. This relationship may be viewed as analogous to the r_{dm} problem in beef cattle. Jensen et al. (1991) reported a correlation of -0.47 when the bulls were fed a diet of concentrates whereas the correlation became +0.47 when the bulls were on a roughage diet. Meyer (1992b) studied three different breeds yielding positive (Angus) and negative (Hereford, Zebu Cross) genetic correlations for direct and maternal. Data originated partly from experimental stations and partly from field data. A negative r_{dm} could be amplified by the management system. Tawah et al. (1993) suggested that negative correlation estimates between direct and maternal effects may reflect adaptation of the animals to a dry tropical environment where food resources are scarce. In such an environment, small cows tend to meet their nutritional requirements for maintenance and growth of their calves more easily than larger cows. The larger cows would produce smaller calves, especially at weaning, than would smaller cows of similar age.

When there is a large negative correlation between direct and maternal effects, only selection with different weighting ratios on maternal and direct breeding values in male

and female lines can provide meaningful genetic gain in litter size (Roehe & Kennedy, 1993a). In this crossbreeding scheme, males of the dam line should be selected for the highest direct response, which can be achieved by selection on direct effects only. The females of the dam line should be selected for an optimum weighting ratio of maternal and direct breeding values. A complete pedigree is important to get greatest separation of maternal and direct estimated breeding values when maternal effects are included in the evaluation model (Roehe and Kennedy, 1993a).

An alternative approach for decreasing the negative correlation between direct and maternal genetic effects is to use multivariate analyses instead of univariate. Some literature references describing this advantage are listed in Table 2.3. In field datasets, usually not all traits are recorded for all animals or for all herds and therefore univariate analyses for genetic evaluation of animals for that trait are implemented. In multivariate analyses, a dataset with animals recorded for the traits of interest is necessary. Swalve (1993) used univariate and multivariate methods for estimation of direct and maternal (co)variance components for growth traits in Australian Simmental beef cattle. In the dataset, just 52.7% of animals were recorded for birth weight, 12.4% for weaning weight and 12.1% for yearling weight. Herds with the same trait recorded were grouped together. Herds were extracted if they exceeded 500 birth weights, 500 weaning weights, or 400 yearling weights. Swalve (1993) reported low negative correlations of direct-maternal genetic effects when multivariate analysis was used compared to univariate analyses. The effects of correlation between traits and the covariance between direct and maternal

genetic effects specifically seem to agree with lower estimates of direct-maternal genetic correlation in multivariate analyses compared to univariate analyses.

2.7. What is simulation?

2.7.1. Simulation Value

Simulations are widely used in all scientific research for understanding the behavior of stochastic systems. "Simulation means deriving a model of a system with suitable inputs and observing the corresponding outputs." (Bratley et al.1987). In a simulation study we can quickly try out our ideas at a fraction of the cost of trying them in actual experiments. Thus, there are many process improvements that we can make using simulation such as higher efficiency and better management the system (Axelrod, 1997).

Simulation is a way of conducting scientific studies with two standard methods of induction and deduction. Induction is the discovery of patterns in experimental data. Deduction, on the other hand, involves specifying a set of hypotheses and proving consequences that can be derived from those assumptions (Axelrod, 1997).

2.7.2. Programming the simulation model

For programming of a simulation model, considering the following goals is necessary:

- a) Validity b) Usability c) Extendibility

The first goal for programming a simulation model is validity. Validity of the program means that the program must correctly implement the model. This kind of validity is called "internal validity". But sometimes getting internal validity is harder than it might

seem. For example the programmer needs to know whether unexpected results which are obtained from the simulation model are reflections of a mistake in the program, or are an unexpected consequence of the model itself (Axelrod, 1997).

Usability of the program is a key goal particularly if a program could be used by other users. The usability of a program is important to allow the users to interpret its output and understand how it works, especially if there are alternative scenarios and parameters to be selected.

The third goal of a simulation program is extendibility of the program. The purpose of extendibility is to allow flexibility to adjust the program for other uses. A good programmer needs to think about this efficiency before starting to write a program. A program would be much more useful if it is designed for this purpose in advance.

The major advantage of simulation studies is the ability to define the true values of simulated scenarios and test the hypothesis in different models. Researchers have control over the data and therefore are able to evaluate the impact of each factor under different conditions in which the true values are known. Further, simulation studies in comparison with real life experiments have some advantages. For example experimenting in real life is costly. It is not only the capital expenditure of hiring new staff or purchasing new equipment but also the cost of the implication of these decisions. In real life it is very difficult to repeat the exact circumstances again and the chance to test different ideas under the exact same condition occurs rarely. In simulation studies we are able to test different models and ideas in a very short time.

Table 2.1. Literature estimates of direct and maternal parameters

Authors (year) Country/ Model ¹ / Method ²	Species/ Breed	Trait ³	# records	r_{dm}	h^2_d	h^2_m
Baker (1980)	Beef	BW PWG WW	-	0.0 to -0.42 -0.05 to -0.45 -0.07 to -0.72	0.40 0.26 0.30	0.19 0.24 0.52
Burfening et al., (1981) USA/ IND/ H-III	Beef/ Simmental	BW	11,552	-0.24	0.21	0.11
Graser and Hammond (1985) AUS/ S-MGS/ REML	Beef/ Simmental	WW	-	0.04	0.10	0.13
Quass et al., (1985) USA/ S-MGS/ A-REML	Beef/ Simmental	BW WW	497,409 768,419	-0.28 -0.22	0.16 0.12	0.06 0.08
Wright et al., (1987) USA/ S-MGS/ A-REML	Beef/ Simmental	WW	114,899	0.16	0.12	0.09
Cantet et al., (1988) USA/ S-MGS/ A-REML	Beef/ Hereford	BW WW	4,600 4,423	-0.05 -0.57	0.18 0.32	0.21 0.27
Trus and Wilton (1988) CAN/ S-MGS/ H-IV	Beef/ Simmental	BW PWG	23,784 20,870	-0.22 -0.45	0.34 0.43	0.20 0.20
Trus and Wilton (1988) CAN/ S-MGS/	Dairy/ Shorthorn	BW PWG	-	+0.55 -0.14	0.27 0.39	0.20 0.26
Garrick et al., (1989) USA/ S-MGS/ REML	Beef/ Simmental	BW WW	590,202 812,972	-0.38 -0.32	0.44 0.36	0.12 0.19
Mrode & Thompson (1990) UK/ AM/REML	Beef/ Simmental	WW YW	8,890 5,890		0.19 0.27	0.07 0.03
Southwood & Kennedy (1990) CAN/ AM/ DFREML	Swine/ Yorkshire	NOBN NOBA NOWN	2,960	-0.44 -0.22 -0.71	0.12 0.10 0.11	0.05 0.04 0.08
Southwood & Kennedy (1990) CAN/ AM/ DFREML	Swine/ Landrace	NOBN NOBA NOWN	4,225	-0.91 -0.92 -0.82	0.25 0.17 0.09	0.05 0.08 0.06
Mackinnon et al. (1991) AUS/ AM/	Beef/ Zebu cross	BW WW	- -	+0.01 0.0	0.61 0.20	0.11 0.32
Woodward et al., (1992) USA/ SM/ REML	Beef/ Simmental	BW WW	12,583 11,993		0.28 0.18	
Swalve (1993) AUS/ AM/ DFREML	Beef/ Simmental	BW WW YW	3,452 2,380 1,608	-0.26 to -0.36 -0.39 to -0.52 -0.08 to -0.22	0.42 0.38 0.34	0.08 0.18 0.03
Eler et al. (1995) USA/ AM/ DFREML	Beef/ Nelore Brazilian Breed	BW WW YW	6,780 6,911 4,831	-0.72 -0.32 0.09	0.22 0.13 0.16	0.12 0.13 0.10
Robinson (1996a) AUS/ AM/ DFREML	Beef/ Angus	BW WW YW FW	5,747 13,376 6,292 5,268	-0.61 -0.52 -0.72 -0.70	0.47 0.29 0.33 0.28	0.17 0.14 0.12 0.06
C. Lee et al. (1997) USA/ AM/ DFREML	Beef/ Simmental	WW	45,336	-0.34	0.32	0.20
Meyer (1997) AUS/ AM/ DFREML	Beef/ Polled Herefords Beef/ Herefords Beef/ Angus(AUS) Beef/ Angus(NZ) Beef/ Limousin	WW WW WW WW WW	61,787 79,434 87,389 57,375 16,635	-0.64 -0.65 -0.62 -0.52 -0.64	0.25 0.28 0.38 0.25 0.40	0.22 0.21 0.18 0.14 0.26
Dodenhoff et al., (1998) USA/ AM/ AI-REML	Beef/ Hereford	WW YW	2,811 2,706	-0.22 -0.35	0.18 0.13	0.18 0.20
Dodenhoff et al. (1999) USA/ AM/ AI-REML	Beef/ 9 parental breed Beef/ 3 composite breed	WW WW	1,450 3,100	-0.37 to +0.64 +0.08 to +0.51	0.1 to 0.34 0.2 to 0.34	0.04 to 0.25 0.03 to 0.08

Table 2.1. Literature estimates of direct and maternal parameters (*continue ...*)

Authors (year) Country/ Model ¹ / Method ²	Species/ Breed	Trait ³	# records	r_{dm}	h^2_d	h^2_m
Diop et al. (1998) USA/ AM/ AI-REML	Beef/ Gobra Senegal Breed	BW	3,909	-0.17	0.08	0.03
		WW	3,425	-0.58	0.20	0.21
		YW	2,764	-0.52	0.26	0.16
Luo et al. (1999) CAN/ S-MGS/ Bayesian	Dairy/ Holstien	CE	312,281	-0.16	0.05	0.03
		SB	312,281	-0.24	0.04	0.06
Quintanilla et al. (1999) Spain/ AM/ Bayesian	Beef/ Bruna dels (Spanish breed)	WW	2,218	-0.24	0.22	0.08
Varona et al. (1999) USA/ AM/ Bayesian	Beef/ Gelbvieh	BW	2,366	-0.35	0.26	0.05
		CD	2,106	-0.32	0.18	0.01
Boettcher et al. (2000) CAN/ S-MGS/ Bayesian	Dairy/ Holstein	CE	94,000	+0.38	0.14	0.08
Duangjinda et al. (2001) USA/ AM/ Method R	Beef/ Hereford	WW	255,790	-0.32	0.24	0.14
	Beef/ Gelbvieh	WW	381,389	-0.31	0.28	0.08
	Beef/ Charolais	WW	252,456	-0.46	0.33	0.15
Maniatis & Pollott (2003) UK/ AM/ DFREML	Sheep/ Suffolk	BW	Full data	-0.36	0.14	0.10
		BW	50% dam rec	-0.40 to -0.51	0.20	0.12
		BW	10% dam rec	-0.46 to -0.99	0.21	0.13
Roso (2004) CAN/ AM/ AI-REML	Beef herds of Ontario Pure & cross breed	PWG	869,050	-0.63	0.32	0.20
Iwaisaki et al. (2005) JAP/ AM/ REML	Beef/ Gelbvieh	WW	82,138	-0.25	0.28	0.08
	Beef/ Limousin	WW	88,639	-0.58	0.39	0.15

¹ Models: AM= Animal Model, S-MGS= Sire-Maternal Grandsire, SM= Sire Model, IND= Indirect Method (results from separate runs of a sire and maternal-grandsire model are combined),

² Methods: H-III = Henderson's Method III, H-IV= Henderson's Method IV, REML= Restricted Maximum Likelihood, A-REML= Approximated REML, DFREML: Derivative free REML, Bayesian method (Gibbs sampling).

³ Traits: BW: Birth weight, WW= Weaning weight, YW= Yearling weight, FW= Final weight, PWG= Pre-weaning gain, NOBN= Number of piglets born, NOBA= Number of piglets born alive, NOWN= Number of piglets weaned, CD= Calving difficulty, CE= Calving ease, SB=Stillbirth.

Table 2.2. Coefficients for the covariance components contributing to the resemblance between relatives in a model which includes maternal effects.

Covariances ^b	Components ^a			
	σ_d^2	σ_m^2	σ_{dm}	σ_c^2
Individual	1	1	1	1
Dam-offspring	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{5}{4}$	0
Sire-offspring	$\frac{1}{2}$	0	$\frac{1}{4}$	0
Full-sibs	$\frac{1}{2}$	1	1	1
Maternal half-sibs	$\frac{1}{4}$	1	1	0
Paternal half-sibs	$\frac{1}{4}$	0	0	0
Mat. granddam-offspring	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{5}{8}$	0
Mat. grandsire-offspring	$\frac{1}{4}$	0	$\frac{1}{8}$	0

^a σ_d^2 = direct additive genetic variance; σ_m^2 = maternal additive genetic variance; σ_{dm} = direct-maternal genetic covariance; σ_c^2 = permanent environmental variance.

^b Adapted from Willham (1963) and Thompson (1976).

Table 2.3. Estimates of direct-maternal genetic correlation (r_{dm}) from univariate and multivariate analyses of weaning weight in beef cattle.

Reference	Breed	# of records	Univariate estimate	Multivariate estimate
Swalve (1993)	Simmental	9,595	-0.52	-0.39
Meyer (1992a)	Poll Hereford	30,506	-0.67	-0.42
Meyer (1992b)	Charolais	6,448	-0.8	-
Eler et al. (1995)	Nelore	27,549	-0.32	-0.13
Robinson (1996a)	Angus	13,376	-0.52	-0.45
Dodenhoff et al. (1999)	Charolais	1,336	-0.12	0.07
	Limousin	1,409	-0.18	0.01

Chapter 3

3) Material & Methods

3.1. Simulation Method

A stochastic simulation of two traits in a closed breeding herd of 400 cows with 50 sires per year with random mating was carried out to examine the influence of population structure on accuracy of direct and maternal variance component estimation over nine overlapping generations. Five different population types (PT1 to PT5) were simulated on the basis of a different proportion of dams with performance records (Table 3.1).

Table 3.1. Structure of the simulated populations

Population Type (PT)	(PT1)	(PT2)	(PT3)	(PT4)	(PT5)
Proportion of dams with record or Missing rate →	10% (0.9)	20% (0.8)	50% (0.5)	90% (0.1)	100% (0.0)
No. of animals in base generation	<u>Sire</u> <u>Dam</u> 50 400	<u>Sire</u> <u>Dam</u> 50 400	<u>Sire</u> <u>Dam</u> 50 400	<u>Sire</u> <u>Dam</u> 50 400	<u>Sire</u> <u>Dam</u> 50 400
No. of dams with Records	~109	~218	~544	~979	~1088
No. of dams contributed in all matings	~1088	~1088	~1088	~1088	~1088
No. of animals	~4229	~3794	~3468	~3359	~3250
No. of records	~2880	~2880	~2880	~2880	~2880
Number of generations	9	9	9	9	9
Pregnancy rate	80%	80%	80%	80%	80%
Female replacement rate	30%	30%	30%	30%	30%
Male replacement rate	50%	50%	50%	50%	50%

~ Average over 100 replicates

3.1.1. Data simulation

Data were generated using a stochastic procedure similar to that described by Gerstmayer (1992) and Van Vleck (1994). The base population consisted of 50 males and 400 females that were assumed to be unrelated, unselected and sampled randomly from a conceptually infinite population. Animals in the base generation (generation 0) were mated at random ($400/50 = 8$ females per male) to produce 320 progeny (80% pregnancy rate), giving 160 males and 160 females, in generation one. Ten generations were simulated including the base generation. After two generations, sires were replaced to prevent high inbreeding rates. Each sire had a chance to become a parent of future progeny for two generations.

Simulation of data was performed on the basis of the following univariate model:

$$y = \text{mean} + S + A + a + m + pe + e$$

where,

y = phenotypic record,

S = sex of individuals (male =1; female =2),

A = age of dam (2, 3, 4, 5, and 6 years),

a = direct additive genetic effect,

m = maternal additive genetic effect,

pe = maternal permanent environmental effect,

e = random residual.

Values for **e** and **pe** were randomly drawn from a normal distribution with mean zero and variance σ_e^2 ($e \sim N(0, \sigma_e^2)$) and σ_{pe}^2 ($pe \sim N(0, \sigma_{pe}^2)$), respectively. Base animal additive and maternal genetic values were also generated from random normal distributions with means equal to zero and variances of σ_a^2 and σ_m^2 respectively. As additive direct and

maternal effects are genetically correlated, values for the two traits were generated simultaneously. Genetic values for animals of later generations (generation 1 to 9) were simulated as follows:

$$\mathbf{a} = \frac{1}{2} \mathbf{a}_s + \frac{1}{2} \mathbf{a}_d + \mathbf{MSa} \quad \mathbf{m} = \frac{1}{2} \mathbf{m}_s + \frac{1}{2} \mathbf{m}_d + \mathbf{MSm}$$

$$\begin{pmatrix} \mathbf{MSa} \\ \mathbf{MSm} \end{pmatrix} = \begin{pmatrix} T_{11} & 0 \\ T_{12} & T_{22} \end{pmatrix} \begin{pmatrix} V_1 \\ V_2 \end{pmatrix}$$

$$\text{where } \begin{pmatrix} V_1 \\ V_2 \end{pmatrix} \sim N(0, I) \quad \text{and} \quad \begin{pmatrix} \mathbf{T} & \mathbf{T}' \\ \begin{pmatrix} T_{11} & 0 \\ T_{12} & T_{22} \end{pmatrix} & \begin{pmatrix} T_{11} & T_{12} \\ 0 & T_{22} \end{pmatrix} \end{pmatrix} = \frac{1}{2} \begin{pmatrix} \sigma^2_a & \sigma_{am} \\ \sigma_{am} & \sigma^2_m \end{pmatrix}$$

where $\mathbf{T}$ is the lower triangular matrix generated by a Cholesky decomposition, $\mathbf{a}_s$ and $\mathbf{a}_d$ are direct and $\mathbf{m}_s$ and $\mathbf{m}_d$ represent maternal additive genetic values of sire and dam of an individual respectively. The value of $\mathbf{MS}$ is the Mendelian sampling effect of an individual which was assumed to be independent of $\mathbf{a}_s$, $\mathbf{a}_d$, $\mathbf{m}_s$ and $\mathbf{m}_d$ (Bulmer, 1971). The inbreeding rates were computed using the algorithm of Meuwissen and Luo (1992) in the VCE package (Table 3.2). The average inbreeding rate (Table 3.2) was very small (2%) in the simulated population, and was not taken into account in the model of analysis or when Mendelian sampling was generated.

Table 3.2. Inbreeding rate in the pedigree file

Inbreeding (%)	# of animals
0	2502
0 < 5	634
5 < 10	43
10 < 15	26
25 < 30	19
30 < 35	1
Average inbreeding	2%

3.1.2. Simulation of fixed effects

Three fixed effects including sex (S), age of dam (A) and generation (G) were simulated for each individual. Two sex groups (50% male and 50% female) were equally assigned per generation by using random uniform distribution. Depending on the sex, trait means were altered by ± 5 units. Base means were 100 and 200 units for trait 1 and trait 2, respectively. Frequency of sexes after nine generations of random mating is shown in Table 3.3.

Table 3.3. Frequency of sex classes after 9 generations of random mating

Sex	Frequency	Percent	Cumulative Frequency	Cumulative Percent
Male (1)	1440	50.00	1440	50.00
Female (2)	1440	50.00	2880	100.00

Age of dam was categorized into one of five groups. The percentage of dams in generation 0 of age 2, 3, 4, 5 and 6 were 15%, 45%, 25%, 10% and 5%, respectively. The trait mean was increased as the age of dam increased. For example, a 2 year old dam had a 2 unit increase in the trait means. Frequencies of ages of dam after nine generations of random mating are presented in Table 3.4.

Table 3.4. Frequency of Age of dam after 9 generations of random mating

Age (yr)	Frequency	Percent	Cumulative Frequency	Cumulative Percent
1	796	25.07	796	25.07
2	709	22.33	1505	47.40
3	602	18.96	2107	66.36
4	497	15.65	2604	82.02
5	390	12.28	2994	94.30
6	158	4.98	3152	99.28
7	23	0.72	3175	100.00

Nine overlapping generations, as well as the base population, were simulated for each population type in order to have enough records of individuals for estimation of variance components and enough dam-offspring pairs for estimation of maternal variances. After nine generations of random mating, 2,880 performance records were generated for the full data set (PT5).

3.1.3. Selection and replacement strategy

No selection schemes were used on either trait for any population structure. Random mating was applied in each generation. In terms of replacement, half of the sires were randomly selected from the males of the current generation and the other half randomly kept from the previous generation. Each sire stayed in service for a maximum of two generations. Thirty percent of the dams were randomly selected from the females of the current generation and the rest (70%) were kept randomly from the previous generation. Therefore, 30% of females in each generation were culled. Culling strategy for dams was based on two criteria. Dams were culled which failed to become pregnant and produce progeny, and dams were culled based on age. Older dams had a higher chance to be culled. As a result, dams had an opportunity to have at most five progeny. The average number of progeny per dam was 2.6 in all data sets. Frequency of dams classified by their number of progeny is shown in Table 3.5.

To simulate five population types, PT5 was first created as a complete dataset (with all female offspring later becoming dams of offspring for subsequent generations) and then other population types (PT4 to PT1) were created from PT5 by manipulating the number of dams with records. Based on this strategy, the number of dams which contributed to

the matings in each population type was the same. However, the number of dams with performance records decreased from PT5 to PT1 in order to break the link of a dam to her progeny (Table 3.1). According to this plan, some of the dam-offspring links in the data were removed gradually from PT5 to PT1 until only 10% of female offspring appeared as a dam (PT1). As the number of animals with records in the data file was constant in all scenarios, depending on the missing rates and the number of dams with no records, some dam IDs were replaced with new ID numbers in the data and pedigree files.

Table 3.5. Frequency of progeny per dam after 9 generations of random mating

Progeny/dam	Frequency	Percent	Cumulative Frequency	Cumulative Percent
1	331	30.76	331	30.76
2	248	23.05	579	53.81
3	171	15.89	750	69.70
4	129	11.99	879	81.69
5	197	18.31	1076	100

3.1.4. Prior values of variance components (True values)

On the basis of the three different ratios (1:3, 1:1, and 3:1) of direct to maternal genetic variances, three parameter sets for each trait of interest were investigated (Table 3.6). Three genetic correlations (-0.5, 0.0, +0.5) between direct and maternal components were investigated within each parameter set Table 3.6.

Three different values (0.0, 0.3, and 0.8) of genetic correlation between two traits, indicated as zero, medium, and high, were investigated. Overall 135 scenarios were simulated based on these criteria. One hundred replicates were used for each scenario.

Table 3.6. Values for the parameter set of trait 1 and trait 2

Trait	Parameter Set		σ_d^2	σ_m^2	r_{dm}
	Direct:Maternal	Scenario			
1	1:3	1	10	30	- 0.5
		2	10	30	0.0
		3	10	30	+ 0.5
	1:1	4	20	20	- 0.5
		5	20	20	0.0
		6	20	20	+ 0.5
	3:1	7	30	10	- 0.5
		8	30	10	0.0
		9	30	10	+ 0.5
2	3:1	1	30	10	- 0.5
		2	30	10	0.0
		3	30	10	+ 0.5
	1:1	4	20	20	- 0.5
		5	20	20	0.0
		6	20	20	+ 0.5
	1:3	7	10	30	- 0.5
		8	10	30	0.0
		9	10	30	+ 0.5

Phenotypic variance ($\sigma_p^2 = 100$),
 Permanent environmental variance ($\sigma_{pe}^2 = 5$)
 Residual variance ($\sigma_e^2 = 55$)

3.1.5. Pedigree information

For all scenarios, full pedigree information, composed of animal, sire, and dam identifications (ID), was used. As the number of animals with records in the data file was constant in all scenarios, depending on the missing rates and the number of dams with no records, some dam IDs were replaced with new ID numbers in the data and pedigree files. Consequently, the number of animals in the pedigree file increased as the missing rate of dams increased. The dam and her record were in the data, but the link to her progeny was broken.

3.1.6. Assumptions of the simulation

- Two traits within a closed herd composed of nine overlapping fixed size generations were included. Overlapping generations were utilized to give a more complex relationship structure.
- Animals in the base population were unselected, non-inbred, unrelated, and sires had no prior records of performance.
- Five population types were assumed depending on percentage of dams with records available (10, 20, 50, 90, or 100%).
- Dams were randomly mated to sires in each generation.
- A pregnancy rate of 80% for females and an equal sex ratio were included in each generation.
- For estimating variance components, all observations were used.
- Number of parities per cow and culling rate of sires were restricted to 5 and 50% respectively, in order to keep generation intervals short, to maintain equal family size, and to lower the rate of inbreeding.
- For each population type and parameter set, 100 replicates were generated.
- Sex of offspring, age of dam, and generation were fixed effects in the model.
- In order to have enough records for dams in each population type, particularly in PT1, the number of dams was set to 400 in the base generation of each scenario.

3.2. Statistical Analysis

All simulation procedures were programmed using the SAS package. Variance components were estimated using restricted maximum likelihood (REML) with an average information algorithm (Johnson and Thompson, 1995) through the DMU

statistical package (Madsen and Jensen, 2002). The standard error squared (SE)² of the mean (100 replicates) for each scenario was used as a weighting factor in the statistical analyses. The SE of the estimates was used as a criterion for precision and bias of estimates was used as a criterion of accuracy of estimates. Total bias (%) of the whole set of estimated parameters at one time was also calculated and was used as an indicator of bias percentage of all parameters in different population structure.

3.2.1. Model of analysis

Estimation of variance components was accomplished utilizing the same multi-trait linear model as used to generate the data:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Zd} + \mathbf{Mm} + \mathbf{Wp} + \mathbf{e}$$

For two traits in a combined analysis, the multi-trait animal model can be presented as follows:

$$\begin{bmatrix} \mathbf{y}_1 \\ \mathbf{y}_2 \end{bmatrix} = \begin{bmatrix} \mathbf{X}_1 & 0 \\ 0 & \mathbf{X}_2 \end{bmatrix} \begin{bmatrix} \mathbf{b}_1 \\ \mathbf{b}_2 \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_1 & 0 \\ 0 & \mathbf{Z}_2 \end{bmatrix} \begin{bmatrix} \mathbf{d}_1 \\ \mathbf{d}_2 \end{bmatrix} + \begin{bmatrix} \mathbf{M}_1 & 0 \\ 0 & \mathbf{M}_2 \end{bmatrix} \begin{bmatrix} \mathbf{m}_1 \\ \mathbf{m}_2 \end{bmatrix} + \begin{bmatrix} \mathbf{W}_1 & 0 \\ 0 & \mathbf{W}_2 \end{bmatrix} \begin{bmatrix} \mathbf{p}_1 \\ \mathbf{p}_2 \end{bmatrix} + \begin{bmatrix} \mathbf{e}_1 \\ \mathbf{e}_2 \end{bmatrix} \quad (3.1)$$

where

- $\mathbf{y}_i$ = vector of observation for the i th trait ($i = 1, 2$)
- $\mathbf{b}_i$ = vector of fixed effects for the i th trait
- $\mathbf{d}_i$ = vector of random direct genetic effects
- $\mathbf{m}_i$ = vector of random maternal genetic effects
- $\mathbf{p}_i$ = vector of permanent environmental effects
- $\mathbf{X}_i, \mathbf{Z}_i, \mathbf{M}_i,$ and $\mathbf{W}_i$ = incidence matrices relating records of the i th trait to fixed, direct, maternal genetic and permanent environmental effects respectively
- $\mathbf{e}_i$ = vector of random residual effects

The mixed model equations (MME) for the best linear unbiased prediction (BLUP) of $\mathbf{d}$, $\mathbf{m}$, $\mathbf{p}$, and estimable functions of $\mathbf{b}$ in equation 3.1 were as follows:

$$\begin{bmatrix} \hat{\mathbf{b}} \\ \hat{\mathbf{d}} \\ \hat{\mathbf{m}} \\ \hat{\mathbf{p}} \end{bmatrix} = \begin{bmatrix} \mathbf{X}'\mathbf{R}^{-1}\mathbf{X} & \mathbf{X}'\mathbf{R}^{-1}\mathbf{Z} & \mathbf{X}'\mathbf{R}^{-1}\mathbf{M} & \mathbf{X}'\mathbf{R}^{-1}\mathbf{W} \\ \mathbf{Z}'\mathbf{R}^{-1}\mathbf{X} & \mathbf{Z}'\mathbf{R}^{-1}\mathbf{Z} + \mathbf{k}_1 & \mathbf{Z}'\mathbf{R}^{-1}\mathbf{M} + \mathbf{k}_2 & \mathbf{Z}'\mathbf{R}^{-1}\mathbf{W} \\ \mathbf{M}'\mathbf{R}^{-1}\mathbf{X} & \mathbf{M}'\mathbf{R}^{-1}\mathbf{Z} + \mathbf{k}_2 & \mathbf{M}'\mathbf{R}^{-1}\mathbf{M} + \mathbf{k}_3 & \mathbf{M}'\mathbf{R}^{-1}\mathbf{W} \\ \mathbf{W}'\mathbf{R}^{-1}\mathbf{X} & \mathbf{W}'\mathbf{R}^{-1}\mathbf{Z} & \mathbf{W}'\mathbf{R}^{-1}\mathbf{M} & \mathbf{W}'\mathbf{R}^{-1}\mathbf{W} + \mathbf{k}_4 \end{bmatrix}^{-1} \begin{bmatrix} \mathbf{X}'\mathbf{R}^{-1}\mathbf{Y} \\ \mathbf{Z}'\mathbf{R}^{-1}\mathbf{Y} \\ \mathbf{M}'\mathbf{R}^{-1}\mathbf{Y} \\ \mathbf{W}'\mathbf{R}^{-1}\mathbf{Y} \end{bmatrix} \quad (3.2)$$

where,

$$\mathbf{y} = \begin{bmatrix} \mathbf{y}_1 \\ \mathbf{y}_2 \end{bmatrix}, \quad \hat{\mathbf{b}} = \begin{bmatrix} \hat{\mathbf{b}}_1 \\ \hat{\mathbf{b}}_2 \end{bmatrix}, \quad \hat{\mathbf{d}} = \begin{bmatrix} \hat{\mathbf{d}}_1 \\ \hat{\mathbf{d}}_2 \end{bmatrix}, \quad \hat{\mathbf{m}} = \begin{bmatrix} \hat{\mathbf{m}}_1 \\ \hat{\mathbf{m}}_2 \end{bmatrix}, \quad \hat{\mathbf{p}} = \begin{bmatrix} \hat{\mathbf{p}}_1 \\ \hat{\mathbf{p}}_2 \end{bmatrix}$$

$$\mathbf{X} = \begin{bmatrix} \mathbf{X}_1 & 0 \\ 0 & \mathbf{X}_2 \end{bmatrix}, \quad \mathbf{Z} = \begin{bmatrix} \mathbf{Z}_1 & 0 \\ 0 & \mathbf{Z}_2 \end{bmatrix}, \quad \mathbf{M} = \begin{bmatrix} \mathbf{M}_1 & 0 \\ 0 & \mathbf{M}_2 \end{bmatrix}, \quad \mathbf{W} = \begin{bmatrix} \mathbf{W}_1 & 0 \\ 0 & \mathbf{W}_2 \end{bmatrix}$$

$$k_1 = G_1 \otimes A^{-1}, \quad k_2 = G_2 \otimes A^{-1}, \quad k_3 = G_3 \otimes A^{-1}, \quad k_4 = G_4 \otimes I_C,$$

$$G_1 = \begin{bmatrix} \sigma^2_{d1} & \sigma_{d1d2} \\ \sigma_{d1d2} & \sigma^2_{d2} \end{bmatrix}^{-1}, \quad G_2 = \begin{bmatrix} \sigma_{d1m1} & \sigma_{d1m2} \\ \sigma_{d2m1} & \sigma_{d2m2} \end{bmatrix}^{-1},$$

$$G_3 = \begin{bmatrix} \sigma^2_{m1} & \sigma_{m1m2} \\ \sigma_{m1m2} & \sigma^2_{m2} \end{bmatrix}^{-1}, \quad G_4 = \begin{bmatrix} \sigma^2_{p1} & \sigma_{p1p2} \\ \sigma_{p1p2} & \sigma^2_{p2} \end{bmatrix}^{-1}.$$

The (co)variance matrix for residual effects, R , is as follows:

$$R = R_0 * I_N \quad R_0 = \begin{bmatrix} \sigma^2_{e1} & \sigma_{e1e2} \\ \sigma_{e2e1} & \sigma^2_{e2} \end{bmatrix}$$

where

N is the number of records, C is the number of cows, and I is an identity matrix.

In the above equations “ $\otimes$ ” denotes the direct product of the matrices involved and A is the additive relationship matrix.

When two traits with maternal effects were used in the model, the structure of the (co)variance matrix would be different compared to single trait analysis. As well, the number of estimated (co)variances will increase. For example, in this study, 16 (co)variance components needed to be estimated; three for permanent environmental effects, three for residual effects and 10 for direct and maternal genetic effects.

3.2.2. REML Analysis

In the field of animal breeding, REML is one of the most used procedures for estimating variance components (Thompson, 1962). In general, the algorithms which are utilized to obtain REML estimates can be grouped in accordance to the order of derivatives used. There are typically three groups of algorithms: 1) first and second derivatives of the likelihood (or approximation of second derivatives), 2) first derivatives only, and 3) derivative free methods. The REML procedure maximizes the joint likelihood of all error contrasts rather than of the data as in maximum likelihood. In the original description of REML, Patterson and Thompson (1971) suggested that the score equations for the variance components may be solved iteratively using the Fisher scoring (FS) algorithm. For many applications, particularly in animal breeding, this strategy presents computational difficulties due to the large size of the matrices to be inverted and multiplied. Thompson (1977) presented an overview of the methodology with particular reference to animal breeding applications and showed how some of the computational burdens of the FS algorithm may be overcome. In some situations use of observed information might be preferred to the use of expected information. Johnson and Thompson (1995) applied AI-REML in an animal breeding context. They found it more

efficient when compared to the Derivative Free (DF) and Expectation Maximization (EM) algorithms. AI-REML converged five times faster than the DF algorithm and 15 times faster than EM algorithm. The Newton-Raphson method uses first and second derivatives to compute the estimates of genetic parameters that maximize the likelihood function. The logarithm of the restricted maximum likelihood function is (e.g., Graser et al., 1987)

$$L = -\frac{1}{2}[\text{constant} + \ln|V| + \ln|X'V^{-1}X| + y'Py]$$

where,

$$P = V^{-1} - V^{-1}X(X'V^{-1}X)^{-1}X'V^{-1}$$

The Newton-Raphson method uses the matrix of second derivatives (Hessian, $\mathbf{H}$) to maximize the likelihood function at $m + 1^{\text{st}}$ iterations,

$$\theta^{m+1} = \theta^m - (H^m)^{-1} K^m$$

In the above equation θ is the vector of parameters and K is the vector of first derivatives of the likelihood function (the gradient or score function) for which the i th element can be written as:

$$k_i = \frac{\partial L}{\partial \theta_i} = -\frac{1}{2} \left[\text{tr} \left(P \frac{\partial V}{\partial \theta_i} \right) - y'P \frac{\partial V}{\partial \theta_i} Py \right]$$

In Fisher's method of scoring, $\mathbf{H}$ is replaced with its expected value, $E[\mathbf{H}]$:

$$\theta^{m+1} = \theta^m - (E[H^m])^{-1} K^m$$

Where, $-E[\mathbf{H}]$ is also called an *information matrix*. The matrices H and $E[\mathbf{H}]$ can be written as:

$$H = \frac{\partial^2 L}{\partial \theta_i \partial \theta_j} = \frac{1}{2} \text{tr} \left(P \frac{\partial V}{\partial \theta_i} P \frac{\partial V}{\partial \theta_j} \right) - y'P \frac{\partial V}{\partial \theta_i} P \frac{\partial V}{\partial \theta_j} Py$$

and

$$E[H] = E\left[\frac{\partial^2 L}{\partial \theta_i \partial \theta_j}\right] = -\frac{1}{2} \text{tr}\left(P \frac{\partial V}{\partial \theta_i} P \frac{\partial V}{\partial \theta_j}\right).$$

Both the Hessian and its expected value include terms that are computationally demanding. Johnson and Thompson (1995) noticed that the trace parts drop out if the two expressions are averaged:

$$AvI = \frac{1}{2}(H + E[H]) = -\frac{1}{2} y' P \frac{\partial V}{\partial \theta_i} P \frac{\partial V}{\partial \theta_j} P y$$

Taking advantage of algebraic simplifications makes computing the average information matrix feasible in some cases. AI algorithm is useful for a comparatively large number of highly correlated measurements where a covariate function of low order suffices to describe the data adequately. Convergence of the algorithm is reliable; however, processing time and memory requirements are often prohibitive for large datasets or for models with many covariance parameters. A reduced number of iterations is a significant advantage for using AI algorithm over both DF and EM.

3.2.3. Convergence Criteria (CC)

In order to obtain breeding values using Best Linear Unbiased Prediction (BLUP), for the analysis of large amounts of data, large sets of mixed model equations (MME) need to be solved iteratively, which also involves considerable computing time. In practice, breeders only require the solutions periodically to select their best individuals, so that computing time is not usually a limiting factor. In simulation studies involving genetic evaluation of individuals by BLUP, many rounds of evaluation are required for each simulated population. Several replicates are usually needed to obtain accurate results from stochastic simulations, and therefore computing time becomes a limiting factor.

One of the factors which drastically affects computing time in iterative methods is the criterion for ceasing iterations, or the convergence criterion. Major disadvantages for iterative methods can be a slow convergence rate or no convergence at all under certain circumstances. The more inflexible the convergence criterion, the more iteration, and hence longer computing time are required.

Quaas et al. (1984) stated that there is no certain answer to the question, “how does one know when to stop?” However, a number of possible convergence criteria (CC) that can be used to assess the point to terminate the iteration processes are as follows:

1. Maximum absolute change, refers to the difference between two consecutive solutions for any effect in the model, from one iteration to another is less than a certain value.
2. Sums of squares of changes in solutions from one round to the next are less than a certain value.
3. Sums of squares of differences between consecutive solutions divided by the sum of squares of new solutions, is less than a certain value.

That is,

$$\text{Convergence Criterion} = \frac{\sum_{j=1}^n (\hat{\mathbf{b}}_{ij} - \hat{\mathbf{b}}_{i-1,j})^2}{\sum_{j=1}^t \hat{\mathbf{b}}^2_{ij}}$$

where, $\hat{\mathbf{b}}_{ij}$ is the solution for element $\mathbf{j}$ after $\mathbf{i}$ iterations (Schaeffer, 1993). These criteria have units associated with them and are not scale free, which means that a particular value of a convergence criterion does not have the same meaning for all traits.

Meaningful comparisons of two CC for different traits can only be identified by experience. Using the first criterion, a maximum absolute change of less than 10^{-6} of the mean might suffice to terminate the iteration (Schaeffer, 1993). Quaas et al. (1984) used the square root of criterion 3 and suggested that 10^{-4} could be sufficient.

VanVleck and Dwyer (1985) stated that for the purpose of ranking animals, a less precise stopping point could be sufficient as compared to when genetic evaluations are used to predict genetic trends. Also all previous discussions of CC have focused on genetic evaluations of real data where computing time is often not an important factor. Less severe criteria would probably be more appropriate in simulation studies to achieve a reasonable accuracy of evaluation. In this study, the convergence criterion for AI-REML was when the function value ($-2 \log L$) was less than 10^{-6} for both traits.

3.2.4. Bias

Bias is a term which refers to how far the average statistic lies from the parameter it is estimating, that is, the error which arises when estimating a quantity. Bias is defined as the average difference between the estimate of a parameter and its unknown true value. Bias can be used as an indicator of the accuracy of prediction. When there is no difference between true and predicted values, the correlation between true and predicted is one. If the differences between true and predicted values increase, the accuracy will decrease. So, calculating bias of (co)variance estimates helps us to find out how much the estimates are far from the true values and could be used as an indicator of accuracy of prediction. A bias of 10% for example will not be a problem for estimating genetic

parameters, while it will have serious effects on the prediction of genetic values in selection schemes (Clement et al. 2001). In this study, bias of four parameters of trait 1 such as direct genetic variance, maternal genetic variance, and maternal permanent environmental variance and also direct-maternal covariance was calculated for each population structure. Total bias (%) of the whole set of estimated parameters (13 parameters) for traits 1 and 2 were calculated by using the Euclidean Norm method (see Appendix 3).

3.2.5. Standard Error (SE)

Standard error is a measure of an estimate's variability. The greater the standard error in relation to the size of the estimate, the less reliable the estimate. Standard error can be defined as a statistical estimate of the population standard deviation based on the mean and standard deviation of one sample which is calculated by dividing the standard deviation of the sample by the square root of the number of subjects in the sample (Kenney and Keeping, 1962). Standard error as a statistical measure of variation in a population of means can be a good criterion to indicate how well sample estimates represent population parameters. Standard error tells us the typical distance between a population mean (μ) and the mean of a sample (M) drawn from that population. If we really want to know how good our estimate of the mean is and how much variation were found around this particular estimate of the mean, we need to calculate the standard error. The standard errors (SE) of the (co)variance estimates were used as a criterion for the reliability of the estimation in this study.

3.2.6. Software Packages (SAS, DMU, PERL) used in this study

3.2.6.1. SAS

SAS software is a combination of a statistical package, a data-base management system, and a high level programming language (Cody & Smith, 1997). Like SPSS, BMDP, SYSTAT, and other statistical packages, SAS software can be used to describe a collection of data and produce a variety of statistical analyses.

SAS software was used for writing the simulation program in this study. All statistical analyses which were necessary for summarizing the results and also extracting the data from DMUAI files were done by SAS.

3.2.6.2. DMU

DMU is a package for analysing multivariate mixed models written by Per Madsen & Just Jensen, Danish Institute of Agricultural Sciences (DIAS), Dept of Animal Breeding and Genetics, Research Centre Folium, in Denmark. The DMU package was developed over a period of several years, mostly in response to the needs of various research projects. The name DMU stems from a working name used for initial procedures in the package. These procedures were used to do multivariate analysis by restricted maximum likelihood based on a derivative-free approach. This version of the DMU package is written in FORTRAN 90/95 and most dimensions are dynamic. The modules DMU1 and DMUAI were used for (co)variance estimates in this research.

DMU1. The program reads a driver file containing descriptions of data, model and variance structure, prior variances and covariances and auxiliary input to the other modules. The information in the driver file is checked. The data files are read and recoded. If specified, the pedigree file is read and recoded and if requested, inbreeding coefficients and the inverse of the numerator relationship matrix are computed and stored. The relationship matrix depends on the amount of pedigree information available and on assumptions about inbreeding. Therefore pedigree information can be specified in different ways.

DMUAI. This module can be used for estimation of (co)variance components using Average Information Restricted Maximum Likelihood (AI-REML) (Jensen et al. 1997). The algorithm is based on the use of Average Information (AI) as second differentials of the likelihood function. The AI is obtained by averaging the information matrices based on observed and expected information. The module can also use Expectation Maximisation (EM) to maximise the restricted likelihood function. Asymptotic standard errors of estimated (co)variance components are obtained from the Average Information matrix. The standard errors of interclass correlations and correlations between random effects (e.g. genetic correlations) were computed based on a Taylor series approximation. AI-REML can yield updates of the parameter vector that are outside the parameter space. To overcome this problem different methods are implemented in DMUAI.

Estimated parameters

DMUAI writes an ASCII file with estimated (co)variance components (PAROUT). The format of this file is the same as used for the prior (co)variances read by DMU1. This file can thus be used as priors for subsequent analyses.

Standard errors of estimated parameters

DMUAI also writes an ASCII file containing estimated (co)variance components, their asymptotic standard errors and correlations among the estimates (PAROUT_STD). The information in this file can be used to calculate asymptotic standard errors of functions of the estimated (co)variance components.

The DMU package can handle a maximum of 31 traits in one analysis. This can not be changed by the user.

Estimates of (co)variance components (σ^2_d , σ^2_m , σ^2_{pe} , σ^2_e , and σ_{dm}) and estimates of the effects included in the model were obtained using the DMU program (Madsen and Jensen, 2002).

3.2.6.3. PERL

PERL is a general-purpose scripting language originally developed for text manipulation and now used for a wide range of tasks including system administration, web development, network programming, and more.

A PERL script consists of a sequence of declarations and statements which run from the top to the bottom. Loops, subroutines and other control structures allow you to jump around within the code. PERL is a free-form language; you can format and indent it however you like. PERL script statements are simply written in a straight forward fashion. There is no need to have a main function.

PERL was used in this study for implementing three programs (SAS, DMU1, and DMUAI) simultaneously. Following chart give the procedures of the analyses in the PERL program.

Data Analysis diagram in PERL program

Chapter 4

Results and Discussion

4.1. Estimation of (co) variance components

Estimates of variance components and genetic parameters for two traits, with their standard errors for each population type were extracted from DMU output files. All estimates were obtained using restricted maximum likelihood (REML) based on the average information algorithm. An animal model for two traits with several fixed and random effects was used. For each trait in the analysis, convergence was considered to have been reached when the value of $-2\log L$ was less than 10^{-6} . Direct genetic variances (σ^2_d), maternal genetic variances (σ^2_m), genetic covariances between direct and maternal (σ_{dm}), and maternal permanent environmental variance (σ^2_{pe}) for traits 1 and 2 are presented in Tables 4-1 to 4-15. The direct-maternal genetic correlation (r_{dm}), direct heritability (h^2_d), and maternal heritability (h^2_m) for both traits were calculated after convergence. Standard errors of the mean of 100 replicates of each component and bias were calculated for all parameters. Total bias as a percentage of the whole set of estimated genetic parameters for traits 1 and 2 also was calculated by using the Euclidean norm procedure.

4.2. Model for analyzing the results

(Co) variance component estimates was obtained from each scenario were analysed with the following model to determine the significance of each factor on (co)variance estimation.

$$V = \text{mis} + t + \text{par} + r + (\text{2 way interactions}) + (\text{3 way interactions})$$

where V = (co)variance estimate of interest (e.g. σ_{dl}^2 , σ_{ml}^2 , σ_{dlml} , etc.)

mis = missing rate of dam's record (0.0, 0.1, 0.5, 0.8, and 0.9)

t = correlation between two traits (0.0, 0.3, and 0.8)

par = parameter set (values of direct variance; 10, 20, and 30)

r = correlation between direct and maternal (-0.5, 0.0, +0.5)

2 way interactions: (mis×t, mis×par, mis×r, t×par, t×r, par×r)

3 way interactions: (mis×t×par, mis×par×r, mis×t×r, t×par×r)

× = interaction between factors (two and three way interactions)

mis, t, par, and r were treated as classification effects. Proc GLM in SAS was used to test the significance of each factor on (co)variance estimates. A summary of analyses of variance is presented in Table 4.16.

4.2.1. Factors affecting variance component estimates

Based on the results in Table 4.16, all main effects (*mis*, *t*, *par*, and *r*) significantly affected the (co)variance estimates. The proportion of dams without records (*mis*) was found to depend on genetic parameter sets (*par*), correlation between direct and maternal effects (*r*), and to some extent on the correlation between the two traits (*t*). Most two way interactions were significant but *misxr*, *parxr* and *misxpar* interactions had significant effects for all parameter estimates. Some three way interactions also were significant; particularly the *misxparxr* interaction which had a major impact on the (co)variance estimates.

4.2.1.1. Impact on estimates of maternal variance of trait1 (σ^2_{m1})

There were significant differences in the variance component estimates due to different proportions of dams without records (*mis*) within different levels of correlation between direct and maternal genetic effects (*r*), different levels of correlation between traits (*t*) and different parameter sets (*par*). The *misxparx* interaction could take many forms, referred to as cross-over interactions and it would be difficult to explain all the underlying circumstances in such interactions.

Missing Rates: By increasing the missing rate from 0 to 0.1, the estimates of maternal genetic variance increased in all cases, and were overestimated, particularly when the direct and maternal correlation was positive. When the missing rate increased from 0.1 to 0.9, and direct and maternal correlation was negative the estimates decreased and were underestimated (Figure 4-1, graph At1 to Ct3). There were no significant differences between maternal variance estimates when the missing rate was either 0.8 or 0.9 within each level of correlation between direct and maternal effects ($P>0.05$). Less upward biased estimates were found at a missing rate of 0.9, when maternal variance was greater than direct variance, *t* was 0.8, and the direct and maternal correlation was negative (Figure 4.1, graph At1 to At3).

Direct-Maternal Correlations: There were significant differences ($P>0.05$) between maternal variance estimates within the correlation between direct and maternal (*r*) effects in all levels of missing rates. More biased estimates were obtained when the correlation between direct and maternal effects was either negative or positive. Trends of variance

estimates over missing rates were similar within each level of correlation between direct-maternal but with different magnitude. The most upward biased estimates were obtained when the missing rate was 0.8 or 0.9, direct-maternal correlation was negative, t was zero, and maternal variance was greater than direct variance (Figure 4.1, graph At1).

Trait Correlations: The trends of maternal variances across missing rates were found to be more similar when the correlation between traits was high ($t = 0.8$), particularly for a negative direct-maternal correlation but greater differences were detected when the true maternal variance and the true direct variance was not equal (Figure 4-1, graphAt3, Bt3, and Ct3). Less biased estimates were obtained when the direct-maternal correlation was zero and true direct and maternal variances were equal to 20 (Figure 4-1, graph Bt1 to Bt3). Indeed, no significance effect on maternal variance estimates across missing rate was observed by increasing the correlation between traits from zero to 0.8.

As shown in most graphs of Figure 4.1, underestimates of maternal variance were obtained when the missing rate was high ($mis = 0.9$) and direct-maternal correlation was negative. When only 10% of dams have performance records, the maternal variance estimates were the lowest particularly when true maternal variance was greater than direct variance. Generally, when the percentage of dams without records was high, a low bias of maternal genetic variance was obtained when the correlation between direct and maternal effects was zero and the true direct and maternal variances were equal.

4.2.1.2. Impact on estimates of maternal permanent environmental variance of trait1 (σ^2_{pe1})

Missing Rates: By increasing the missing rate from 0 to 0.1, the estimates of maternal permanent environmental variances decreased in all cases and were biased downward. When the missing rate increased from 0.1 to 0.9, the estimates decreased and were biased downward (Figure 4-2, graph At1 to Ct3) except when the direct-maternal correlation was negative and direct variance was 10 or 20 (Figure 4-2, graph At1 to Bt3). There were no significant differences between maternal permanent environmental variance estimates when missing rate was either 0.5 or 0.8, the direct-maternal correlation was negative, and direct and maternal variance were equal to 20, within each level of t (Figure 4-2, graph Bt1 to Bt3). The most reliable estimates was found between missing rates of 0 and 0.1, when maternal variance was greater than direct variance, t was 0.8, and the correlation between direct-maternal was negative (Figure 4-2, graph At3).

Direct-Maternal Correlations: There were significant differences ($P < 0.05$) between maternal permanent environmental variances at different levels of the correlation between direct and maternal(r) effects and missing rates from 0.1 to 0.9. More biased estimates were obtained when the correlation between direct and maternal was positive ($r = + 0.5$) and the true direct variance was greater than the true maternal variance (Figure 4-2, graph Ct1 to Ct3). As shown in most graphs, trends of variance estimates over missing rates were similar, particularly when the direct-maternal correlation was zero or positive. The most upward biased estimates were obtained when the missing rate was 0.8 or 0.9 and correlation between direct and maternal was also positive (Figure 4.2, graph Ct1 to Ct3).

Trait Correlations: The trends of maternal permanent environmental variances over missing rates were found to be similar at all levels of correlation between traits. The correlation between the two traits had no significant effect on variance estimates, but greater differences were detected when the true maternal variance was smaller than the true direct variance (Figure 4.2, graph Ct1 to Ct3). Most biased estimates were obtained when there was no correlation between traits and correlation of direct-maternal was positive (Figure 4.2, graph Ct1).

Maternal permanent environmental variance estimates varied the most when the correlation between direct and maternal was zero or negative and the correlation between traits was zero (Figure 4.2, graph At1). In most graphs of Figure 4.2, underestimates of maternal permanent environmental variance were obtained when the proportion of dams without records was the highest ($mis = 0.9$). There were no significant differences on variance estimates at missing rates of 0.8 or 0.9 when the direct and maternal correlation was positive. Generally, less biased estimates were found when the direct-maternal correlation was negative and the true maternal variance was greater than true direct variance (Figure 4.2, graph At1).

4.2.1.3. Impact on estimates of direct-maternal covariance of trait1 (σ_{d1m1})

Missing Rates: By increasing the missing rate from 0 to 0.9, the estimates of direct-maternal covariance increased in almost all cases, and were biased upward, except when the missing rate was 0.1, the direct-maternal correlation was negative, trait correlation was zero or 0.3, and maternal variance was greater or equal to the direct variance (Figure 4.3, graph At1, At2, Bt1, Bt2). When the missing rate increased from 0.1 to 0.5, the

estimates increased and were biased upward when trait correlation was zero (Figure 4.3, graph At1, Bt1, Ct1), but by increasing the correlation between traits, estimates were almost constant. There were significant differences between direct-maternal covariance estimates when missing rate was 0.5, 0.8 or 0.9 in all levels of correlation between direct and maternal effects ($P < 0.05$). Less biased estimates were found for a missing rate of 0.1, when true direct and maternal variance were equal to 20, in all levels of correlation between direct and maternal (Figure 4.3, graph Bt1 to Bt3).

Direct-Maternal Correlations: There were no significant differences ($P > 0.05$) between direct-maternal covariances over missing rate when the correlation between direct and maternal was negative and maternal variance was greater than direct variance (Figure 4.3, graph At1 to At3). More biased estimates were obtained when the correlation between direct and maternal was positive ($r = +0.5$), the trait correlation was zero, and true direct variance was greater than true maternal variance (Figure 4.3, graph Ct1). Trends of covariance estimates over missing rates were almost similar when correlation of direct-maternal was zero or positive. The most upward biased estimates were obtained when the missing rate was 0.9, the trait correlation was zero and the correlation between direct and maternal was also negative (Figure 4.3, graph At1, to At3).

Trait Correlations: The trends of direct-maternal covariances over missing rates were found to be similar in different levels of the correlation between traits, but greater differences were detected when the correlation between traits was 0.8 (Figure 4.3, graph Ct3). The most biased estimates were obtained for a missing rate of 0.9, when there was

no correlation between traits, direct and maternal correlation was positive, and true direct variance was greater than true maternal variance (Figure 4.3, graph Ct1).

Direct-maternal covariance estimates varied the most when the correlation between traits was zero and direct and maternal variances were equal to 20. As shown in most graphs of Figure 4.3, overestimates of the direct-maternal covariance were obtained when the proportion of dams without records was the highest ($mis = 0.9$) and the direct-maternal correlation was positive. Generally, no significant difference of direct-maternal covariance estimates was observed from a missing rate of 0.0 to 0.5, but by increasing missing rate from 0.5 to 0.9 these estimates had significant differences ($P < 0.05$).

4.2.1.4. Impact on estimates of direct variance of trait1 (σ^2_{d1})

Missing Rates: By increasing the missing rate from 0 to 0.1, the estimates of direct variances decreased in all cases, and were biased downward (Figure 4-4, graph At1 to Ct3). When the missing rate increased from 0.1 to 0.5, the estimates were almost constant. Trends of direct variance estimates across missing rates were very similar in all levels of direct-maternal genetic correlation when true direct and maternal variances were equal (Figure 4.4, graph Bt1 to Bt3). There were no significant differences between direct variance estimates when the missing rate was either 0.1 or 0.5 within each level of correlation between traits and also correlation between direct and maternal. The most reliable estimates were found at a missing rate of 0.0, when direct variance was smaller than maternal variance, trait correlation was 0.3, in all levels of the correlation between direct and maternal (Figure 4.4, graph At2).

Direct-Maternal Correlations: There were no significant differences ($P > 0.05$) between direct variances when the correlation between direct and maternal (r) effects was zero or positive, and direct variance was equal or greater than maternal. More biased estimates were obtained when the correlation between direct-maternal was negative ($r = -0.5$). Trends of variance estimates over missing rates were similar when correlation of direct-maternal was zero or positive, particularly between missing rate of 0.1 and 0.5. The most upward biased estimate was obtained when the missing rate was high ($\text{mis} = 0.9$), correlation between direct-maternal was negative, and true direct variance was greater than maternal variance (Figure 4-4, graph Ct1 to Ct3).

Trait Correlations: The trends of direct variances over missing rates were found to be similar particularly when the correlation between traits was 0.8, and true direct variance was equal or greater than maternal, but greater differences were detected when the true maternal variance was greater than the direct variance (Figure 4.4, graph At3, Bt3, and Ct3). The most downward biased estimates were obtained when there was no correlation between traits, the direct-maternal correlation was positive, and true direct variance was greater than maternal variance (Figure 4.4, graph Ct1). Generally, the correlation between the two traits had no significant effect on direct genetic variance estimates.

Direct variance estimates varied the most when the correlation between direct and maternal was negative and the correlation between traits was zero. In Figure 4.4, the lowest estimate of direct variance was obtained when the rate of dams without records was medium ($\text{mis} = 0.5$) and the highest estimate of direct variance was obtained when

the rate of dams without records was very high ($mis = 0.9$). Generally, by increasing the correlation between traits, no improvement in direct genetic variance was observed.

4.3. Influence of mis , r , t , and par on SE of the parameter estimates

Influence of the missing rates on SE of (co)variance estimates of traits 1 and 2 in different levels of direct-maternal genetic correlation (r), different levels of correlation between traits (t), and different parameter sets (par) are presented in Figure 4.5 to 4.8.

4.3.1. SE of the maternal variance estimates

Standard errors (SE) of maternal variance estimates are presented in Figure 4-5. The SE of maternal variance estimates was smallest when all dams had performance records ($mis=0.0$). In general, larger SE of maternal variance were obtained when the proportion of dams without records was high ($mis=0.9$), the direct-maternal correlation was negative, and the true maternal variance was greater than the direct variance (Figure 4.5, graphs At1 to At3). A comparison of parameter set B, in which the direct and maternal heritability were of the same magnitude and hence directly comparable, confirmed the adverse effects of negative correlation between direct and maternal genetic effects. Despite decreasing SE with increasing correlation between the two traits, this improvement was not significant over levels of missing rate. Generally, SE of the maternal variance estimates was almost unaffected by the proportion of dams without records and more affected by the parameter sets. For example, when the true maternal variance was 10, the SE of maternal genetic variance increased by 41 percent compared

to the situation when the true maternal variance was 30. The present results confirm the findings of Gerstmayr (1992).

4.3.2. SE of the direct variance estimates

Standard errors (SE) of direct variance estimates are presented in Figure 4.6. The smallest SE of direct variance estimates were obtained when the true direct variance was smaller than true maternal variance and correlation between direct-maternal (r) was positive (Figure 4.6, graphs At1 to At3). Most higher SE of direct variance were obtained when correlation between direct-maternal was negative. The SE of the direct variance was unaffected by the proportion of dams without records, which was expected, because the direct variance in an animal model is estimated by one observation provided by each animal.

4.3.3. SE of the direct-maternal covariance estimates

Standard errors (SE) of direct-maternal covariance estimates are presented in Figure 4.7. The smallest SE of direct-maternal covariance estimates were obtained when all dams have records ($\text{mis}=0.0$), and the direct-maternal genetic correlation was positive (Figure 4.7, graphs At1 to Ct3). Greater SE were obtained when the missing rate was high ($\text{mis}=0.8$ or 0.9), the direct-maternal genetic correlation was negative, and the true values of the direct and maternal variance were equal ($d = m = 20$). No indication of improvement for SE by increasing the correlation between traits (t) was observed. The estimation of the direct-maternal covariance, as expected, was affected by the population structure particularly by an increasing missing rate from 0.5 to 0.9. This pattern was very similar to the results of Gerstmayr (1992).

4.3.4. SE of the maternal permanent environmental variance estimates

The standard error (SE) of maternal permanent environmental variance estimates is presented in Figure 4-8. No major differences were observed for the SE of maternal permanent environmental variance over missing rates. Smaller SE were obtained when the true maternal variance was smaller than direct and direct-maternal genetic correlation was positive (Figure 4.8, graphs Ct1 to Ct3). The correlation between the two traits (t) had no significant effect on SE.

4.4. Bias of (co)variance estimates

Bias averaged over the missing rates for direct, maternal, and maternal permanent environmental variance estimates, and direct-maternal covariance estimates are presented in Figures 4.9 to 4.12.

4.4.1. Bias of maternal genetic variance estimates

Average bias of maternal genetic variance estimates over missing rates at different levels of direct and maternal correlation (r), different levels of correlation between traits (t), and different values of parameter sets (par) are presented in Figure 4.9. Larger bias of maternal genetic variance estimates was obtained when the missing rate was high ($mis = 0.8$ or 0.9), trait correlation was 0.8 , the direct-maternal correlation was positive, and the true direct variance was greater than maternal variance (Figure 4.9, graph Ct3). When there was no correlation between traits, large bias was obtained when the missing rate was 0.9 , the direct-maternal correlation was negative and the true maternal variance was greater than the true direct variance (Figure 4.9, graph At1). Generally, most bias was

obtained when the missing rate was high, the direct and maternal correlation was negative or positive, and the true maternal variance was not equal to the true direct variance (Figure 4.9, graphs At1 to At3 and Ct1 to Ct3). By decreasing the true value of maternal variance from 30 to 10, the estimation of maternal variance components changed from an underestimate to an overestimate (e.g. compare graphs At1 with Ct1). When the true direct and maternal variances were equal, a larger bias was obtained with a missing rate of 0.5 when direct-maternal correlation was positive (Figure 4.9, graphs Bt1 to Bt3). The bias was statistically significant for full data sets ($\text{mis} = 0.0$) only when the correlation between direct and maternal was zero or positive and the true maternal variance was greater than the true direct variance (Figure 4.9, graphs At1 to At3).

4.4.2. Bias of maternal permanent environmental variance estimates

The average bias of maternal permanent environmental variance estimates over missing rates at different levels of correlation between direct and maternal (r), different levels of correlation between traits (t) and different values of parameter sets (par) are presented in Figure 4.10. The direction of the bias of the estimates was opposite compared with the bias in genetic maternal variance (compare Figure 4.9 and 4.10). For example, in Figure 4-9 when the true maternal variance was 10, almost all maternal genetic variance estimates were overestimated, but in Figure 4.10 all maternal environmental variance estimates were underestimated. The largest bias for maternal permanent environment occurred with a missing rate of 0.8 or 0.9, particularly when the true maternal variance was smaller than the direct variance and the direct-maternal correlation was positive (Figure 4.10, graphs Ct1 to Ct3). Less biased estimates of the maternal permanent

environmental variance were obtained when the direct-maternal correlation was negative and the ratio of true maternal and direct variance was equal to 20 (Figure 4.10, graphs Bt1 to Bt3). The bias of estimates increased over missing rates with a decreasing true value of maternal variance from 30 to 10, when the direct-maternal genetic correlation was zero or positive. By increasing the correlation between two traits, no improvement of bias was observed which means the correlation between two traits had no effect on bias.

4.4.3. Bias of direct genetic variance estimates

The average bias of direct genetic variance estimates over missing rates at different levels of direct-maternal correlation (r), different levels of correlation between traits (t) and different values of parameter sets (par) are presented in Figure 4.11. The direct genetic variance was overestimated when missing rate was 0.8 or 0.9 (Figure 4.11, graphs At1 to Ct3). Generally, the largest bias for direct genetic variance was obtained when the missing rate was high ($mis = 0.9$), the true direct variance was greater than the true maternal variance, and direct-maternal correlation was negative (Figure 4.11, graph Ct3). Direct variances were underestimated the most when the missing rate was 0.5 or less. All direct variance estimates were overestimated with an increasing true value of the direct variance from 10 to 30, the bias of estimates also increased particularly for a missing rate of 0.9. There was no significant bias when the missing rate was zero at all levels of trait and direct-maternal correlations. The correlation between the two traits had no significant effect on estimates of direct genetic variance.

4.4.4. Bias of direct-maternal genetic covariance estimates

The average bias of direct-maternal genetic covariance estimates over missing rates at different levels of direct and maternal correlation (r), different levels of correlation between traits (t), and different values of parameter sets (par) are presented in Figure 4.12. The bias of the direct-maternal covariance estimates increased with increasing missing rates, but significant differences in bias were only observed when missing rate was 0.8 and 0.9. The largest bias was obtained when the missing rate was 0.9, trait correlation was zero, the direct-maternal correlation was positive, and the true direct variance was greater than the true maternal variance (Figure 4.12, graph Ct1). When the direct-maternal genetic correlation was negative ($r = -0.5$), less bias was observed for direct-maternal covariance estimates in all cases, particularly when the true maternal variance was greater than the true direct variance (Figure 4.12, graphs At1 to At3). Correlation between traits (t) had no major effects on bias of direct-maternal covariance estimates. A small improvement was observed when the true direct variance was greater than the true maternal variance (Figure 4.12, compare graphs Ct1 with Ct2 and Ct3).

4.4.5. Total bias (%) of the whole set of parameter estimates

Total bias (%) of the whole set of parameter estimates was calculated for traits 1 and 2 by using the Euclidean Norm method and the results are presented in Table 4.13. Twenty six (co)variance estimates were considered in obtaining this indicator. Total bias was obtained over missing rates at different levels of genetic correlation between direct and maternal (r), different levels of correlation between two traits (t), and different values of parameter sets (par). The largest total bias (12.5%) for whole set was obtained when the missing rate was high ($mis = 0.9$), the trait correlation was zero, the true direct and

maternal variances were equal and the direct-maternal genetic correlation was positive (Figure 4.13, graph Bt1). The smallest total bias (1%) for the whole set was obtained when the missing rate was zero ($\text{mis}=0.0$) and the direct and maternal genetic correlation was negative (Figure 4.13, graph At3). In general, the largest total bias percentages were obtained when the missing rate was high ($\text{mis}=0.8$ or 0.9) and the direct and maternal genetic correlation was positive. With an increasing correlation between two traits from 0 to 0.8, total bias percentage decreased. Trend of total bias (%) over missing rates was similar for all parameter sets.

Discussion:

Accuracy of variance component estimates is required in animal evaluation systems and is problematic for traits with maternal effects. Improvement of such traits requires knowledge of the genetic background of the maternal component effect. However, genetic analysis of maternally influenced traits has proven difficult, and extremely negative estimates of the genetic correlation between the direct and maternal effects can result in a severe problem for selection based on these traits with a detrimental effect on response to selection. An understanding of the genetic variation in maternal effects and the relationship between direct and maternal genetic effects is essential for formulating optimum breeding programs. If a negative genetic correlation exists between the direct and maternal genetic effects, the dam either passes to her offspring a beneficial set of alleles for the direct effect and a poor set of alleles for the maternal effect or the other way around. Therefore, improvement by selecting on phenotype would be difficult. For example let $\mathbf{P}_x$ represent the phenotype of individual $\mathbf{X}$. Assume that $\mathbf{P}_x$ is composed

additively of two phenotypic values, one being influenced by the genotypic value of **X** and the other by the genotypic value of the dam of **X**, say **W**. The direct and maternal effect values will be denoted by **d** for the direct and **m** for the maternal, then:

$$\mathbf{P}_x = \mathbf{P}_{dx} + \mathbf{P}_{mw}$$

where $\mathbf{P}_{dx}$ is the phenotypic value for the direct effect and $\mathbf{P}_{mw}$ is the phenotypic value for the maternal effect. For a simple trait, the phenotypic value is usually composed of the sum of the genotypic value and an environmental value.

$$\begin{aligned}\mathbf{P}_{dx} &= \mathbf{G}_{dx} + \mathbf{E}_{dx} \\ \mathbf{P}_{mw} &= \mathbf{G}_{mw} + \mathbf{E}_{mw}\end{aligned}$$

where $\mathbf{G}_{dx}$ and $\mathbf{E}_{dx}$ are the genotypic and environmental direct effects of **X** and $\mathbf{G}_{mw}$ and $\mathbf{E}_{mw}$ are the genotypic and environmental maternal effects of **W**.

Based on Willham's model, the sum of genetic values of individual **X** for direct and maternal genetic effects can be written as: $(\mathbf{G}_{dx} + \mathbf{G}_{mx})$

The compositions of several covariances between relatives are considered when a direct and a maternal effect are investigated (Table 2-2). For instance, the fraction of selection differential that would be realized if selection were on $\mathbf{P}_x$ was defined by Willham (1972) as the regression of $(\mathbf{G}_{dx} + \mathbf{G}_{mx})$ on $\mathbf{P}_x$. The covariance term is the sum of the sire-offspring and the dam-offspring covariance.

$$\text{Cov}(\mathbf{G}_{dx} + \mathbf{G}_{mx}, \mathbf{P}_x) = \sigma^2_{Gd} + 3/2 \sigma_{GdGm} + 1/2 \sigma^2_{Gm} \quad (4.1)$$

Based on equation 4.1, it is obvious that if direct-maternal covariance (σ_{GdGm}) is negative, less progress can be made by selection than when it is zero or positive. Furthermore, when direct and maternal variances are equal ($\sigma^2_{Gd} = \sigma^2_{Gm}$), selection for the maternal effect is less accurate because it is based on one record of a relative, the dam, instead of on the animal's own performance record.

Selection programs for beef cattle focus on birth weight and weights or gain during later stages (e.g. weaning weight, yearling weight, and yearling gain) of the life of the animal. Therefore, for the evaluation of beef cattle, not only is a differentiation of genetic and environmental causes of phenotypic variation needed, but the genetic part has to be separated into direct and maternal effects. Both direct and maternal effects that contribute to the growth of young beef cattle need to be taken into account in genetic improvement programs, particularly in cross-breeding studies. For example, in cross breeding systems both the breed correlation between the direct and maternal effect and the individual within-breed genetic correlations are important. The former indicates what currently exists and how it can be exploited while the latter indicates how breeds can be manipulated to better fit a given cross breeding system. Most studies involving the covariance between relatives have emphasized the estimation of this genetic correlation. Numerous estimates of direct and maternal parameters for traits in livestock such as beef and dairy cattle, sheep and swine can be found in the literature and some of them are presented in Table 2.1. Data structure has been reported as a possible cause of the negative correlation between direct and maternal genetic effects in a few previous studies (Meyer, 1992a ; Gerstmayr, 1992 ; Maniatis et al., 2003 ; Roso, 2004).

The main objective of this study was to investigate the influence of data structure on (co)variance estimates through simulation. A stochastic simulation of two traits in a closed breeding herd with overlapping generations and random mating was carried out to examine the influence of population structure on the bias of direct and maternal variance component estimates over nine generations. Results obtained in this study were compared to the results from previous studies of Gerstmayr (1992) and Maniatis et al. (2003) specifically.

4.5. Comparison of simulation procedures

4.5.1. Gerstmayr study

Gerstmayr (1992) investigated the impact of data structure on the reliability of the estimated genetic parameters in an animal model with maternal effects. The effect of the number of offspring per dam on the maternal heritability and the influence of the number of dams with recorded performance on the direct-maternal genetic correlation using several sets of genetic parameters were of particular interest in her study. She simulated a closed random mating population with overlapping generations and a fixed population size within generation. Animals from the base generation had no records. The influence of the proportion of dams without a record was investigated by generating populations with an increasing proportion of dams drawn from the base generation. Based on this strategy, she simulated five generations in which 0, 20, 40, 60, 80, and 100 percent of the dams were randomly chosen from the base generation. The approximate standard deviation (SD) of the genetic parameter estimates was used as a criterion for the reliability of the estimates. No indication of bias was found from the results in any of the

populations. The effect of population structure was found to be independent of the genetic parameters. With a true strongly negative correlation, the differences between the populations were more pronounced. The SD of all estimated parameters was smallest when most of the dams had their own performance record. There was a strong increase in the SD of the maternal heritability when 80 to 100 percent of dams were without a record. The SD of all parameters increased when the covariance between direct and maternal genetic effects was negative. The correlation between direct and maternal effects along with the proportion of their variances had a stronger influence on the reliability of the estimates than aspects of the population structure. The most inaccurate estimates were obtained when the genetic correlation was large and negative, and the maternal variance was the same or smaller than the direct variance. One progeny per dam led to decreased accuracy of all estimates compared with larger progeny groups. Gerstmayr (1992) concluded that to obtain getting accurate variance estimates for maternal effects, larger data sets with a better structure (e.g. more dams with records, and more progeny per dam) are required if the parameters are not known.

4.5.2. Maniatis and Pollott study

Maniatis & Pollott (2003) investigated the impact of data structure on the estimates of genetic (co)variance components of early growth in sheep using an animal model with maternal effects. The objectives of their work were to study the effect of particular genetic relationships, the number of offspring per dam and the influence of the proportion of dams with recorded performance on parameter estimates using farm records. Data used for the analysis came from the “Suffolk Sire Reference Scheme Ltd” in UK. The study

was based on an analysis of 8-week birth weight of sheep. With 50% of dams having records, the direct-maternal correlations decreased in magnitude compared with those obtained from families that had only 10% of dams with records. The magnitude of negative correlation estimates between direct and maternal effects declined with increasing number of progeny records. Both the number of progeny per dam and the proportion of mothers with recorded performance considerably influenced the parameter estimates. With a small progeny group per dam and limited information from recorded dams, the direct-maternal correlation had the highest negative value. Keeping progeny group size constant but increasing the number of dams with recorded performance produced a considerably lower negative correlation. A high proportion of both dams and maternal grand-dams with their own records were essential for estimating maternal effects and the covariance between direct and maternal genetic effects.

4.6. Impact of data structure on (co)variance estimates

Population structure had a significant effect on (co)variance estimates in the present study. Because of the similar patterns between results for trait 1 and trait 2, only results of trait 1 have been discussed.

4.6.1. Impact of data structure on estimates of maternal variance

By increasing the missing rate of dam's records from 0 to 0.1, the estimates of maternal genetic variance increased in all cases and were overestimated. When the missing rate increased from 0.1 to 0.9, the estimates decreased and were underestimated when the direct-maternal correlation was negative. This indicated that maternal variance estimates

depended on missing rate and the genetic correlation between direct and maternal. Further, a quadratic trend also existed in addition to a linear trend. Linear and quadratic contrast analyses for genetic maternal variance were examined (Appendix1.b). For a missing rate of 0.9, the largest upward bias and also the largest standard error were obtained, which is in agreement with the results of Gerstmayr (1992). The higher proportion of dams without records caused a further increase in the SE. If only ten percent of the dams had a record ($\text{mis}=0.9$), the SE of the genetic maternal variance increased by 26 percent compared to the population with all dams having a record. This could be explained by the fact that most covariances were estimated using only the relationships amongst animals, and just ten percent of dams provided direct information about this component by expressing it in both their records and the records of their progeny.

Gerstmayr (1992) found that by increasing the proportion of dams without records, the standard deviations of maternal variance estimates were increased. The largest standard deviation was obtained when the direct-maternal genetic correlation was negative and the proportion of dams without records was high, which agreed with results of the present study. Gerstmayr (1992) obtained largest standard deviation for maternal variance estimates when the true maternal variance was the same or smaller than the true direct variance. Instead, in this study the largest standard error was obtained when the true maternal variance was greater than the true direct variance. This may have been caused by different parameter sets, and different simulation assumptions, along with different methods of estimation in these two studies. The genetic correlation between the two traits had no major effects on maternal genetic variance estimates.

Earlier studies have indicated that the estimation of maternal effects and their covariance components is inherently problematic because the expressions of those effects lag by one generation behind the direct effects in their expression (Willham, 1980). This genetic lag between parent and offspring represents the coefficient of dam-offspring relationship. Datasets having sufficient dam-offspring pairs would yield improved separation of the direct and maternal effects.

4.6.2. Impact of data structure on estimates of maternal permanent environmental variance

The smallest estimate of maternal permanent environmental variance was obtained when the proportion of dams without records was high ($\text{mis} = 0.9$), the correlation between direct and maternal was positive, and the true direct variance was greater than the true maternal variance. This situation was almost in contrast with the estimation of maternal genetic variance. The smallest estimate of maternal genetic variance was obtained when the direct and maternal correlation was negative, and the true maternal variance was greater than the true direct variance. The present results confirm the results of Maniatis et al. (2003) who found a reduction in maternal heritability (m^2) and an increase in permanent environmental variance (C^2) when the direct-maternal correlation was high and negative. Maniatis et al. (2003) showed a substantial increase of the maternal heritability accompanied by a much less negative direct and maternal correlation (r_{dm}) and consequently a smaller C^2 which was in agreement with the results of the present study. When each dam in the data had three or four progeny records, the m^2 parameter increased markedly (by 70%), which coincided with the decrease in C^2 by 75%. In setting up the design matrices that relate records through the dam to their maternal effects,

estimates of the maternal additive genetic component are for all animals in the analysis while estimates of permanent environmental variance are only for dams with progeny records. When the missing rate went up, the average progeny per dam (2.6) was decreased. Therefore, with only an average of 2.6 offspring per dam the incidence matrices for the maternal genetic and maternal permanent environmental effects tended to be similar. This may cause difficulties in separating the maternal genetic and maternal environmental effects, which depend on the magnitude of the covariances between the dam effects relative to their variances. The small estimate of the maternal variance along with the large estimate for permanent environment could also verify this. The separation between the maternal genetic component and maternal permanent environmental effects requires repeated records on individual mothers and the presence of these mothers in the data. The links between the dam and her female progeny was broken with an increasing missing rate. The smallest estimate of permanent environmental variance was obtained when the missing rate was high, similar to the results of Maniatis et al. (2003).

4.6.3. Impact of data structure on estimates of direct-maternal covariance

The largest bias for the direct-maternal covariance estimates were obtained when the missing rate was high ($\text{mis} = 0.8$ or 0.9) and the direct-maternal genetic correlation was positive, together with a maternal variance the same or smaller than the direct variance. Maniatis et al. (2003) reported that with a small size of progeny group per dam and limited information from recorded dams, the direct-maternal genetic correlation had the largest negative value (-0.99). Gerstmayr (1992) reported that the standard deviation (SD) of the direct-maternal correlation increased by increasing the proportion of dams without

records. This trend was also observed in the present study in the case of standard error (SE) of estimates. Although there were no significant differences observed between SE of estimates as missing rate increased, a larger SE was obtained when the missing rate was high ($\text{mis} = 0.9$). Gerstmayr (1992) did not find any bias in any of the populations in her study, which does not agree with the results of this study.

The bias of direct-maternal covariance estimates increased with increasing missing rates, but a significant bias was only observed when the missing rate was 0.8 and 0.9. This case could be explained by the fact that just a few dams provided direct information about this component and most covariances were estimated by using only the relationships amongst animals. In fact, when a large number of dams have missing data, there could be serious consequences for the direct-maternal covariance estimate. The trend of bias for direct-maternal genetic covariance estimates as missing rate increases indicated that these may have been inflated by data structure, i.e. that the proportion of dams without records has a significant effect on direct-maternal covariance estimates. This bias trend rapidly increased for missing rates greater than 0.5, which indicates existence of a quadratic trend for this parameter in addition to linear trend (see Appendix1). The results showed that the genetic covariance between direct and maternal could depend on the structure of the data and availability of dams with performance records in the population, particularly when the number of dams with records is very low in the data set. The sign of this covariance also has an effect on the bias of this parameter. The largest bias was obtained when the sign was positive. Based on the findings presented here, there is strong evidence to suggest that the proportion of mothers with recorded performance considerably

influenced the parameter estimates. The present results confirmed the findings of Gerstmayr (1992) and Maniatis et al. (2003). The results showed that the genetic correlation between direct and maternal depends on the structure of the data and availability of dams with performance records in the data set. When the number of dams with records was small ($mis = 0.8$ or 0.9), the direct-maternal covariance estimate was far from the true value. When the missing rate was smaller than 0.5, the estimation of this covariance was not significantly different from the true value. Thus, low to medium missing rates (0.0 to 0.5) had no effect on the bias of the direct-maternal genetic covariance.

Boettcher et al. (2000) reported a positive correlation between direct-maternal genetic effects of calving ease (CE) in Canadian dairy cattle. This result contradicted many previous estimates, including those currently used for national evaluation. Some estimates of direct and maternal parameters for dairy cattle traits such as calving ease and stillbirth rate are presented in Table 2.1. A common assumption has been that direct and maternal effects should be negatively correlated, because small calves will be born more easily, but will grow up to be small cows and will experience calving problems. Boettcher et al. (2000) suggested that an estimate of direct-maternal genetic correlation in the range of 0.20 to 0.40 seems appropriate for genetic evaluation of CE.

The results of the current study also showed that the smaller SE of estimates for direct-maternal genetic covariance were obtained when the correlation between direct and maternal effects was positive and all dams had performance records.

4.6.4. Impact of data structure on estimates of direct variance

Direct variance estimates had linear trends over the missing rate. Generally overestimated direct variances were obtained when the missing rate was high ($\text{mis} = 0.9$). The standard errors (SE) of the direct variances were almost unaffected by the proportion of dams without records. This was expected because the direct variance in an animal model is estimated by one observation provided by each animal. This was the given structure for all populations. The largest SE was obtained when the direct variance was greater than the maternal variance. The SE for the negative correlation was larger than that of the positive one. Gerstmayr (1992) reported that estimation was most reliable if the direct variance was markedly smaller than the maternal variance, which is somewhat contrary to the situation with some traits in livestock. For example, in the majority of growth traits for beef cattle, the direct variance is greater than the maternal variance, as presented in Table 2.1.

The largest bias of direct variance was obtained when the proportion of dams without records was high ($\text{mis}=0.9$), the true direct variance was greater than the maternal and the genetic correlation of direct and maternal was negative. In fact, one component contains much information about the other, regardless if they vary in the same or in the opposite direction. This could explain the larger bias of direct variance when the direct-maternal correlation is negative. In addition, the numbers of full sibs and maternal half-sibs in this data set are also decreased compared to the full data set and consequently, both direct and

maternal variances were biased considerably. This result agrees with the findings of Maniatis et al. (2003).

4.6.5. Impact of data structure on total bias of the whole set of estimates

In general, the largest total bias percentage was obtained when the missing rate was high ($\text{mis}=0.8$ or 0.9) and trait correlation was zero. By increasing the proportion of dams without records the link between dam and offspring was decreased and there was insufficient information for accurate estimates of parameters, particularly for maternal variance and direct-maternal genetic covariance estimates. When the genetic correlation between two traits was zero ($t=0$), all elements of covariance between the two traits in the (co)variance matrix were zero. In other words, a lack of information for these covariances in the matrix could lead to more bias in the estimation of these parameters. The largest total bias percentage was obtained when the direct and maternal genetic correlation was positive ($r = +0.5$). In order to find out which one of (co)variances had larger bias compared to others when direct-maternal correlation was positive and when it was negative, bias for all (co)variances to be examined just for one parameter set. (see Appendix2). Results showed that some (co)variances such as direct-maternal covariances for traits 1 and 2, maternal genetic variances for both traits, and also maternal permanent environmental variance for trait 2 had larger bias when r was positive compared to when that correlation was negative. With an increasing correlation between the two traits from 0 to 0.8, total bias percentage decreased. When the genetic correlation of the two traits was large ($t = 0.8$), a smaller total bias for parameter estimates was obtained (Figure 4.13, e.g. compare graph At1 with At3).

Table 4-1: Estimated Variance components and genetic parameters for two traits under different population types
100% of dams have record (mis = 0.0) and correlation between two traits is zero (t = 0.0)

Trait1

Parameters	Γ_{dm}^a	σ_{d1}^2	(SE) ^b	σ_{m1}^2	(SE)	σ_{d1m1}	(SE)	σ_{pe1}^2	(SE)	h_{d1}^2	h_{m1}^2	Γ_{d1m1}
True variances		10		30				5		0.1	0.3	
	-0.5	9.9746	0.3211	29.8871	0.4857	-8.4489	0.3074	4.8977	0.3154	0.1091	0.3269	-0.4893
	0.0	9.9640	0.3234	30.5239	0.4880	0.1245	0.2885	4.6397	0.3200	0.0992	0.3041	0.0071
	+0.5	9.9779	0.3041	30.7034	0.4986	8.6975	0.2637	4.5061	0.3254	0.0915	0.2817	0.4969
True variances		20		20				5		0.2	0.2	
	-0.5	20.0985	0.4487	19.9997	0.4441	-9.8255	0.3318	4.7868	0.2988	0.2230	0.2219	-0.4900
	0.0	20.0470	0.4381	20.3840	0.4489	0.1538	0.3079	4.6408	0.3061	0.1998	0.2032	0.0076
	+0.5	19.9802	0.4102	20.4149	0.4453	10.1224	0.2794	4.6006	0.3075	0.1812	0.1852	0.5012
True variances		30		10				5		0.3	0.1	
	-0.5	30.2382	0.5478	10.0062	0.3773	-8.5365	0.3407	4.7462	0.2679	0.3306	0.1094	-0.4907
	0.0	30.1343	0.5233	10.1810	0.3885	0.1517	0.3159	4.6803	0.2825	0.3007	0.1016	0.0086
	+0.5	30.0963	0.4874	10.3056	0.3616	8.7225	0.2748	4.6182	0.2829	0.2766	0.0947	0.4952

Trait2

Parameters	Γ_{dm}	σ_{d2}^2	(SE)	σ_{m2}^2	(SE)	σ_{d2m2}	(SE)	σ_{pe2}^2	(SE)	h_{d2}^2	h_{m2}^2	Γ_{d2m2}
True variances		30		10				5		0.3	0.1	
	-0.5	30.8890	0.5475	10.5573	0.3678	-9.0934	0.3297	4.7909	0.2453	0.3380	0.1155	-0.5035
	0.0	30.8708	0.5586	10.5817	0.3636	-0.4422	0.2988	4.7585	0.2611	0.3087	0.1058	-0.0244
	+0.5	30.8206	0.5430	10.5447	0.3393	8.2275	0.2580	4.7112	0.2714	0.2839	0.0971	0.4563
True variances		20		20				5		0.2	0.2	
	-0.5	20.7697	0.4381	20.4761	0.4327	-10.3101	0.3256	4.8318	0.2518	0.2305	0.2272	-0.4999
	0.0	20.7559	0.4584	20.5331	0.4453	-0.3249	0.2985	4.7677	0.2741	0.2074	0.2052	-0.0157
	+0.5	20.6621	0.4479	20.5066	0.4193	9.6952	0.2560	4.6810	0.2891	0.1879	0.1865	0.4710
True variances		10		30				5		0.1	0.3	
	-0.5	10.5505	0.3163	30.3525	0.4963	-8.8209	0.3066	4.8717	0.2694	0.1153	0.3318	-0.4929
	0.0	10.5427	0.3358	30.4223	0.5201	-0.1748	0.2844	4.7814	0.2930	0.1053	0.3040	-0.0097
	+0.5	10.4840	0.3277	30.4400	0.4937	8.5140	0.2426	4.6581	0.3051	0.0965	0.2802	0.4765

^a Correlation between direct and maternal ; ^b Standard errors

Table 4-2: Estimated Variance components and genetic parameters for two traits under different population types
100% of dams have record (mis = 0.0) and correlation between two traits is 0.3 (t = 0.3)

Trait1

Parameters	r_{dm}^a	σ_{d1}^2	(SE) ^b	σ_{m1}^2	(SE)	σ_{d1m1}	(SE)	σ_{pe1}^2	(SE)	h_{d1}^2	h_{m1}^2	r_{d1m1}
True variances		10		30				5		0.1	0.3	
	-0.5	10.0092	0.3218	29.9634	0.4748	-8.5076	0.3018	4.8613	0.3138	0.1094	0.3277	-0.4912
	0.0	9.9837	0.3233	30.5728	0.4769	0.0804	0.2846	4.6216	0.3198	0.0994	0.3046	0.0046
	+0.5	9.9832	0.3049	30.6819	0.4882	8.6921	0.2641	4.5242	0.3246	0.0916	0.2815	0.4966
True variances		20		20				5		0.2	0.2	
	-0.5	20.0985	0.4487	19.9999	0.4442	-9.8256	0.3318	4.7867	0.2988	0.2230	0.2219	-0.4900
	0.0	20.0470	0.4381	20.3843	0.4490	0.1536	0.3079	4.6406	0.3061	0.1998	0.2032	0.0076
	+0.5	19.9803	0.4102	20.4152	0.4453	10.1221	0.2794	4.6004	0.3075	0.1812	0.1852	0.5011
True variances		30		10				5		0.3	0.1	
	-0.5	30.1901	0.5408	9.9661	0.3810	-8.4901	0.3401	4.7605	0.2685	0.3301	0.1089	-0.4894
	0.0	30.1173	0.5211	10.1460	0.3938	0.1829	0.3171	4.6935	0.2821	0.3006	0.1012	0.0104
	+0.5	30.0787	0.4864	10.3215	0.3642	8.7233	0.2732	4.6090	0.2819	0.2765	0.0948	0.4950

Trait2

Parameters	r_{dm}	σ_{d2}^2	(SE)	σ_{m2}^2	(SE)	σ_{d2m2}	(SE)	σ_{pe2}^2	(SE)	h_{d2}^2	h_{m2}^2	r_{d2m2}
True variances		30		10				5		0.3	0.1	
	-0.5	30.8663	0.5295	10.3793	0.3473	-9.0228	0.3219	5.0132	0.2406	0.33758	0.1135	-0.5041
	0.0	30.7685	0.5284	10.4271	0.3463	-0.3752	0.2908	4.9786	0.2655	0.30762	0.1042	-0.0209
	+0.5	30.6419	0.5030	10.4426	0.3255	8.2865	0.2505	4.9200	0.2805	0.28222	0.0961	0.4632
True variances		20		20				5		0.2	0.2	
	-0.5	20.7296	0.4213	20.1985	0.4190	-10.1947	0.3253	5.0577	0.2499	0.2300	0.2241	-0.4982
	0.0	20.6694	0.4332	20.3418	0.4329	-0.2616	0.2978	4.9856	0.2835	0.20655	0.2032	-0.0127
	+0.5	20.5246	0.4126	20.4437	0.4070	9.6932	0.2545	4.8738	0.3036	0.18669	0.1859	0.4732
True variances		10		30				5		0.1	0.3	
	-0.5	10.489	0.2977	30.0201	0.4910	-8.6707	0.3035	5.0751	0.2721	0.11468	0.3282	-0.4886
	0.0	10.4862	0.3148	30.2561	0.5110	-0.1162	0.2863	4.9544	0.3028	0.10476	0.3022	-0.0065
	+0.5	10.4096	0.3003	30.4403	0.4801	8.4449	0.2473	4.8149	0.3194	0.09581	0.2801	0.4744

^a Correlation between direct and maternal ; ^b Standard errors

Table 4-3: Estimated Variance components and genetic parameters for two traits under different population types
100% of dams have record (mis = 0.0) and correlation between two traits is 0.8 (t = 0.8)

Trait1

Parameters	r_{dm}^a	σ_{d1}^2	(SE) ^b	σ_{m1}^2	(SE)	σ_{d1m1}	(SE)	σ_{pe1}^2	(SE)	h_{d1}^2	h_{m1}^2	r_{d1m1}
True variances		10		30				5		0.1	0.3	
	-0.5	10.1410	0.3090	30.1644	0.4406	-8.6703	0.2809	4.7612	0.3039	0.1109	0.3299	-0.4957
	0.0	10.0578	0.3149	30.6561	0.4378	-0.0516	0.2724	4.6035	0.3117	0.1002	0.3055	-0.0029
	+0.5	10.0589	0.2978	30.6272	0.4543	8.6215	0.2589	4.5944	0.3162	0.0923	0.2811	0.4912
True variances		20		20				5		0.2	0.2	
	-0.5	20.0980	0.4487	19.9901	0.4423	-9.8232	0.3315	4.7950	0.2975	0.2230	0.2218	-0.4900
	0.0	20.0477	0.4382	20.3718	0.4473	0.1555	0.3077	4.6511	0.3047	0.1998	0.2031	0.0076
	+0.5	20.0304	0.4117	20.4123	0.4416	10.0824	0.2761	4.6297	0.3057	0.1817	0.1851	0.4986
True variances		30		10				5		0.3	0.1	
	-0.5	29.9786	0.4979	9.9200	0.3608	-8.3552	0.3097	4.7499	0.2602	0.3279	0.1085	-0.4840
	0.0	30.0207	0.4996	10.1028	0.3882	0.2436	0.3010	4.7114	0.2750	0.2997	0.1008	0.0139
	+0.5	30.0246	0.4778	10.4239	0.3597	8.6872	0.2611	4.5622	0.2695	0.2760	0.0958	0.4910

Trait2

Parameters	r_{dm}	σ_{d2}^2	(SE)	σ_{m2}^2	(SE)	σ_{d2m2}	(SE)	σ_{pe2}^2	(SE)	h_{d2}^2	h_{m2}^2	r_{d2m2}
True variances		30		10				5		0.3	0.1	
	-0.5	30.3810	0.4979	10.1103	0.3169	-8.6959	0.2971	5.0336	0.2558	0.3321	0.1105	-0.4961
	0.0	30.2543	0.4974	10.2189	0.3242	-0.0604	0.2803	5.0307	0.2784	0.3022	0.1020	-0.0034
	+0.5	30.1598	0.4708	10.3295	0.3104	8.5209	0.2520	4.9825	0.2828	0.2775	0.0950	0.4827
True variances		20		20				5		0.2	0.2	
	-0.5	20.3739	0.4254	19.7695	0.4330	-9.8779	0.3334	5.1958	0.2973	0.2260	0.2193	-0.4921
	0.0	20.2661	0.4226	20.1306	0.4395	0.0188	0.2980	5.0789	0.3211	0.2022	0.2009	0.0009
	+0.5	20.1504	0.3925	20.3707	0.4194	9.8590	0.2515	4.9756	0.3272	0.1830	0.1850	0.4866
True variances		10		30				5		0.1	0.3	
	-0.5	10.1732	0.2758	29.5156	0.4977	-8.3445	0.2783	5.2574	0.3278	0.1112	0.3227	-0.4815
	0.0	10.1852	0.2890	30.0165	0.5087	0.1324	0.2642	5.0787	0.3366	0.1016	0.2994	0.0075
	+0.5	10.1392	0.2730	30.5143	0.4939	8.4744	0.2360	4.8679	0.3415	0.0931	0.2804	0.4817

^a Correlation between direct and maternal ; ^b Standard errors

Table 4-4: Estimated Variance components and genetic parameters for two traits under different population types
90% of dams have record (mis = 0.1) and correlation between two traits is zero ($t = 0.0$)

Trait1

Parameters	Γ_{dm}^a	σ_{d1}^2	(SE) ^b	σ_{m1}^2	(SE)	σ_{d1m1}	(SE)	σ_{pe1}^2	(SE)	h_{d1}^2	h_{m1}^2	Γ_{d1m1}
True variances		10		30				5		0.1	0.3	
	-0.5	9.7453	0.2802	30.4621	0.4981	-8.6991	0.2928	4.7454	0.2766	0.1067	0.3337	-0.5048
	0.0	9.8277	0.2835	30.7604	0.4923	-0.0632	0.2906	4.4940	0.2651	0.0983	0.3077	-0.0036
	+0.5	9.9280	0.2617	30.8531	0.4618	8.5649	0.2770	4.3191	0.2633	0.0914	0.2842	0.4893
True variances		20		20				5		0.2	0.2	
	-0.5	19.7005	0.4212	20.5012	0.4321	-9.9548	0.3113	4.6140	0.2560	0.2191	0.2280	-0.4953
	0.0	19.7781	0.4112	20.7342	0.4475	0.0438	0.2944	4.3906	0.2559	0.1979	0.2075	0.0021
	+0.5	19.8040	0.3695	20.7824	0.4318	10.0689	0.2748	4.2449	0.2553	0.1803	0.1892	0.4963
True variances		30		10				5		0.3	0.1	
	-0.5	29.7401	0.5548	10.4305	0.3533	-8.5318	0.3036	4.5518	0.2356	0.3260	0.1143	-0.4844
	0.0	29.7515	0.5210	10.6081	0.3814	0.1629	0.2777	4.3693	0.2451	0.2978	0.1062	0.0091
	+0.5	29.7660	0.4700	10.6966	0.3662	8.8106	0.2498	4.2446	0.2431	0.2743	0.0986	0.4940

Trait2

Parameters	Γ_{dm}	σ_{d2}^2	(SE)	σ_{m2}^2	(SE)	σ_{d2m2}	(SE)	σ_{pe2}^2	(SE)	h_{d2}^2	h_{m2}^2	Γ_{d2m2}
True variances		30		10				5		0.3	0.1	
	-0.5	29.2060	0.5461	9.8631	0.3696	-7.8194	0.3257	5.0167	0.2842	0.3191	0.1077	-0.4607
	0.0	29.1653	0.5113	10.0684	0.3894	0.8475	0.2935	4.8945	0.3001	0.2909	0.1004	0.0494
	+0.5	29.2193	0.4739	10.3920	0.3754	9.3719	0.2634	4.7222	0.2991	0.2682	0.0954	0.5378
True variances		20		20				5		0.2	0.2	
	-0.5	19.3809	0.4566	19.8862	0.4329	-9.2888	0.3188	5.0928	0.2888	0.2148	0.2204	-0.4731
	0.0	19.3121	0.4215	20.0914	0.4643	0.7892	0.2855	4.9762	0.3125	0.1924	0.2001	0.0400
	+0.5	19.3606	0.3775	20.3518	0.4683	10.6856	0.2728	4.8432	0.3207	0.1753	0.1842	0.5383
True variances		10		30				5		0.1	0.3	
	-0.5	9.5454	0.3193	29.8104	0.4997	-8.0502	0.2917	5.1562	0.2985	0.1042	0.3257	-0.4772
	0.0	9.5042	0.3020	30.0710	0.5245	0.6963	0.2609	5.0580	0.3225	0.0946	0.2993	0.0411
	+0.5	9.5826	0.2671	30.3386	0.5299	9.2391	0.2649	4.9698	0.3331	0.0877	0.2778	0.5418

^a Correlation between direct and maternal ; ^b Standard errors

Table 4-5: Estimated Variance components and genetic parameters for two traits under different population types
90% of dams have record (mis = 0.1) and correlation between two traits is 0.3 (t = 0.3)

Trait1

Parameters	Γ_{dm}^a	σ_{dl}^2	(SE) ^b	σ_{ml}^2	(SE)	σ_{dlm1}	(SE)	σ_{pe1}^2	(SE)	h_{dl}^2	h_{ml}^2	Γ_{dlm1}
True variances		10		30				5		0.1	0.3	
	-0.5	9.7682	0.2800	30.5319	0.4946	-8.7513	0.2938	4.7376	0.2754	0.1070	0.3344	-0.5067
	0.0	9.8404	0.2848	30.8144	0.4903	-0.0989	0.2899	4.4897	0.2651	0.0984	0.3082	-0.0056
	+0.5	9.9270	0.2651	30.8630	0.4633	8.5462	0.2763	4.3295	0.2648	0.0914	0.2843	0.4882
True variances		20		20				5		0.2	0.2	
	-0.5	19.7005	0.4211	20.5012	0.4321	-9.9548	0.3113	4.6139	0.2560	0.2191	0.2280	-0.4953
	0.0	19.7780	0.4112	20.7340	0.4475	0.0439	0.2944	4.3907	0.2559	0.1979	0.2075	0.0027
	+0.5	19.8041	0.3694	20.7812	0.4316	10.0690	0.2748	4.2459	0.2551	0.1803	0.1892	0.4963
True variances		30		10				5		0.3	0.1	
	-0.5	29.7109	0.5505	10.3869	0.3497	-8.4924	0.2994	4.5534	0.2334	0.3257	0.1138	-0.4834
	0.0	29.7358	0.5184	10.5720	0.3816	0.1863	0.2775	4.3686	0.2442	0.2977	0.1058	0.0105
	+0.5	29.7691	0.4654	10.6935	0.3664	8.8282	0.2490	4.2306	0.2419	0.2744	0.0985	0.4948

Trait2

Parameters	Γ_{dm}	σ_{d2}^2	(SE)	σ_{m2}^2	(SE)	σ_{d2m2}	(SE)	σ_{pe2}^2	(SE)	h_{d2}^2	h_{m2}^2	Γ_{d2m2}
True variances		30		10				5		0.3	0.1	
	-0.5	29.3984	0.5303	9.8167	0.3346	-7.9038	0.3243	5.1103	0.2601	0.3210	0.1072	-0.4652
	0.0	29.3148	0.5021	9.9958	0.3585	0.8240	0.2965	4.9601	0.2772	0.2922	0.0996	0.0481
	+0.5	29.3442	0.4737	10.3204	0.3503	9.3500	0.2654	4.7473	0.2860	0.2693	0.0947	0.5372
True variances		20		20				5		0.2	0.2	
	-0.5	19.5122	0.4531	19.7458	0.3964	-9.3279	0.3179	5.2404	0.2593	0.2162	0.2187	-0.4752
	0.0	19.4202	0.4223	19.9438	0.4348	0.7984	0.2912	5.0864	0.2832	0.1934	0.1986	0.0405
	+0.5	19.4606	0.3853	20.2212	0.4452	10.7027	0.2754	4.9038	0.3017	0.1762	0.1831	0.5395
True variances		10		30				5		0.1	0.3	
	-0.5	9.6588	0.3215	29.5389	0.4571	-8.0539	0.2841	5.3694	0.2688	0.1055	0.3227	-0.4768
	0.0	9.5745	0.3092	29.8295	0.4852	0.7070	0.2591	5.2232	0.2869	0.0953	0.2970	0.0418
	+0.5	9.6570	0.2783	30.1958	0.5097	9.2659	0.2600	5.0402	0.3119	0.0884	0.2764	0.5426

^a Correlation between direct and maternal ; ^b Standard errors

Table 4-6: Estimated Variance components and genetic parameters for two traits under different population types
90% of dams have record (mis = 0.1) and correlation between two traits is 0.8 (t = 0.8)

Trait1

Parameters	Γ_{dm}^a	σ_{dl}^2	(SE) ^b	σ_{ml}^2	(SE)	σ_{dlm1}	(SE)	σ_{pe1}^2	(SE)	h_{dl}^2	h_{ml}^2	Γ_{dlm1}
True variances		10		30				5		0.1	0.3	
	-0.5	9.8876	0.2691	30.6630	0.4788	-8.9044	0.2827	4.7604	0.2655	0.1082	0.3358	-0.5113
	0.0	9.8951	0.2820	30.9128	0.4818	-0.2259	0.2808	4.5223	0.2626	0.0989	0.3092	-0.0129
	+0.5	9.9392	0.2678	30.8304	0.4585	8.4655	0.2695	4.4209	0.2657	0.0916	0.2841	0.4830
True variances		20		20				5		0.2	0.2	
	-0.5	19.6999	0.4212	20.4800	0.4308	-9.9503	0.3113	4.6330	0.2534	0.2191	0.2278	-0.4953
	0.0	19.7785	0.4112	20.7155	0.4472	0.0463	0.2946	4.4070	0.2539	0.1979	0.2073	0.0022
	+0.5	19.8186	0.3697	20.7699	0.4298	10.0608	0.2744	4.2610	0.2539	0.1804	0.1891	0.4958
True variances		30		10				5		0.3	0.1	
	-0.5	29.7085	0.5088	10.3443	0.3201	-8.4861	0.2678	4.5873	0.2219	0.3258	0.1134	-0.4840
	0.0	29.7269	0.4962	10.5001	0.3651	0.2129	0.2657	4.3888	0.2356	0.2977	0.1051	0.0120
	+0.5	29.8121	0.4449	10.6951	0.3528	8.8069	0.2402	4.2206	0.2330	0.2748	0.0985	0.4932

Trait2

Parameters	Γ_{dm}	σ_{d2}^2	(SE)	σ_{m2}^2	(SE)	σ_{d2m2}	(SE)	σ_{pe2}^2	(SE)	h_{d2}^2	h_{m2}^2	Γ_{d2m2}
True variances		30		10				5		0.3	0.1	
	-0.5	29.7641	0.4695	10.1579	0.2903	-8.4159	0.3102	4.9657	0.2211	0.3254	0.1110	-0.4840
	0.0	29.6976	0.4598	10.2676	0.3194	0.3384	0.2902	4.7908	0.2381	0.2966	0.1025	0.0193
	+0.5	29.6897	0.4337	10.4299	0.3063	8.9462	0.2518	4.5979	0.2517	0.2732	0.0959	0.5083
True variances		20		20				5		0.2	0.2	
	-0.5	19.7565	0.4264	19.9318	0.3882	-9.6756	0.3200	5.1237	0.2402	0.2192	0.2211	-0.4875
	0.0	19.7219	0.4037	20.1400	0.4204	0.4446	0.2995	4.8910	0.2505	0.1968	0.2009	0.0223
	+0.5	19.7663	0.3626	20.3497	0.4032	10.3952	0.2720	4.6575	0.2612	0.1794	0.1847	0.5183
True variances		10		30				5		0.1	0.3	
	-0.5	10.0001	0.2851	29.5287	0.4216	-8.3966	0.2519	5.3796	0.2563	0.1094	0.3231	-0.4886
	0.0	9.8600	0.2853	29.8490	0.4630	0.4018	0.2520	5.1191	0.2607	0.0984	0.2979	0.0234
	+0.5	9.9005	0.2563	30.3221	0.4618	8.9683	0.2461	4.7754	0.2675	0.0909	0.2784	0.5176

^a Correlation between direct and maternal ; ^b Standard errors

Table 4-7: Estimated Variance components and genetic parameters for two traits under different population types
50% of dams have record (mis = 0.5) and correlation between two traits is zero (t = 0.0)

Trait1

Parameters	Γ_{dm}^a	σ_{d1}^2	(SE) ^b	σ_{m1}^2	(SE)	σ_{d1m1}	(SE)	σ_{pe1}^2	(SE)	h_{d1}^2	h_{m1}^2	Γ_{d1m1}
True variances		10		30				5		0.1	0.3	
	-0.5	9.7331	0.3273	29.3597	0.4536	-8.4542	0.3202	5.3999	0.2709	0.1067	0.3218	-0.5001
	0.0	9.8423	0.3087	30.1928	0.4586	0.1449	0.2922	4.5596	0.2674	0.0985	0.3024	0.0084
	+0.5	9.9482	0.2810	30.7224	0.4895	8.9158	0.2556	3.8939	0.2762	0.0917	0.2832	0.5099
True variances		20		20				5		0.2	0.2	
	-0.5	19.7565	0.4459	19.7503	0.4118	-9.7813	0.3635	4.9861	0.2547	0.2199	0.2198	-0.4957
	0.0	19.7925	0.4214	20.5694	0.4216	0.2558	0.3258	4.1222	0.2511	0.1982	0.2060	0.0126
	+0.5	19.7570	0.3911	21.1205	0.4306	10.4377	0.2782	3.4243	0.2540	0.1799	0.1923	0.5109
True variances		30		10				5		0.3	0.1	
	-0.5	29.7691	0.541	10.2748	0.3560	-8.3659	0.3701	4.4261	0.2367	0.3264	0.1126	-0.4783
	0.0	29.6537	0.5139	10.8328	0.3625	0.4199	0.3341	3.7811	0.2352	0.2976	0.1085	0.0234
	+0.5	29.5335	0.4847	11.4114	0.3367	9.1841	0.2847	3.1647	0.2255	0.2724	0.1052	0.5002

Trait2

Parameters	Γ_{dm}	σ_{d2}^2	(SE)	σ_{m2}^2	(SE)	σ_{d2m2}	(SE)	σ_{pe2}^2	(SE)	h_{d2}^2	h_{m2}^2	Γ_{d2m2}
True variances		30		10				5		0.3	0.1	
	-0.5	29.4811	0.5292	9.6478	0.4243	-8.0827	0.3868	4.9539	0.2591	0.3228	0.1056	-0.4792
	0.0	29.1180	0.5086	10.3420	0.4359	0.8258	0.3384	4.1920	0.2780	0.2913	0.1034	0.0475
	+0.5	28.7811	0.4732	11.0370	0.3797	9.4898	0.2681	3.5555	0.2623	0.2653	0.1017	0.5324
True variances		20		20				5		0.2	0.2	
	-0.5	19.6647	0.4156	19.0439	0.5286	-9.5775	0.4053	5.6401	0.2951	0.2184	0.2115	-0.4949
	0.0	19.3952	0.4109	19.9683	0.5483	0.7289	0.3566	4.6559	0.3145	0.1937	0.1994	0.0370
	+0.5	19.1225	0.3856	20.8827	0.4762	10.7314	0.2821	3.8069	0.2938	0.1738	0.1898	0.5370
True variances		10		30				5		0.1	0.3	
	-0.5	9.6969	0.2903	28.5646	0.5758	-8.3370	0.3798	6.1630	0.3172	0.1062	0.3128	-0.5009
	0.0	9.5839	0.2899	29.6117	0.6081	0.5523	0.3342	5.1582	0.3448	0.0956	0.2956	0.0327
	+0.5	9.4941	0.2802	30.7425	0.5440	9.1431	0.2720	4.2046	0.3227	0.0872	0.2824	0.5351

^a Correlation between direct and maternal ; ^b Standard errors

Table 4-8: Estimated Variance components and genetic parameters for two traits under different population types
50% of dams have record (mis = 0.5) and correlation between two traits is 0.3 (t = 0.3)

Trait1

Parameters	r_{dm}^a	σ_{dl}^2	(SE) ^b	σ_{ml}^2	(SE)	σ_{dlml}	(SE)	σ_{pe1}^2	(SE)	h_{dl}^2	h_{ml}^2	r_{dlml}
True variances		10		30				5		0.1	0.3	
	-0.5	9.7305	0.3272	29.4043	0.4530	-8.4808	0.3188	5.3831	0.2679	0.1066	0.3223	-0.5013
	0.0	9.8272	0.3085	30.1903	0.4570	0.1406	0.2934	4.5641	0.2668	0.0984	0.3024	0.0081
	+0.5	9.9367	0.2794	30.7157	0.4854	8.8951	0.2562	3.9063	0.2771	0.0916	0.2831	0.5091
True variances		20		20				5		0.2	0.2	
	-0.5	19.7565	0.4459	19.7505	0.4119	-9.7814	0.3635	4.9859	0.2547	0.2199	0.2198	-0.4951
	0.0	19.7925	0.4214	20.5694	0.4216	0.2558	0.3258	4.1222	0.2511	0.1982	0.2067	0.0126
	+0.5	19.7571	0.3911	21.1203	0.4306	10.4376	0.2782	3.4245	0.2540	0.1799	0.1923	0.5109
True variances		30		10				5		0.3	0.1	
	-0.5	29.832	0.5328	10.3576	0.3511	-8.4198	0.3627	4.3865	0.2361	0.3271	0.1135	-0.4790
	0.0	29.6762	0.5108	10.8253	0.3604	0.4347	0.3307	3.7835	0.2355	0.2973	0.1084	0.0242
	+0.5	29.5530	0.4840	11.4073	0.3364	9.1895	0.2827	3.1679	0.2253	0.2725	0.1052	0.5004

Trait2

Parameters	r_{dm}	σ_{d2}^2	(SE)	σ_{m2}^2	(SE)	σ_{d2m2}	(SE)	σ_{pe2}^2	(SE)	h_{d2}^2	h_{m2}^2	r_{d2m2}
True variances		30		10				5		0.3	0.1	
	-0.5	29.5322	0.5175	9.8347	0.3842	-8.2113	0.3820	4.8479	0.2527	0.3233	0.1076	-0.4818
	0.0	29.2027	0.4973	10.5122	0.4020	0.6614	0.3322	4.0873	0.2734	0.2922	0.1052	0.0377
	+0.5	28.8986	0.4632	11.1350	0.3618	9.3847	0.2654	3.4461	0.2618	0.2665	0.1027	0.5231
True variances		20		20				5		0.2	0.2	
	-0.5	19.6543	0.3997	19.2130	0.5025	-9.7099	0.3990	5.5553	0.2913	0.2184	0.2135	-0.4996
	0.0	19.4141	0.3982	20.1388	0.5229	0.5328	0.3478	4.5477	0.3102	0.1941	0.2013	0.0269
	+0.5	19.1835	0.3750	20.9811	0.4566	10.6355	0.2741	3.6758	0.2886	0.1745	0.1909	0.5301
True variances		10		30				5		0.1	0.3	
	-0.5	9.7913	0.2709	28.7580	0.5486	-8.5571	0.3481	6.0981	0.3147	0.1073	0.3152	-0.5099
	0.0	9.5746	0.2791	29.7082	0.5935	0.3948	0.3224	5.0779	0.3393	0.0957	0.2970	0.0234
	+0.5	9.5035	0.2730	30.8036	0.5290	9.0664	0.2613	4.0720	0.3148	0.0874	0.2833	0.5299

^a Correlation between direct and maternal ; ^b Standard errors

Table 4-9: Estimated Variance components and genetic parameters for two traits under different population types
50% of dams have record (mis = 0.5) and correlation between two traits is 0.8 (t = 0.8)

Trait1

Parameters	Γ_{dm}^a	σ_{dl}^2	(SE) ^b	σ_{ml}^2	(SE)	σ_{dlm1}	(SE)	σ_{pe1}^2	(SE)	h_{dl}^2	h_{ml}^2	r_{dlm1}
True variances		10		30				5		0.1	0.3	
	-0.5	9.7902	0.3083	29.5053	0.4378	-8.5536	0.3029	5.3532	0.2622	0.1073	0.3234	-0.5033
	0.0	9.8071	0.2995	30.1063	0.4445	0.1045	0.2853	4.6408	0.2674	0.0982	0.3017	0.0060
	+0.5	9.9277	0.2703	30.5644	0.4687	8.7710	0.2555	4.0833	0.2788	0.0916	0.2820	0.5035
True variances		20		20				5		0.2	0.2	
	-0.5	19.7569	0.4459	19.7416	0.4115	-9.7805	0.3635	4.9955	0.2541	0.2199	0.2197	-0.4952
	0.0	19.7935	0.4214	20.5508	0.4207	0.2572	0.3257	4.1394	0.2491	0.1983	0.2058	0.0127
	+0.5	19.7730	0.3895	21.0866	0.4269	10.4215	0.2779	3.4656	0.2504	0.1801	0.1920	0.5103
True variances		30		10				5		0.3	0.1	
	-0.5	29.7333	0.4872	10.1599	0.3043	-8.2976	0.3231	4.5097	0.2291	0.3261	0.1114	-0.4774
	0.0	29.6508	0.4897	10.7698	0.3335	0.4334	0.3106	3.8386	0.2311	0.2971	0.1079	0.0242
	+0.5	29.5915	0.4739	11.3674	0.3322	9.1256	0.2731	3.2655	0.2244	0.2729	0.1048	0.4975

Trait2

Parameters	Γ_{dm}	σ_{d2}^2	(SE)	σ_{m2}^2	(SE)	σ_{d2m2}	(SE)	σ_{pe2}^2	(SE)	h_{d2}^2	h_{m2}^2	r_{d2m2}
True variances		30		10				5		0.3	0.1	
	-0.5	29.4944	0.5025	10.2514	0.3225	-8.4095	0.3621	4.5672	0.2369	0.3233	0.1123	-0.4836
	0.0	29.3676	0.5046	10.8674	0.3412	0.3215	0.3460	3.8755	0.2478	0.2943	0.1089	0.0180
	+0.5	29.2971	0.4781	11.3729	0.3198	9.0193	0.3024	3.2938	0.2393	0.2704	0.1050	0.4941
True variances		20		20				5		0.2	0.2	
	-0.5	19.6920	0.4049	19.6641	0.4374	-9.8972	0.3732	5.1861	0.2720	0.2191	0.2188	-0.5029
	0.0	19.6219	0.4002	20.5300	0.4544	0.2038	0.3363	4.2300	0.2763	0.1965	0.2056	0.0101
	+0.5	19.5503	0.3804	21.1324	0.4107	10.4132	0.2830	3.4354	0.2565	0.1781	0.1925	0.5123
True variances		10		30				5		0.1	0.3	
	-0.5	9.8370	0.2601	29.0333	0.4674	-8.5965	0.2966	5.7314	0.2969	0.1079	0.3185	-0.5086
	0.0	9.7597	0.2692	29.9148	0.5200	0.1184	0.2818	4.7903	0.3069	0.0978	0.2999	0.0069
	+0.5	9.7813	0.2666	30.6961	0.4841	8.8651	0.2432	3.9531	0.2767	0.0902	0.2831	0.5116

^a Correlation between direct and maternal ; ^b Standard errors

Table 4-10: Estimated Variance components and genetic parameters for two traits under different population types
20% of dams have record (mis = 0.8) and correlation between two traits is zero (t = 0.0)

Trait1

Parameters	r_{dm}^a	σ_{dl}^2	(SE) ^b	σ_{ml}^2	(SE)	σ_{dlml}	(SE)	σ_{pe1}^2	(SE)	h_{dl}^2	h_{ml}^2	I_{dlml}
True variances		10		30				5		0.1	0.3	
	-0.5	10.3029	0.3261	28.7057	0.5341	-8.3132	0.3816	5.7659	0.2784	0.1127	0.3142	-0.4834
	0.0	10.3365	0.3254	29.5940	0.4794	0.9183	0.3622	4.3392	0.2680	0.1033	0.2959	0.0525
	+0.5	10.5063	0.3028	30.5758	0.4474	9.7828	0.3216	3.1496	0.2573	0.0967	0.2815	0.5458
True variances		20		20				5		0.2	0.2	
	-0.5	20.4009	0.4619	19.1848	0.4716	-9.4508	0.4119	5.1209	0.2605	0.2265	0.2130	-0.4777
	0.0	20.3540	0.4564	20.0826	0.4320	1.2135	0.3945	3.6719	0.2473	0.2034	0.2007	0.0600
	+0.5	20.3896	0.4281	21.0086	0.3915	11.5105	0.3436	2.4945	0.2319	0.1854	0.1910	0.5561
True variances		30		10				5		0.3	0.1	
	-0.5	30.3564	0.5715	9.8654	0.3931	-7.7548	0.4099	4.2013	0.2418	0.3319	0.1078	-0.4481
	0.0	30.2303	0.5570	10.5684	0.3694	1.4586	0.3938	3.0956	0.2334	0.3020	0.1055	0.0816
	+0.5	30.2182	0.5236	11.4244	0.3291	10.2396	0.3314	2.1977	0.2140	0.2781	0.1051	0.5511

Trait2

Parameters	r_{dm}	σ_{d2}^2	(SE)	σ_{m2}^2	(SE)	σ_{d2m2}	(SE)	σ_{pe2}^2	(SE)	h_{d2}^2	h_{m2}^2	I_{d2m2}
True variances		30		10				5		0.3	0.1	
	-0.5	29.9784	0.5157	9.9718	0.4253	-8.4100	0.3881	4.6684	0.2258	0.3280	0.1091	-0.4864
	0.0	29.8417	0.5160	10.4252	0.4325	0.8433	0.3632	3.6436	0.2374	0.2986	0.1043	0.0478
	+0.5	29.6879	0.5009	10.9657	0.3540	9.9295	0.3096	2.6805	0.2249	0.2738	0.1011	0.5503
True variances		20		20				5		0.2	0.2	
	-0.5	20.0783	0.4110	19.4335	0.5470	-10.2962	0.4043	5.6311	0.2288	0.2230	0.2159	-0.5212
	0.0	20.0203	0.4153	20.095	0.5478	0.3637	0.3827	4.2949	0.2553	0.2003	0.2011	0.0181
	+0.5	19.9394	0.4041	20.591	0.4476	11.0144	0.3258	3.1116	0.2455	0.1817	0.1876	0.5435
True variances		10		30				5		0.1	0.3	
	-0.5	10.0094	0.2908	28.8876	0.6329	-9.1510	0.3793	6.2936	0.2504	0.1096	0.3164	-0.5381
	0.0	10.0174	0.2956	29.5339	0.6182	-0.0085	0.3689	5.0824	0.2728	0.1003	0.2958	-0.0004
	+0.5	10.1121	0.2863	30.1104	0.5032	9.2130	0.3122	3.8942	0.2727	0.0933	0.2778	0.5279

^a Correlation between direct and maternal ; ^b Standard errors

Table 4-11: Estimated Variance components and genetic parameters for two traits under different population types
20% of dams have record (mis = 0.8) and correlation between two traits is 0.3 (t = 0.3)

Trait1

Parameters	I_{dm}^a	σ_{d1}^2	(SE) ^b	σ_{m1}^2	(SE)	σ_{d1m1}	(SE)	σ_{pe1}^2	(SE)	h_{d1}^2	h_{m1}^2	I_{d1m1}
True variances			10		30			5		0.1	0.3	
	-0.5	10.3375	0.3213	28.7262	0.5338	-8.3409	0.3837	5.7600	0.2780	0.1131	0.3144	-0.4840
	0.0	10.3466	0.3218	29.5724	0.4791	0.9211	0.3656	4.3479	0.2672	0.1034	0.2957	0.0526
	+0.5	10.4903	0.3001	30.5600	0.4467	9.7860	0.3230	3.1613	0.2552	0.0966	0.2814	0.5465
True variances			20		20			5		0.2	0.2	
	-0.5	20.4009	0.4619	19.1848	0.4716	-9.4508	0.4119	5.1209	0.2605	0.2265	0.2130	-0.4777
	0.0	20.3540	0.4564	20.0827	0.4320	1.2135	0.3945	3.6718	0.2473	0.2034	0.2007	0.0600
	+0.5	20.3895	0.4281	21.0091	0.3914	11.5101	0.3435	2.4945	0.2319	0.1854	0.1910	0.5561
True variances			30		10			5		0.3	0.1	
	-0.5	30.2646	0.5717	9.8124	0.3855	-7.6913	0.4063	4.2022	0.2410	0.3309	0.1073	-0.4463
	0.0	30.1855	0.5580	10.5646	0.3667	1.4564	0.3903	3.0983	0.2344	0.3016	0.1055	0.0815
	+0.5	30.2071	0.5250	11.4334	0.3303	10.2276	0.3303	2.1960	0.2147	0.2780	0.1052	0.5503

Trait2

Parameters	I_{dm}	σ_{d2}^2	(SE)	σ_{m2}^2	(SE)	σ_{d2m2}	(SE)	σ_{pe2}^2	(SE)	h_{d2}^2	h_{m2}^2	I_{d2m2}
True variances			30		10			5		0.3	0.1	
	-0.5	30.0162	0.5364	10.1299	0.4242	-8.4545	0.4049	4.5227	0.2324	0.3285	0.1108	-0.4848
	0.0	29.9200	0.5340	10.6234	0.4346	0.7708	0.3863	3.5177	0.2533	0.2993	0.1062	0.0432
	+0.5	29.7982	0.5073	11.2114	0.3550	9.7990	0.3265	2.6002	0.2423	0.2746	0.1033	0.5361
True variances			20		20			5		0.2	0.2	
	-0.5	20.1852	0.4269	19.6432	0.5410	-10.4095	0.4242	5.4634	0.2430	0.2243	0.2183	-0.5227
	0.0	20.1320	0.4265	20.3710	0.5416	0.2204	0.4067	4.1438	0.2768	0.2014	0.2038	0.0108
	+0.5	20.0552	0.4038	20.8849	0.4523	10.8566	0.3464	3.0182	0.2694	0.1826	0.1901	0.5304
True variances			10		30			5		0.1	0.3	
	-0.5	10.1129	0.2967	29.1152	0.6208	-9.2919	0.4016	6.1082	0.2632	0.1108	0.3191	-0.5415
	0.0	10.1173	0.2957	29.8826	0.5996	-0.1962	0.3944	4.8981	0.2936	0.1013	0.2992	-0.0112
	+0.5	10.2033	0.2778	30.4785	0.5129	9.0187	0.3359	3.7606	0.2976	0.0940	0.2809	0.5114

^a Correlation between direct and maternal ; ^b Standard errors

Table 4-12: Estimated Variance components and genetic parameters for two traits under different population types
20% of dams have record (mis = 0.8) and correlation between two traits is 0.8 (t = 0.8)

Trait1

Parameters	I_{dm}^a	σ_{d1}^2	(SE) ^b	σ_{m1}^2	(SE)	σ_{d1m1}	(SE)	σ_{pe1}^2	(SE)	h_{d1}^2	h_{m1}^2	I_{d1m1}
True variances			10		30			5		0.1	0.3	
	-0.5	10.4656	0.2949	28.7697	0.5218	-8.4680	0.3738	5.8008	0.2730	0.1145	0.3149	-0.4880
	0.0	10.3356	0.3023	29.5283	0.4777	0.8474	0.3645	4.4476	0.2666	0.1034	0.2954	0.0485
	+0.5	10.3856	0.2864	30.5134	0.4485	9.6786	0.3218	3.2856	0.2535	0.0957	0.2812	0.5436
True variances			20		20			5		0.2	0.2	
	-0.5	20.4007	0.4619	19.1772	0.4705	-9.4499	0.4118	5.1283	0.2592	0.2265	0.2129	-0.4777
	0.0	20.3543	0.4564	20.0644	0.4310	1.2142	0.3945	3.6894	0.2457	0.2034	0.2005	0.0600
	+0.5	20.4043	0.4285	20.9786	0.3915	11.4915	0.3443	2.5371	0.2298	0.1855	0.1907	0.5554
True variances			30		10			5		0.3	0.1	
	-0.5	30.0748	0.5409	9.6488	0.3428	-7.6313	0.3728	4.3663	0.2284	0.3291	0.1055	-0.4479
	0.0	29.9938	0.5410	10.5103	0.3477	1.3914	0.3649	3.2469	0.2315	0.2999	0.1051	0.0783
	+0.5	30.0516	0.5184	11.4477	0.3312	10.1071	0.3185	2.2897	0.2190	0.2768	0.1054	0.5449

Trait2

Parameters	I_{dm}	σ_{d2}^2	(SE)	σ_{m2}^2	(SE)	σ_{d2m2}	(SE)	σ_{pe2}^2	(SE)	h_{d2}^2	h_{m2}^2	I_{d2m2}
True variances			30		10			5		0.3	0.1	
	-0.5	30.0347	0.5239	10.0318	0.3740	-8.0207	0.3758	4.2838	0.2366	0.3287	0.1098	-0.4620
	0.0	29.9400	0.5365	10.7140	0.3762	1.0576	0.3838	3.2967	0.2379	0.2994	0.1071	0.0590
	+0.5	29.8517	0.5169	11.5747	0.3335	9.8253	0.3417	2.3967	0.2189	0.2750	0.1066	0.5285
True variances			20		20			5		0.2	0.2	
	-0.5	20.4153	0.4542	19.6573	0.4941	-10.0721	0.4236	5.1065	0.2691	0.2268	0.2184	-0.5027
	0.0	20.3714	0.4524	20.5287	0.4746	0.5384	0.4171	3.7590	0.2699	0.2036	0.2052	0.0263
	+0.5	20.3647	0.4248	21.2495	0.4151	10.9747	0.3681	2.7052	0.2463	0.1851	0.1931	0.5275
True variances			10		30			5		0.1	0.3	
	-0.5	10.3461	0.3001	29.1171	0.5179	-9.0707	0.3750	5.8566	0.2860	0.1134	0.3192	-0.5226
	0.0	10.3317	0.3057	30.1656	0.5007	-0.0314	0.3819	4.5208	0.2923	0.1034	0.3020	-0.0017
	+0.5	10.4292	0.2904	30.9298	0.4605	9.0253	0.3469	3.4380	0.2762	0.0960	0.2848	0.5025

^a Correlation between direct and maternal ; ^b Standard errors

Table 4-13: Estimated Variance components and genetic parameters for two traits under different population types
10% of dams have record (mis = 0.9) and correlation between two traits is zero ($t = 0.0$)

Trait1

Parameters	r_{dm}^a	σ_{d1}^2	(SE) ^b	σ_{m1}^2	(SE)	σ_{d1m1}	(SE)	σ_{pe1}^2	(SE)	h_{d1}^2	h_{m1}^2	r_{d1m1}
True variances			10		30				5	0.1	0.3	
	-0.5	10.7636	0.3225	28.7275	0.5853	-9.1169	0.4063	6.4317	0.2848	0.1182	0.3157	-0.5184
	0.0	10.6634	0.3251	29.5824	0.5653	0.5411	0.3731	4.8718	0.2898	0.1068	0.2963	0.0304
	+0.5	10.6337	0.3057	30.6746	0.4995	9.9847	0.3041	3.3809	0.2668	0.0977	0.2820	0.5528
True variances			20		20				5	0.2	0.2	
	-0.5	21.0016	0.4500	19.2564	0.5245	-10.0661	0.4459	5.6417	0.2593	0.2337	0.2143	-0.5005
	0.0	20.8178	0.4412	20.0551	0.4850	1.0758	0.3951	4.0360	0.2612	0.2081	0.2005	0.0526
	+0.5	20.6636	0.4149	20.9748	0.4256	12.0008	0.3189	2.5760	0.2307	0.1875	0.1903	0.5764
True variances			30		10				5	0.3	0.1	
	-0.5	31.1038	0.5454	9.8936	0.4051	-8.0686	0.4174	4.5620	0.2422	0.3402	0.1082	-0.4599
	0.0	30.8689	0.5273	10.4763	0.3843	1.6339	0.3737	3.2620	0.2396	0.3081	0.1045	0.0908
	+0.5	30.6891	0.4970	11.2616	0.3306	10.9037	0.3040	2.1653	0.2077	0.2818	0.1034	0.5865

Trait2

Parameters	r_{dm}	σ_{d2}^2	(SE)	σ_{m2}^2	(SE)	σ_{d2m2}	(SE)	σ_{pe2}^2	(SE)	h_{d2}^2	h_{m2}^2	r_{d2m2}
True variances			30		10				5	0.3	0.1	
	-0.5	30.0978	0.4982	10.5155	0.4141	-7.8299	0.3817	4.0543	0.2392	0.3278	0.1145	-0.4401
	0.0	30.0235	0.4949	11.1431	0.4373	1.5974	0.3751	2.8333	0.2368	0.2987	0.1108	0.0873
	+0.5	29.9908	0.4802	11.7939	0.3867	10.6332	0.3274	1.9184	0.2059	0.2749	0.1081	0.5653
True variances			20		20				5	0.2	0.2	
	-0.5	20.2792	0.4108	20.1825	0.4798	-9.8323	0.3968	4.9760	0.2753	0.2241	0.2230	-0.4860
	0.0	20.2406	0.4105	20.8933	0.5249	0.9921	0.3948	3.5540	0.2921	0.2013	0.2078	0.0482
	+0.5	20.2079	0.3984	21.5039	0.4708	11.6234	0.3556	2.3615	0.2498	0.1830	0.1947	0.5575
True variances			10		30				5	0.1	0.3	
	-0.5	10.4077	0.2923	29.8483	0.5253	-8.8395	0.3739	5.6141	0.3090	0.1133	0.3250	-0.5015
	0.0	10.3652	0.2953	30.6527	0.5678	0.4591	0.3765	4.2113	0.3282	0.1031	0.3050	0.0257
	+0.5	10.3749	0.2899	31.1722	0.5327	9.7113	0.3502	3.0978	0.3038	0.0951	0.2857	0.5400

^a Correlation between direct and maternal ; ^b Standard errors

Table 4-14: Estimated Variance components and genetic parameters for two traits under different population types
10% of dams have record (mis = 0.9) and correlation between two traits is 0.3 (t = 0.3)

Trait1

Parameters	I_{dm}^a	σ_{d1}^2	(SE) ^b	σ_{m1}^2	(SE)	σ_{d1m1}	(SE)	σ_{pe1}^2	(SE)	h_{d1}^2	h_{m1}^2	r_{d1m1}
True variances		10		30				5		0.1	0.3	
	-0.5	10.724	0.3243	28.7759	0.5815	-9.1098	0.4045	6.4025	0.2824	0.1178	0.3162	-0.5185
	0.0	10.6219	0.3263	29.6007	0.5637	0.5673	0.3721	4.849	0.2889	0.1063	0.2964	0.0319
	+0.5	10.5947	0.3066	30.7071	0.4974	10.0052	0.3024	3.3528	0.2662	0.0974	0.2823	0.5547
True variances		20		20				5		0.2	0.2	
	-0.5	21.0016	0.4500	19.2564	0.5245	-10.0661	0.4459	5.6417	0.2593	0.2337	0.2143	-0.5005
	0.0	20.8185	0.4413	20.1066	0.4910	1.0796	0.3947	3.9826	0.2621	0.2081	0.2010	0.0527
	+0.5	20.6636	0.4149	20.9746	0.4256	12.0007	0.3189	2.5765	0.2307	0.1875	0.1903	0.5764
True variances		30		10				5		0.3	0.1	
	-0.5	31.1675	0.5402	9.8751	0.4058	-8.1019	0.4167	4.6009	0.2416	0.3409	0.1080	-0.4618
	0.0	30.9154	0.5255	10.4731	0.3835	1.5750	0.3739	3.3101	0.2380	0.3086	0.1045	0.0875
	+0.5	30.7157	0.4965	11.2791	0.3296	10.8551	0.3032	2.1845	0.2085	0.2821	0.1036	0.5832

Trait2

Parameters	I_{dm}^a	σ_{d2}^2	(SE)	σ_{m2}^2	(SE)	σ_{d2m2}	(SE)	σ_{pe2}^2	(SE)	h_{d2}^2	h_{m2}^2	r_{d2m2}
True variances		30		10				5		0.3	0.1	
	-0.5	30.1658	0.5171	10.6710	0.4270	-8.1630	0.3890	4.2602	0.2293	0.3285	0.1162	-0.4549
	0.0	30.0893	0.5088	11.2982	0.4640	1.1973	0.3876	3.0441	0.2381	0.2994	0.1124	0.0649
	+0.5	30.0612	0.4883	11.8813	0.4214	10.3206	0.3362	2.0726	0.2161	0.2756	0.1089	0.5461
True variances		20		20				5		0.2	0.2	
	-0.5	20.3580	0.4214	20.4088	0.4969	-10.2245	0.4138	5.1794	0.2657	0.2248	0.2254	-0.5016
	0.0	20.2903	0.4163	21.1781	0.5544	0.5739	0.4191	3.6842	0.2874	0.2018	0.2106	0.0276
	+0.5	20.2699	0.4015	21.6163	0.5124	11.2815	0.3658	2.5330	0.2621	0.1836	0.1958	0.5389
True variances		10		30				5		0.1	0.3	
	-0.5	10.4912	0.2923	30.0244	0.5324	-9.2082	0.3880	5.8323	0.2968	0.1142	0.3268	-0.5188
	0.0	10.4173	0.2907	30.7764	0.5921	0.0656	0.4003	4.4762	0.3248	0.1036	0.3062	0.0036
	+0.5	10.4237	0.2857	31.2166	0.5714	9.3719	0.3634	3.3280	0.3124	0.0956	0.2863	0.5195

^a Correlation between direct and maternal ; ^b Standard errors

Table 4-15: Estimated Variance components and genetic parameters for two traits under different population types
10% of dams have record (mis = 0.9) and correlation between two traits is 0.8 (t = 0.8)

Trait1

Parameters	I_{dm}^a	σ_{d1}^2	(SE) ^b	σ_{m1}^2	(SE)	σ_{d1m1}	(SE)	σ_{pe1}^2	(SE)	h_{d1}^2	h_{m1}^2	I_{d1m1}
True variances			10		30			5		0.1	0.3	
	-0.5	10.6260	0.3156	28.7646	0.5402	-9.0315	0.3763	6.3901	0.2730	0.1167	0.3160	-0.5165
	0.0	10.4917	0.3198	29.5725	0.5428	0.6485	0.3555	4.8601	0.2846	0.1050	0.2961	0.0368
	+0.5	10.4405	0.3004	30.7597	0.4899	9.9687	0.2908	3.3697	0.2651	0.0960	0.2829	0.5562
True variances			20		20			5		0.2	0.2	
	-0.5	21.0016	0.4500	19.2556	0.5245	-10.0661	0.4459	5.6426	0.2592	0.2337	0.2143	-0.5005
	0.0	20.8256	0.4414	20.0764	0.4879	1.0761	0.3952	4.015	0.2605	0.2082	0.2007	0.0526
	+0.5	20.6664	0.4144	20.9705	0.4251	11.9945	0.3187	2.5853	0.2300	0.1875	0.1903	0.5761
True variances			30		10			5		0.3	0.1	
	-0.5	31.2206	0.5066	9.6812	0.3804	-8.0956	0.3851	4.8382	0.2388	0.3416	0.1059	-0.4656
	0.0	30.9060	0.5092	10.3911	0.3674	1.4394	0.3583	3.5245	0.2361	0.3087	0.1038	0.0803
	+0.5	30.6268	0.4850	11.3638	0.3212	10.6002	0.2898	2.3395	0.2078	0.2816	0.1044	0.5682

Trait2

Parameters	I_{dm}	σ_{d2}^2	(SE)	σ_{m2}^2	(SE)	σ_{d2m2}	(SE)	σ_{pe2}^2	(SE)	h_{d2}^2	h_{m2}^2	I_{d2m2}
True variances			30		10			5		0.3	0.1	
	-0.5	30.3601	0.5244	10.2592	0.3867	-8.2815	0.3671	4.7454	0.2477	0.3315	0.1120	-0.4692
	0.0	30.1743	0.5131	10.9725	0.4038	1.0665	0.3554	3.4732	0.2527	0.3011	0.1094	0.0586
	+0.5	30.0762	0.4854	11.7066	0.3712	10.2405	0.2989	2.3284	0.2342	0.2764	0.1076	0.5457
True variances			20		20			5		0.2	0.2	
	-0.5	20.7647	0.4505	20.1080	0.5120	-10.6044	0.4235	5.6438	0.2851	0.2301	0.2228	-0.5189
	0.0	20.6232	0.4378	20.8600	0.5167	0.3190	0.3941	4.1124	0.2980	0.2056	0.2080	0.0153
	+0.5	20.5360	0.4130	21.4319	0.4792	11.2308	0.3229	2.7587	0.2782	0.1863	0.1944	0.5353
True variances			10		30			5		0.1	0.3	
	-0.5	10.9027	0.3104	29.4350	0.5186	-9.6437	0.3729	6.5016	0.3027	0.1192	0.3218	-0.5383
	0.0	10.7073	0.3067	30.1136	0.5402	-0.2224	0.3684	5.1765	0.3249	0.1069	0.3008	-0.0123
	+0.5	10.6613	0.2901	30.8415	0.5390	9.1410	0.3164	3.8429	0.3161	0.0980	0.2836	0.5041

^a Correlation between direct and maternal ; ^b Standard errors

Table 4-16: Probability of significance of each factor on (co)variance estimates

Source	DF	σ^2_{d1}	σ^2_{m1}	σ_{d1m1}	σ^2_{pe1}	σ^2_{d2}	σ^2_{m2}	σ_{d2m2}	σ^2_{pe2}
mis	4	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001
t	2	0.0064	0.0554	<.0001	<.0001	<.0001	0.0007	<.0001	<.0001
par	2	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001
r	2	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001
mis x t	8	0.0004	0.0078	0.8952	<.0001	<.0001	<.0001	<.0001	<.0001
mis x par	8	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001
mis x r	8	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001
t x par	4	<.0001	<.0001	<.0001	<.0001	<.0001	0.0008	0.2408	<.0001
t x r	4	0.6727	0.8086	0.0002	0.0033	0.1465	0.0002	0.0154	0.0025
par x r	4	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001
mis x t x par	16	<.0001	0.4509	<.0001	<.0001	<.0001	0.001	<.0001	<.0001
mis x par x r	16	<.0001	<.0001	<.0001	<.0001	<.0001	0.0003	<.0001	<.0001
mis x t x r	16	0.405	0.1163	0.2396	0.0367	<.0001	<.0001	<.0001	<.0001
t x par x r	8	0.0001	<.0001	<.0001	<.0001	0.329	0.4082	0.7388	0.4749

Source	DF	σ^2_{d1}	σ^2_{m1}	σ_{d1m1}	σ^2_{pe1}	σ^2_{d2}	σ^2_{m2}	σ_{d2m2}	σ^2_{pe2}
mis	4	**	**	**	**	**	**	**	**
t	2	*	*	**	**	**	*	**	**
par	2	**	**	**	**	**	**	**	**
r	2	**	**	**	**	**	**	**	**
mis x t	8	*	*	ns	**	**	**	**	**
mis x par	8	**	**	**	**	**	**	**	**
mis x r	8	**	**	**	**	**	**	**	**
t x par	4	**	**	**	**	**	*	ns	**
t x r	4	ns	ns	*	*	ns	*	*	*
par x r	4	**	**	**	**	**	**	**	**
mis x t x par	16	**	ns	**	**	**	*	**	**
mis x par x r	16	**	**	**	**	**	*	**	**
mis x t x r	16	ns	ns	ns	*	**	**	**	**
t x par x r	8	**	**	**	**	ns	ns	ns	ns

** P<0.0001 ; * P<0.05 ; ns = non-significant

Figure 4-1: Interaction effect of **mis × par × r** on estimation of σ^2_{m1} in different levels of correlation between two traits ($t_1 = 0.0, t_2 = 0.3, t_3 = 0.8$) and different parameter sets (A, B, C)

(A) $\sigma^2_{d1}=10$; (B) $\sigma^2_{d1}=20$; (C) $\sigma^2_{d1}=30$

Figure 4-2: Interaction effect of **mis × par × r** on estimation of σ^2_{pe1} in different levels of correlation between two traits ($t_1 = 0.0, t_2 = 0.3, t_3 = 0.8$) and different values of parameter set (A, B, C)

(A) $\sigma^2_{d1}=10$; (B) $\sigma^2_{d1}=20$; (C) $\sigma^2_{d1}=30$

Figure 4.3. Interaction effect of **mis** $\times$ **par** $\times$ **r** on estimation of σ_{d1m1} in different levels of correlation between two traits ($t_1 = 0.0$, $t_2 = 0.3$, $t_3 = 0.8$) and different parameter sets (A, B, C)

(A) $\sigma_{d1}^2=10$; (B) $\sigma_{d1}^2=20$; (C) $\sigma_{d1}^2=30$

—●— $r = -0.5$ —■— $r = 0.0$ -▲- $r = +0.5$

Figure 4.4. Interaction effect of **mis** $\times$ **par** $\times$ **r** on estimation of σ^2_{d1} in different levels of correlation between two traits ($t_1 = 0.0$, $t_2 = 0.3$, $t_3 = 0.8$) and different parameter sets (A, B, C)

(A) $\sigma^2_{d1}=10$; (B) $\sigma^2_{d1}=20$; (C) $\sigma^2_{d1}=30$

Figure 4.5. Influence of missing rate on SE of maternal variance estimates (σ^2_{m1}) in different levels of r , different levels of t ($t_1 = 0.0$, $t_2 = 0.3$, $t_3 = 0.8$) and different parameter sets (A, B, C)

(A) $\sigma^2_{d1}=10$; (B) $\sigma^2_{d1}=20$; (C) $\sigma^2_{d1}=30$

Figure 4.6. Influence of missing rate on SE of direct variance estimates (σ^2_{d1}) in different levels of r , different levels of t ($t_1 = 0.0$, $t_2 = 0.3$, $t_3 = 0.8$) and different parameter sets (A, B, C)

(A) $\sigma^2_{d1}=10$; (B) $\sigma^2_{d1}=20$; (C) $\sigma^2_{d1}=30$

Figure 4.7. Influence of missing rate on SE of direct-maternal covariance estimates (σ_{d1m1}) in different levels of r , different levels of t ($t_1 = 0.0$, $t_2 = 0.3$, $t_3 = 0.8$) and different parameter sets (A, B, C)

(A) $\sigma^2_{d1}=10$; (B) $\sigma^2_{d1}=20$; (C) $\sigma^2_{d1}=30$

Figure 4.8. Influence of missing rate on SE of maternal permanent environmental variance estimates (σ^2_{pe1}) in different levels of r , different levels of t ($t_1 = 0.0$, $t_2 = 0.3$, $t_3 = 0.8$) and different parameter sets (A, B, C)

(A) $\sigma^2_{d1}=10$; (B) $\sigma^2_{d1}=20$; (C) $\sigma^2_{d1}=30$

Figure 4.9. Average bias of maternal variance estimates of trait1 over missing rate in different levels of r , different levels of t ($t_1 = 0.0$, $t_2 = 0.3$, $t_3 = 0.8$) and different parameter sets (A, B, C)

(A) $\sigma^2_{d1}=10$; (B) $\sigma^2_{d1}=20$; (C) $\sigma^2_{d1}=30$

Figure 4.10. Average bias of maternal permanent environmental variance estimates of trait1 over missing rate in different levels of r , different levels of t ($t_1 = 0.0$, $t_2 = 0.3$, $t_3 = 0.8$) and different parameter sets (A, B, C)

(A) $\sigma^2_{d1}=10$; (B) $\sigma^2_{d1}=20$; (C) $\sigma^2_{d1}=30$

Figure 4.11. Average bias of direct genetic variance estimates of trait1 over missing rate in different levels of r , different levels of t ($t_1 = 0.0$, $t_2 = 0.3$, $t_3 = 0.8$) and different parameter sets (A, B, C)

(A) $\sigma^2_{d1}=10$; (B) $\sigma^2_{d1}=20$; (C) $\sigma^2_{d1}=30$

Figure 4.12. Average bias of direct-maternal genetic covariance estimates of trait1 over missing rate in different levels of r , different levels of t ($t_1 = 0.0$, $t_2 = 0.3$, $t_3 = 0.8$) and different parameter sets (A, B, C)

(A) $\sigma^2_{d1}=10$; (B) $\sigma^2_{d1}=20$; (C) $\sigma^2_{d1}=30$

Figure 4.13. Bias (%) of the whole set of estimated genetic parameters for traits 1 and 2 over missing rate in different levels of **r**, different levels of **t** ($t_1 = 0.0$, $t_2 = 0.3$, $t_3 = 0.8$), and different parameter sets (**A, B, C**)

(A) $\sigma^2_{d1}=10, \sigma^2_{d2}=30$; (B) $\sigma^2_{d1}=20, \sigma^2_{d2}=20$; (C) $\sigma^2_{d1}=30, \sigma^2_{d2}=10$

Chapter 5

5) Conclusions and recommendations

5.1. Introduction

The general objective of this project was to consider the impact of population structure on the accuracy of (co)variance component estimation for traits that are affected by maternal effects. For estimating variance components, the Restricted Maximum Likelihood (REML) method via Average Information (AI) algorithm was used.

The specific objectives were:

- a) To determine the influence of the proportion of dams with records on (co)variance estimates. Five population types were formed with different percentages of dams with records, namely 10, 20, 50, 90, or 100%.
- b) To determine the influence of the sign of the genetic correlation between direct and maternal genetic effects on (co)variance estimates. Three different values of this correlation were considered: -0.5, 0.0, and +0.5
- c) To determine the influence of the magnitude of the genetic correlation between two traits on (co)variance estimates. Three levels of correlation between traits were considered: 0.0, 0.3, and 0.8.
- d) To determine the influence of different ratios of direct to maternal variances on (co)variance estimates. Three different ratios of direct to maternal true variance were considered: 1:3, 1:1, and 3:1.

In order to address these objectives, the same stochastic simulation was used to generate data for each population.

5.2. Variance component estimation

For each population structure (135 scenarios), sixteen (co)variances were estimated using the AI-REML method using the DMU software package. Variance component estimates were compared by their empirical sampling properties such as standard error (SE) and bias. SE was used to assess the precision of the estimates and bias was used as a criterion of comparison between true and estimated variances. Total bias percentage of the whole set of estimated parameters was used as an indicator of the bias in all parameter estimates simultaneously in each population structure.

5.2.1. Standard Error (SE)

The SE of the (co)variance estimates are presented in Figures 4.5 to 4.8. Generally, the proportion of dams with records (*mis*) had no influence on the SE of the maternal, direct, and permanent environmental variance estimates. For the direct-maternal covariance estimates, a larger SE was obtained when the missing rate was high ($mis = 0.8$ or 0.9). The influence of the parameter sets (ratio of direct to maternal variance) on the SE of the estimates was stronger than that of the population structure. A larger SE was obtained when the direct-maternal correlation was negative ($r = -0.5$). The correlation between two traits (*t*) had no major influence on the SE of the estimates.

5.2.2. Bias

Bias for maternal, permanent environmental and direct variances as well as for direct-maternal covariance was reported in chapter 4 in Figures 4.9 to 4.12. In general, the proportion of dams without records (missing rate) and the sign of the direct and maternal correlation had a greater effect on bias of the estimates than different parameter sets and correlation between two traits. A larger bias was obtained when the missing rate was high ($\text{mis}=0.8$ or 0.9) and the direct-maternal correlation was positive. In the case of the direct genetic variance, the larger bias was obtained when the direct-maternal correlation was negative. Larger differences in bias were detected when direct variance was greater than maternal variance. This variance ratio exists for most growth traits in livestock particularly in beef cattle. A smaller bias of direct-maternal covariance was obtained when the direct-maternal correlation was negative. In fact, this negative correlation between the direct and maternal effects exists biologically in most livestock growth traits (see Table 2.1). Bias of the genetic maternal variance estimates in the full data structure was unexpected. This may be caused by some simulation assumptions for replacement of dams in each generation such as the strategy for culling dams when they have more than 5 progeny or when they are older than 7 years.

5.2.3. Total bias (%)

Bias percentage for the whole set of estimated genetic parameters for traits 1 and 2 was reported in Chapter 4 in Figure 4-13. This parameter shows the percentage bias that would exist in the whole set of parameter estimates in each population structure at one time. The largest bias percentage was obtained when the missing rate was 0.9, the direct-

maternal correlation was positive ($r = +0.5$) and the variance ratio between direct and maternal was equal (1:1). Bias of the whole set of estimates was influenced by population structure and direct-maternal correlation. With an increasing correlation between traits, the percentage of total bias decreased.

5.3. Recommendations and future studies

Both direct and maternal effects should be considered in selection decisions when traits are known to be influenced by maternal effects. Many studies suggest that when the maternal component is more important, selection for direct effect alone can reduce overall genetic progress. A negative genetic correlation between direct and maternal effect will reduce the genetic progress even more. Therefore, consideration of such effects in the genetic evaluation of animals requires reliable estimates of the (co)variance components. The results of this study showed that the ratio of direct and maternal variances along with the sign of the correlation between direct and maternal effects had a major influence on the SE of the (co)variance estimates compared with aspects of the proportion of dams with records (mis) and the correlation between two traits. The factors such as mis , r , and par had a significant impact on the bias of (co)variance estimates but the correlation between the two traits (t) had a limited effect.

The populations simulated in this study were idealized in several aspects. First, animals were randomly mated and culled in each generation and there was no selection. Second, the fixed factors (sex, age of dam, generation) were balanced for each population type. Third, parameters to be estimated were known which never holds in reality. Also, some

important assumptions which rarely if ever occur in reality included equal sex ratio, equal family size, fixed generation size, and no inbreeding effects. Therefore, applying the conclusions of this simulation study to real populations will provide an indication of the potential accuracy and bias but the actual magnitude will differ. With real data, the problem becomes more complex and there are several additional causes of bias. For further studies, some factors that exist in real animal populations could be considered in the simulation such as:

- 1) Selection of animals based on their phenotypic records or total merit (direct breeding value plus maternal breeding value).
- 2) Simulating populations with differentially missing data for traits 1 and 2.
- 3) Treating one trait as affected by maternal effects and the other trait for direct genetic effects alone.
- 4) The influence of fixed effects on (co)variance estimates.
- 5) Inbreeding effects.
- 6) More than two traits (multiple-traits)
- 7) Using different values for parameters sets and genetic correlations between direct and maternal for each trait
- 8) Simulating populations with more records and a larger data set.
- 9) The influence of a negative genetic correlation between traits on (co)variance estimates
- 10) Other gene interactions in addition to additive effects such as dominance and epistatic effects

Despite some limited assumptions, the results of this study showed that reliable estimates of maternal effects were obtained when several well-linked generations of records and many relationships between relatives related to the mother were available. Large data sets with good structure (i.e. more dams with records and more progeny per dam) are required, particularly when parameters are not known. Roehre & Kennedy (1993) concluded that with 3 million records and only 100 dam-offspring pairs, the reliability of the estimated correlation between direct and maternal effects will be low. Results of the present study showed that by increasing the proportion of dams without records from 0.5 to 0.9, all (co)variance estimates such as maternal variance, permanent environmental variance and direct-maternal covariance are biased and are not accurate for using in genetic evaluation systems. The results also showed that larger bias for direct-maternal covariance occurred when there was a positive correlation between direct and maternal effects. Based on the results of this study by using a negative genetic correlation ($r = -0.5$) between direct and maternal effects, the (co)variance estimates would be less biased and more accurate, which may be useful for genetic evaluation for traits subject to maternal effects when a negative correlation exist between direct and maternal genetic effects. However, for expanding this result further studies are needed.

Fitting an appropriate model to estimate parameters for traits subject to direct and maternal genetic influence is also necessary to obtain unbiased estimates. A good definition of the biological model is important because direct and maternal effects can interact depending on environmental conditions. For example, in this study only genetic

covariances such as direct-direct, maternal-maternal and direct-maternal were considered in the model while environmental covariances between these parameters were assumed to be zero. Several authors (e.g. Baker, 1980 ; Cantet et al., 1988) emphasized the possibility of a negative environmental covariance between dam and offspring (σ_{EC}) which was expected to bias the estimate of the direct-maternal genetic correlation downwards. By assuming a non-zero σ_{EC} , Cantet et al. (1988) obtained large negative estimates of the direct-maternal genetic covariance for birth weight (BW) and weaning weight (WW) in Herefords accompanied by positive estimates of σ_{EC} . Koerhuis and Thompson (1997) found that models accounting for environmental dam-offspring covariances yielded estimates of genetic correlations that were somewhat more negative than estimates obtained when ignoring environmental covariances. Bijma (2006) reported that, even with a moderate environmental direct-maternal correlation of -0.3, the estimated direct-maternal genetic correlation may be biased substantially. So, further studies are needed to consider these environmental factors and their covariances in the model (e.g. environmental covariances between dam and offspring records) for maternal effects evaluation.

In general, results of the present study showed that the parameter sets (par) along with the direct-maternal correlation (r) had major influences on the SE of the (co)variance estimates in comparison to the proportion of dams with records (mis) and the correlation between traits (t). The proportion of dams with records had greater impact on the bias and total bias percentage of the estimates. However, complete data sets with more links of dam-offspring as well as more progeny per dam are required for estimating maternal genetic parameters with high reliability in the single and multiple trait situations.

Chapter 6

References:

Ahlschwede, W. T., and Robison, O. W. 1971a. Prenatal and postnatal influences on growth and backfat in swine. *J. Anim. Sci.* 32:10-16.

Ahlschwede, W. T., and Robison, O. W. 1971b. Maternal effects on weights and backfat of swine. *J. Anim. Sci.* 33:1206-1215.

Axelrod, R. 1997. Advancing the art of simulation in the social sciences. Paper prepared for the school of public policy, University of Michigan, Ann Arbor, USA.

Baker, R. L. 1980. The role of maternal effects on the efficiency of selection in beef cattle. A review. *Proc. N. Z. Soc. Anim. Prod.* 40:285-303.

Bertrand, J. K., and Benyshek, L. L. 1987. Variance and covariance estimates for maternally influenced beef growth traits. *J. Anim. Sci.* 64:728-734.

Bijma, P. 2006. Estimating maternal genetic effects in livestock. *J. Anim. Sci.* 84: 800-806.

Boettcher, P., Luo, M., Schaeffer, L. R., and Dekkers, J. 2000. Estimates of genetic parameters for calving ease in first and second lactations. Report to the technical committee of the Genetic Evaluation Board, Canada.

Bondari, K., Willham, R. L., and Freeman, A. E. 1978. Estimates of direct and maternal genetic correlations for pupa weight and family size of *Triboleum*. *J. Anim. Sci.* 47: 358-365.

Bradford G. E. 1972. The role of maternal effects in animal breeding: VII. Maternal effects in sheep. *J. Anim. Sci.* 35:1324-1334.

Bratley, P., Fox, B., and Schrage, L. 1987. A guide to simulation. second edition. New York: Springer-Verlag

Bulmer, M. G. 1971. The effect of selection on genetic variability. *Am. Nat.* 105:201-211.

Burfening, P. J., Kress, D. D., and Friedrich, R. L. 1981. Calving ease and growth rate of Simmental sired calves. III. Direct and maternal effects. *J. Anim. Sci.* 53:1210-1216.

Cantet, R. J. C., Kress, D. D., Anderson, D. C., Doornbos, D. E., Burfening, P. J., and Blackwell, R. L. 1988. Direct and maternal variances and covariances and maternal phenotypic effects on pre-weaning growth of beef cattle. *J. Anim. Sci.* 66: 648-660.

Cheverud, J. M. 1983. Evolution by kin selection: a quantitative genetic model illustrated by maternal performance in mice. *Evolution.* 38:766-777.

Clement, V., Bibe, B., Verrier, E., Elsen, E. J., Manfredi, E., Bouix, J., and Hanocq, E. 2001. Simulation analysis to test the influence of model adequacy and data structure on the estimation of genetic parameters for traits with direct and maternal effects. *Genet. Sel. Evol.* 33:369-395.

Cody, R. P., and Smith, J. K. 1997. Applied statistics and the SAS programming language. 4th edition, (445 pages), Prentice-Hall, Inc.

Cundiff, L. V. 1972. The role of maternal effects in animal breeding. VIII. Comparative aspects of maternal effects. *J. Anim. Sci.* 35: 1335-1337.

Dickerson, G. E. 1947. Composition of hog carcasses as influenced by heritable differences in rate and economy of gain. *Res. Bul. Iowa Agric. Exp. Sta.* 354: 489-524.

Diop, M., and Van Vleck, L. D. 1998. Estimates of genetic parameters for growth traits of Gobra cattle. *Anim. Sci.* 66:349-355.

Dodenhoff, J., Van Vleck, L. D., Kachman, S. D. and Koch, R. M. 1998. Parameter estimates for direct, maternal and grandmaternal genetic effects for birth weight and weaning weight in Hereford cattle. *J. Anim. Sci.* 76: 2521-2527.

Dodenhoff, J., Van Vleck, L. D., and Gregory, K. E. 1999. Estimation of direct, maternal, and grandmaternal genetic effects for weaning weight in several breeds of beef cattle. *J. Anim. Sci.* 77:840-845.

Duangjinda, M., Bertrand, J. K., Misztal, I., and Druet, T. 2001. Estimation of additive and non-additive genetic variances in Hereford, Gelbvieh, and Charolais by method R. *J. Anim. Sci.* 79:2997-3001.

Eisen, E. J. 1967. Mating designs for estimating direct and maternal genetic variances and direct-maternal covariances. *Can. J. Genet. Cytol.* 9:13-22.

Eler, J.P., Van Vleck, L. D., Ferraz, J. B. S. and Lobo, R.B. 1995. Estimation of variances due to direct and maternal effects for growth traits of Nelore cattle. *J. Anim. Sci.* 73: 3253-3258.

El Oksh, H. A., Sutherland, T. M., and Williams, J. S. 1967. Prenatal and postnatal influence on growth of mice. *Genetics.* 57:79-94.

Falconer, D. S. 1965. Maternal effects and selection response. *Proceedings of the XIth international congress of genetics. The Hague. The Netherlands. Vol. 3: 763-774.*

Fouilly, J. L., and Lefort, G. 1978. Methodes d'estimation des effets directs et maternels en selection animale. *Ann. Genet. Sel. Anim.* 10:475-496.

Garrick, D. J., Pollack, E. J., Quaas, R. L., and Van Vleck, L. D. 1989. Variance heterogeneity in direct and maternal weight traits by sex and percent purebred for Simmental-sired calves. *J. Anim. Sci.* 67:2515-2528.

Gerstmayer, S. 1992. Impact of the data structure on the reliability of the estimated genetic parameters in an animal model with maternal effects. *J. Anim. Breed. Genet.* 109:321-336.

Graser, H. U., and Hammond, K. 1985. Mixed model procedures for the Australian beef industries. I. Multiple traits model for estimation of breeding values for 200-day and final weights for cattle. *J. Aust. Agric. Res.* 36:527-535.

Graser, H. U., Smith, S. P., and Tier, B. 1987. A derivative-free approach for estimating variance components in animal models by Restricted Maximum Likelihood. *J. Anim. Sci.* 64: 1362-1370.

Gregory, K. E., Laster, D. B., Cundiff, L. V., Koch, R. M., and Smith, G. M. 1978. Heterosis and breed maternal and transmitted effects in beef cattle. II. Growth rate and puberty in females. *J. Anim. Sci.* 47:1042-1053.

Griggs, K. M. 1986. The influence of pre-weaning growth of heifers on their maternal ability. B. Rur. Sci. Thesis, University of New England, Armidale, NSW 2351, Australia.

Hohenboken, W. D., and Brinks, J. S. 1971. Relationships between direct and maternal effects on growth in Herefords: II partitioning of covariance between relatives. *J. Anim. Sci.* 32:26-34.

Iwaisaki, H., Tsuruta, S., Misztal, I., and Bertrand, J. K. 2005. Estimation of correlation between maternal permanent environmental effects of related dams in beef cattle. *J. Anim. Sci.* 83: 537-542.

Jensen, J., Madsen, P., Andersen, B. B. 1991. Sire by rearing intensity interactions on feed intake, efficiency, and production of bulls, heifers and cows. Paper presented at the 42th Ann. Meeting of EAAP, Berlin.

Jensen, J., E., Mantysaari, A., Madsen, P., and Thompson, R. 1997. Restricted Maximum Likelihood estimation of (co)variance components in multivariate mixed linear models using average information. *J. Indian Soc. Agr. Stat.* 49:215-236.

Johnson, D. L., and Thompson, R. 1995. Restricted maximum likelihood estimation of variance components for univariate animal models using sparse matrix techniques and average information. *J. Dairy. Sci.* 78:449-456.

Kempthorne, O. 1957. An introduction to genetic statistics. Wiley, New York. Ch. 2, 3.

Kenney, J. F. and Keeping, E. S. 1962. Mathematics of Statistics, Pt. 1, 3rd ed. Princeton, NJ: Van Nostrand.

Kirkpatrick, M., Lande, R. 1989. The Evolution of Maternal Characters. *Evolution.* 43: 485-503.

Koch, R. M. 1972. The role of maternal effects in animal breeding. VI. Maternal effects in beef cattle. *J. Anim. Sci.* 35:1316-1323.

Koch, R. M. and Clark, R. T. 1955. Genetic and environmental relationships among economic characters in beef cattle. III. Evaluating maternal environment. *J. Anim. Sci.* 14: 979-996.

Koerhuis, A. N. M., and Thompson, R. 1997. Models to estimate maternal effects for juvenile body weight in broiler chickens. *Genet. Sel. Evol.* 29: 225-249.

Lee, C., and Pollak, E. J. 1997a. Influence of sire misidentification on sire x year interaction variance and direct-maternal genetic covariance for weaning weight in beef cattle. *J. Anim. Sci.* 75:2858-2863.

Lee, C., and Pollak, E. J. 1997b. Relationship between sire x year interactions and direct-maternal genetic correlation for weaning weight of Simmental cattle. *J. Anim. Sci.* 75:68-75.

Luo, M. F., Boettcher, P. J., Dekkers, J. C. M., and Schaeffer, L. R. 1999. Bayesian analysis for estimation of genetic parameters for calving ease and stillbirth for Canadian Holstein. *J. Dairy. Sci.* 82:1848-1857.

Madsen, P., and Jensen, J. 2002. A user's guide to DMU. Danish Institute of Agricultural Sciences (DIAS), Department of Animal Breeding and Genetics, Denmark.

Mackinnon, M. J., Meyer, K. and Hetzel, D. J. S. 1991. Genetic variation and covariation for growth, parasite resistance and heat tolerance in tropical cattle. *Livest. Prod. Sci.* 27:105-122.

Maniatis, N. and Pollott, G. E. 2003. The impact of data structure on genetic (co)variance components of early growth in sheep, estimated using an animal model with maternal effects. *J. Anim. Sci.* 81: 101-108.

Maurer, R. R. and Gregory, K. E. 1990. Contributions of ovum cytoplasm, uterine environmental and postnatal environment to maternal effects in beef cattle. *J. Anim. Sci.* 68:2319-2332.

Meyer, K. 1992a. Bias and sampling covariances of estimates of variance components due to maternal effects. *Genet. Sel. Evol.* 24:487-509.

Meyer, K. 1992b. Variance components due to direct and maternal effects for growth traits of Australian beef cattle. *Livest. Prod. Sci.* 31: 179-204.

Meyer, K. 1997. Estimates of genetic parameters for weaning weight of beef cattle accounting for direct-maternal environmental covariances. *Livest. Prod. Sci.* 52:187-199.

Mrode, R. A., and Thompson, R. 1990. Genetic parameters for body weight in beef cattle in Britain. *Proc. 4th Wld. Cong. Genet. Appl. Livest. Prod.*, Edinburgh, Vol. XV, 271-275.

Meuwissen, T. H. E., and Luo, Z. 1992. Computing inbreeding coefficients in large populations. *Genet. Sel. Evol.* 24:305-313.

Patterson, H. D., and Thomson, R. 1971. Recovery of inter-block information when block sizes are unequal. *Biometrika*, 58:545-554.

Quaas, R.L., and Pollak, E. J. 1980. Mixed model methodology for farm and ranch beef cattle testing programs. *J. Anim. Sci.* 51:1277-1287.

Quaas, R. L., Anderson, R. D., and Gilmour, A. R. 1984. BLUP method. Handout, AGBU, University of New England, N. S. W., 2351, Australia.

Quaas, R. L., Elzo, M. A., and Pollak, E. J. 1985. Analysis of Simmental data: estimation of direct and maternal (co)variances. *J. Anim. Sci.* 61, Suppl. 1, 221.

Quintanilla, R.L., Varona, M.R., and Piedrafita, J. 1999. Maternal animal model with correlation between environmental effects of related dams. *J. Anim. Sci.* 77: 2904-2917.

Robison, O. W. 1972. The role of maternal effects in animal breeding. V. Maternal effects in swine. *J. Anim. Sci.* 35: 1303-1315.

Robison, O. W. 1981. The influence of maternal effects on the efficiency of selection. A review. *Livest. Prod. Sci.* 8:121-137.

Robinson, D. L. 1996a. Estimation and interpretation of direct and maternal genetic parameters for weights of Australian Angus cattle. *Livest. Prod. Sci.* 45:1-11.

Robinson, D. L. 1996b. Models which might explain negative correlations between direct and maternal genetic effects. *Livest. Prod. Sci.* 45:111-122.

Roehe, R., and Kennedy, B. W. 1993a. The influence of maternal effects on accuracy of evaluation of litter size in swine. *J. Anim. Sci.* 71:2353-2364.

Roehe, R., and Kennedy, B. W. 1993b. Effect of selection for maternal and direct genetic effects on genetic improvement of litter size in swine. *J. Anim. Sci.* 71:2891-2904.

Roso, V. M. 2004. Genetic evaluation of multi-breed beef cattle. Center for Genetic Improvement of Livestock (CGIL), University of Guelph, Canada.

Schaeffer, L. R. 1993. Linear models and computing strategies in animal breeding. Handout, CGIL, University of Guelph, Dept. of Animal and Poultry Science, Canada.

Southwood, O.I., and Kennedy, B. W. 1990. Estimation of direct and maternal genetic variance for litter size in Canadian Yorkshire and Landrace swine using an animal model. *J. Anim. Sci.* 68:1841-1847.

Swalve, H. 1993. Estimation of direct and maternal (co)variance components for growth traits in Australian Simmental beef cattle. *J. Anim. Breed. Genet.* 110: 241-252.

Tawah, C. L., Mbah, D. A., Rege, J. E. O. and Oumate, H. 1993. Genetic evaluation of birth and weaning weights of Gudali and two-breed synthetic Wakwa beef cattle populations under selection in Cameroon: genetic and phenotypic parameters. *Anim. Prod.* 57: 73-79.

Thiede, D. A. 1998. Maternal inheritance and its effect on adaptive evolution: a quantitative genetic analysis of maternal effects in a natural plant population. *evolution.* 52:998-1015.

Thompson, W. A. 1962. The problem of negative estimates of variance components. *Ann. Mat. Stat.* 33:273-289.

Thompson, R. 1976. The estimation of maternal genetic variances. *Biometrics*. 32: 903-917.

Thompson, R. 1977. Estimation of quantitative genetic parameters. *Proceeding of International Conference in Quantitative Genetics*. Iowa State Univ. Press, Ames, 639-657.

Totusek, R., Stephens, O.F., Kropp, J.R., Holloway, S.W., Knosi, J.W. and Whiteman, J.V. 1971. Milk production of range cows. *Okla. Agric. Ext. Sta. Misc. Pub.* 85.

Trus, D., and Wilton, J. W. 1988. Genetic parameters for maternal traits in beef cattle. *Can. J. Anim. Sci.* 86:119-128.

Van Vleck, L. D. 1994. Algorithms for simulation of animal models with multiple traits and with maternal and non-additive genetic effects. *Brazilian Journal of Genetics (Revista Brasileira de Genetica)*, 17:53-57.

Van Vleck, L. D., Louis, D. S., and Miller, J. I. 1977. Expected phenotypic response in weaning weight of beef calves from selection for direct and maternal genetic effects. *J. Anim. Sci.* 44:360-367.

Van Vleck, L. D. and Dwyer, D. J. 1985. Successive overrelaxation, block iteration, and method of conjugate gradients for solving equations for multiple trait evaluation of sires, *J. Dairy. Sci.* 68:760-768.

Varona, L., Misztal, I. and Bertrand, J. K. 1999. Threshold-linear versus linear-linear analysis of birth weight and calving ease using an animal model. II. Comparison of models. *J. Anim. Sci.* 77:2003-2007.

Willham, R. L. 1963. The covariance between relatives for characters composed of components contributed by related individuals. *Biometrics* 19:18-27.

Willham, R. L. 1972. The role of maternal effects in animal breeding: III. Biometrical aspects of maternal effects in animals. *J. Anim. Sci.* 35:1288-1293.

Willham, R. L. 1980. Problems in estimating maternal effects. *Livest. Prod. Sci.* 7:405-418.

Woodward, B. W., Pollak, E. J., and Quaas, R. L. 1992. Parameter estimation for carcass traits including growth information of Simmental beef cattle using Restricted Maximum Likelihood with a multiple-trait model. *J. Anim. Sci.* 70:1098-1109.

Wright, H. B., Pollack, E. J., and Quaas, R. L. 1987. Estimation of variance and covariance components to determine heritabilities and repeatability of weaning weights in American Simmental cattle. *J. Anim. Sci.* 65:975-981.

Appendices

Appendix1 (a): Linear & quadratic contrast of different factors on direct variance

Class	Levels	Values
mis	5	0 0.1 0.5 0.8 0.9
t	3	0 0.3 0.8
par	3	10 20 30
r	3	-0.5 0 0.5
Number of Observations		135

Dependent Variable: **d1**

Weight: wt

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	102	55321.62073	542.36883	122956	<.0001
Error	32	0.14115	0.00441		
Corrected Total	134	55321.76188			

R-Square	Coeff Var	Root MSE	d1 Mean
0.999997	0.400645	0.066416	16.57725

Source	DF	Type III SS	Mean Square	F Value	Pr > F
mis	4	109.04539	27.26135	6180.20	<.0001
t	2	0.05238	0.02619	5.94	0.0064
par	2	54383.39502	27191.69751	6164406	<.0001
r	2	0.48767	0.24384	55.28	<.0001
mis*t	8	0.18035	0.02254	5.11	0.0004
mis*par	8	5.27594	0.65949	149.51	<.0001
mis*r	8	2.69594	0.33699	76.40	<.0001
t*par	4	0.17697	0.04424	10.03	<.0001
t*r	4	0.01040	0.00260	0.59	0.6727
par*r	4	1.02594	0.25648	58.15	<.0001
mis*t*par	16	0.73554	0.04597	10.42	<.0001
mis*par*r	16	0.52047	0.03253	7.37	<.0001
mis*t*r	16	0.07673	0.00480	1.09	0.4050
t*par*r	8	0.20232	0.02529	5.73	0.0001

Contrast	DF	Contrast SS	Mean Square	F Value	Pr > F
mis (linear)	1	55.65420	55.65420	12616.9	<.0001
mis (quadratic)	1	51.78822	51.78822	11740.5	<.0001
t (linear)	1	0.04685	0.04685	10.62	0.0027
t (quadratic)	1	0.00507	0.00507	1.15	0.2916
par (linear)	1	50135.92577	50135.92577	1.137E7	<.0001
par (quadratic)	1	0.11338	0.11338	25.70	<.0001
r (linear)	1	0.44583	0.44583	101.07	<.0001
r (quadratic)	1	0.05718	0.05718	12.96	0.0011

Appendix1(b) : Linear & quadratic contrast of different factors on maternal variance

Class	Levels	Values
mis	5	0 0.1 0.5 0.8 0.9
t	3	0 0.3 0.8
par	3	10 20 3
r	3	-0.5 0 0.5
Number of Observations		135

Dependent Variable: **m1**
Weight: wt

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	102	49378.04019	484.09843	88605.6	<.0001
Error	32	0.17483	0.00546		
Corrected Total	134	49378.21502			

R-Square	Coeff Var	Root MSE	m1 Mean
0.999996	0.402862	0.073916	18.34765

Source	DF	Type III SS	Mean Square	F Value	Pr > F
mis	4	32.76402	8.19100	1499.22	<.0001
t	2	0.03464	0.01732	3.17	0.0554
par	2	48084.62651	24042.31326	4400517	<.0001
r	2	146.81383	73.40691	13435.8	<.0001
mis*t	8	0.14270	0.01784	3.26	0.0078
mis*par	8	36.05236	4.50655	824.84	<.0001
mis*r	8	46.75352	5.84419	1069.67	<.0001
t*par	4	0.23305	0.05826	10.66	<.0001
t*r	4	0.00870	0.00217	0.40	0.8086
par*r	4	1.29789	0.32447	59.39	<.0001
mis*t*par	16	0.09032	0.00565	1.03	0.4509
mis*par*r	16	1.13238	0.07077	12.95	<.0001
mis*t*r	16	0.14271	0.00892	1.63	0.1163
t*par*r	8	0.60071	0.07509	13.74	<.0001

Contrast	DF	Contrast SS	Mean Square	F Value	Pr > F
mis(linear)	1	15.06477	15.06477	2757.34	<.0001
mis(quadratic)	1	8.80917	8.80917	1612.36	<.0001
t (linear)	1	0.01846	0.01846	3.38	0.0753
t (quadratic)	1	0.01567	0.01567	2.87	0.1001
par(linear)	1	46740.31503	46740.31503	8554983	<.0001
par(quadratic)	1	0.00004	0.00004	0.01	0.9315
r (linear)	1	146.80564	146.80564	26870.2	<.0001
r (quadratic)	1	0.13363	0.13363	24.46	<.0001

Appendix1 (c) : Linear & quadratic contrast of different factors on
direct-maternal covariance

Class	Levels	Values
mis	5	0 0.1 0.5 0.8 0.9
t	3	0 0.3 0.8
par	3	10 20 30
r	3	-0.5 0 0.5
Number of Observations		135

Dependent Variable: **d1m1**

Weight: wt

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	102	79491.33329	779.32680	120011	<.0001
Error	32	0.20780	0.00649		
Corrected Total	134	79491.54109			

R-Square	Coeff Var	Root MSE	d1m1 Mean
0.999997	5.020157	0.080584	1.605208

Source	DF	Type III SS	Mean Square	F Value	Pr > F
mis	4	222.10335	55.52584	8550.63	<.0001
t	2	0.36408	0.18204	28.03	<.0001
par	2	39.26455	19.63228	3023.25	<.0001
r	2	75468.42162	37734.21081	5810830	<.0001
mis*t	8	0.02225	0.00278	0.43	0.8952
mis*par	8	17.05964	2.13245	328.38	<.0001
mis*r	8	96.00281	12.00035	1847.98	<.0001
t*par	4	0.39146	0.09786	15.07	<.0001
t*r	4	0.19341	0.04835	7.45	0.0002
par*r	4	373.74484	93.43621	14388.6	<.0001
mis*t*par	16	0.99754	0.06235	9.60	<.0001
mis*par*r	16	1.77936	0.11121	17.13	<.0001
mis*t*r	16	0.13809	0.00863	1.33	0.2396
t*par*r	8	0.35470	0.04434	6.83	<.0001

Contrast	DF	Contrast SS	Mean Square	F Value	Pr > F
mis (linear)	1	202.24730	202.24730	31144.8	<.0001
mis (quadratic)	1	15.07821	15.07821	2321.95	<.0001
t (linear)	1	0.33580	0.33580	51.71	<.0001
t (quadratic)	1	0.02519	0.02519	3.88	0.0576
par (linear)	1	38.67599	38.67599	5955.86	<.0001
par (quadratic)	1	0.39937	0.39937	61.50	<.0001
r (linear)	1	74496.16001	74496.16001	1.147E7	<.0001
r (quadratic)	1	1.26055	1.26055	194.12	<.0001

**Appendix1 (d): Linear & quadratic contrast of different factors on
maternal permanent environmental variance**

Class	Levels	Values
mis	5	0 0.1 0.5 0.8 0.9
t	3	0 0.3 0.8
par	3	10 20 30
r	3	-0.5 0 0.5
Number of Observations		135

Dependent Variable: **pel**
Weight: wt

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	102	1761.437216	17.268992	4897.32	<.0001
Error	32	0.112839	0.003526		
Corrected Total	134	1761.550055			

R-Square	Coeff Var	Root MSE	pel Mean
0.999936	1.433771	0.059382	4.141661

Source	DF	Type III SS	Mean Square	F Value	Pr > F
mis	4	162.6847493	40.6711873	11534.0	<.0001
t	2	0.9954665	0.4977332	141.15	<.0001
par	2	176.3810041	88.1905020	25010.0	<.0001
r	2	694.9289445	347.4644723	98537.6	<.0001
mis*t	8	0.4345572	0.0543196	15.40	<.0001
mis*par	8	108.3946993	13.5493374	3842.46	<.0001
mis*r	8	368.2149801	46.0268725	13052.8	<.0001
t*par	4	0.4550521	0.1137630	32.26	<.0001
t*r	4	0.0695592	0.0173898	4.93	0.0033
par*r	4	7.9248968	1.9812242	561.86	<.0001
mis*t*par	16	0.9809451	0.0613091	17.39	<.0001
mis*par*r	16	5.2205218	0.3262826	92.53	<.0001
mis*t*r	16	0.1182047	0.0073878	2.10	0.0367
t*par*r	8	0.4014288	0.0501786	14.23	<.0001

Contrast	DF	Contrast SS	Mean Square	F Value	Pr > F
Mis (linear)	1	129.2760270	129.2760270	36661.4	<.0001
Mis (quadratic)	1	8.3016941	8.3016941	2354.28	<.0001
t (linear)	1	0.8341781	0.8341781	236.56	<.0001
t (quadratic)	1	0.1556369	0.1556369	44.14	<.0001
par (linear)	1	176.3033485	176.3033485	49997.9	<.0001
par (quadratic)	1	0.7702890	0.7702890	218.45	<.0001
r (linear)	1	694.0467105	694.0467105	196825	<.0001
r (quadratic)	1	1.7572990	1.7572990	498.35	<.0001

Appendix 2: Calculate of bias for all (co)variances of two traits in one parameter set
(d1=m2=10, d2=m1= 30, pe1= pe2=5, t = 0.3, mis = 0.9)

$$\mathbf{G} = \begin{bmatrix} d1 & d1m1 & d1pe1 & d1d2 & d1m2 & d1pe2 \\ & m1 & m1pe1 & m1d2 & m1m2 & m1pe1 \\ & & pe1 & pe1d2 & pe1m2 & pe1pe2 \\ & & & d2 & d2m2 & d2pe2 \\ & & & & m2 & m2pe2 \\ & & & & & pe2 \end{bmatrix}$$

$$\mathbf{G}_1 = \begin{bmatrix} 10 & -8.66 & 0 & 5.19 & -1.50 & 0 \\ & 30 & 0 & -4.50 & 5.19 & 0 \\ & & 5 & 0 & 0 & 1.50 \\ & & & 30 & -8.66 & 0 \\ & & & & 10 & 0 \\ & & & & & 5 \end{bmatrix} \quad \text{when } r = -0.5$$

$$\mathbf{G}_2 = \begin{bmatrix} 10 & 8.66 & 0 & 5.19 & 1.50 & 0 \\ & 30 & 0 & 4.50 & 5.19 & 0 \\ & & 5 & 0 & 0 & 1.50 \\ & & & 30 & 8.66 & 0 \\ & & & & 10 & 0 \\ & & & & & 5 \end{bmatrix} \quad \text{when } r = +0.5$$

$$\hat{\mathbf{G}}_1 - \mathbf{G}_1 = \begin{bmatrix} 0.723 & -0.449 & 0 & 0.333 & -0.532 & 0 \\ & -1.223 & 0 & -0.790 & 0.212 & 0 \\ & & 1.402 & 0 & 0 & 0.540 \\ & & & 0.164 & 0.496 & 0 \\ & & & & 0.670 & 0 \\ & & & & & -0.739 \end{bmatrix}$$

$$\hat{\mathbf{G}}_2 - \mathbf{G}_2 = \begin{bmatrix} 0.594 & 1.344 & 0 & 0.212 & -0.337 & 0 \\ & 0.706 & 0 & 0.367 & 0.475 & 0 \\ & & -1.647 & 0 & 0 & -0.469 \\ & & & 0.054 & 1.667 & 0 \\ & & & & 1.881 & 0 \\ & & & & & -2.927 \end{bmatrix}$$

Appendix 3

In linear algebra, functional analysis and related areas of mathematics, a **norm** is a function which assigns a positive *length* or *size* to all vectors in a vector space, other than the zero vector.

The Euclidean norm is the most common norm, calculated by summing the squares of all coordinates and taking the square root. The Euclidean norm is matrix norm of a $m \times n$ matrix **A** defined as the square root of the sum of the absolute squares of its elements.

$$\|A\|_F = \sqrt{\sum_{i=1}^m \sum_{j=1}^n |a_{ij}|^2} \quad (\text{equ.1})$$

It is also equal to the square root of the matrix trace of $A A^H$, where A^H is the conjugate transpose, i.e.,

$$\|A\|_F = \sqrt{\text{Tr}(A A^H)}. \quad (\text{equ.2})$$

The Euclidean norm method was used for calculating total bias (%) of the whole set of estimated parameters at one time for traits1 and 2 through following formula:

$$\text{TotalBias} = \frac{|\hat{G} - G|}{|G|} \times 100$$

Where G is the true values of (co)variance matrix for both traits and G-hat is the estimated values of (co)variance matrix:

$$G = \begin{bmatrix} d1 & d1m1 & 0 & d1d2 & d1m2 & 0 \\ & m1 & 0 & m1d2 & m1m2 & 0 \\ & & pe1 & 0 & 0 & pe1pe2 \\ & & & d2 & d2m2 & 0 \\ & & & & m2 & 0 \\ & & & & & pe2 \end{bmatrix}$$

The Euclidean norm of G matrix and (G_{hat} – G) was obtained using equ.2 and used for calculation of total bias (%).