MULTIVARIATE ESTIMATION OF VARIANCE AND COVARIANCE COMPONENTS USING RESTRICTED MAXIMUM LIKELIHOOD, IN DAIRY CATTLE.

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ABSTRACT

The multivariate estimation of sire additive and residual variances and covariances by Restricted Maximum Likelihood (REML) is addressed. Particular emphasis is given to its application to dairy cattle data when all traits are explained by the same model and no observations are missing. Special attention is given to the analysis of new traits being included in a sire evaluation programme, for which a model has to be developed and no previous estimates of the population parameters exist.

Results obtained by using either the multivariate Method 3 of Henderson, multivariate REML excluding the Numerator Relationship Matrix (NRM) or by multivariate REML including the NRM were compared. When a large number of traits were fitted simultaneously the variance-covariance matrix estimated by Method 3 was negative-definite (outside the allowable parameter space). REML estimates obtained while ignoring the NRM were biased. The number and sequence of traits fitted in the analysis affected the estimates at convergence. A canonical transformation of the variance-covariance matrix was undertaken to simplify the computation by means of an Expectation Maximisation (EM) algorithm.

Approaches to choosing initial values for their use in iterative methods were compared via their values at convergence and the number of iterations required to converge.

To further simplify the use of multivariate REML, three transformations of the Mixed Model Equations (MME) were integrated: the absorption of proven sire effects taken as fixed, a triangular factorisation of the NRM, and the singular value decomposition of the coefficient matrix in the MME. One statistical algorithm (EM) and one mathematical algorithm (Scoring type) were developed to iteratively solve the REML equations on the transformed scale, such that the transformed coefficient matrix of the MME did not need to be inverted at each iteration and the required quantities to build the REML equations were obtained through vector operations.

Traits other than Production (TOP) from New Zealand Holstein-Friesian dairy cows were analysed (4 management and 13 conformation characteristics), each trait scored using a linear scale from 1 to 9, with extreme values corresponding to extreme phenotypes. Mixed model methodology was used for the analysis of TOP as no significant departure from normality was observed. To model the TOP, the fixed effects of herd, inspector, age, stage of lactation (linear and quadratic) and breed of dam were tested for significance. Only the effects of inspector and herd were significant for all traits, with breed of dam significantly affecting adaptability to milking, shed temperament and stature.

Estimates of phenotypic means and standard deviations, and heritabilities for TOP were: adaptability to milking 5.4 ± 1.7, 0.20; shed temperament 5.5 ± 1.6, 0.12; milking speed 5.7 ± 1.5, 0.11; farmer's overall opinion 5.7 ± 1.7,.14; stature 5.1 ± 1.0, 0.14; weight 4.4 ± 1.0, 0.37; capacity 5.3 ± 1.0, 0.40; rump angle 5.4 ± 0.7, 0.16; rump width 5.2 ± 0.7, 0.08; legs 5.2 ± 0.6, 0.34; udder support 5.3 ± 1.0, 0.63; fore udder 4.9 ± 1.1, 0.48; rear udder 4.9 ± 1.0, 0.33; front teat placement 4.2 ± 0.7, 0.22; rear teat placement 5.2 ± 0.8, 0.22; udder overall 4.8 ± 1.1, 0.42; and dairy conformation 5.3 ± 1.1, 0.32.

Large positive phenotypic correlations among management traits were obtained, while the correlations of these traits with type were small and positive when significant. Large and positive correlations among udder traits were found. All traits related to size were positively correlated amongst themselves. Most of the traits were positively correlated with dairy conformation.

Estimated genetic correlations for stature and weight with other conformation traits were generally negative. With the exception of udder support, all udder traits were positively correlated amongst themselves. Dairy conformation was positively correlated with most traits, except with stature, rump angle, legs, rear udder and udder overall.

The estimates obtained in this study shold be used in the evaluation of Holstein-Friesian sires and cows for TOP in New Zealand.

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CHAPTER I.

GENERAL INTRODUCTION

When undertaking the task of finding estimates of heritabilities and correlations that are to be used in animal selection programmes, both theoretical and practical aspects have to be considered. These deal mainly with the properties of the sample, the model chosen to describe the sampling procedure, the method of computation of the estimates, and the properties of the estimates.

The biology of animals and its interaction with farming practices will impact on the statistical properties of the measurements made on them. Domestic animal species differ in their reproductive physiology and in the length of their life-cycle; that is, they reproduce at different rates and have different generation intervals. The modification of the reproductive rate through artificial breeding, and embryo cloning and transfer may enhance or eliminate some of the natural differences. Some traits are restricted to animals of one sex (eg. ovulation rate), to a given age (eg. weaning weight) or condition (eg. days in calf), these factors affect the kind of selection programme that can be implemented. They also affect

Ideally, all available information should be used in the estimation of population parameters but, this is seldom the case as all records are not always available or validated. Unbalanced size of fixed and random classes is a common finding in field data, and not uncommon in experimental data, imposing restrictions on the statistical methodology that can be used for the study. The methods available frequently involve difficult and tedious computations.

The interpretation of the estimates derived will be limited by the assumptions that were made during the development of the statistical model and by the distribution of the measurements, the underlying traits and unexplained variation.

Often when new traits are considered in a selection programme no previous estimates of the population parameters exist, and sometimes the distribution properties that these traits follow may also be unknown. Thus basic descriptive statistics and tests of goodness of fit are required before preceeding to the modelling of the traits. If several traits are included simultaneously, a multivariate approach is required.

In the present work these problems are addressed with particular emphasis on traits observed in dairy cows. The case studied involves the development of a model by testing fixed and random effects, as well as some covariables, before a method to estimate variance components is chosen. The selection of statistical and computational methods is studied, and practical and theoretical aspects are reviewed.

This thesis consists of three self-contained chapters that deal in sequence with the descriptive study of a new set of traits in a selection programme, their modelling and, the statistical and computational aspects of estimation of their components of variance and covariance, under a multivariate model. A set of management and conformation traits of New Zealand dairy cows is used as an example throughout the study.

In Chapter I an historical review of the measurement, use and evaluation of traits other than production in dairy cows is undertaken. A descriptive study of a set of such traits in New Zealand dairy cows is undertaken and an appropiate model for the multivariate estimation of their variance and covariance components is developed. Restricted Maximum Likelihood (REML) estimation of parameters for traits with equal design matrices under a multivariate model is applied, and the resulting estimates are compared with those obtained by a method of fitting constants.

Further development of a multivariate model is described in Chapter II, in which the importance of including the Numerator Relationship Matrix (NRM), when different from the identity matrix, is shown. A computational strategy for the application of an Expectation Maximisation (EM) algorithm, after a transformation of the vector of observations, is described. The effect of initial values on the rate of convergence of an EM algorithm is studied. The estimates obtained are interpreted and compared with those previously reported in the literature, and a set of recommendations given for the use of the estimates.

Although the desirable properties of REML make it the method of estimation of choice, the number of computations required, and its relative lack of availability in commercial statistical packages, have been limiting factors for its application. The use of a canonical transformation on multivariate models, where traits are affected by the same fixed and random effects, considerably simplifies the computations required by reducing the size of the coefficient matrix of the mixed model equations that is to be inverted. However, the use of slow converging algorithms, that require the inversion of the reduced coefficient matrix at each round of iteration, still represents a large computational effort. Faster algorithms have the disadvantage that an even greater computational effort is needed at each round of iteration. In Chapter III an algorithm that further simplifies the computations is developed, such that the use of EM or Method of Scoring-like algorithms are simpler and faster. This exploits the properties of the singular value decomposition of the coefficient matrix, which allows the inclusion of the NRM. The intention of this section is to make the use of REML more appealing to researchers in the field of animal breeding.

CHAPTER 1

CHAPTER I

MULTITRAIT ANALYSIS OF LINEAR SCORES OF MANAGEMENT AND CONFORMATION CHARACTERISTICS IN NEW ZEALAND HOLSTEIN-FRIESIAN HEIFERS FOR THE ESTIMATION OF THEIR COMPONENTS OF VARIANCE.

1. INTRODUCTION

1.1 Conformation and Dairy Cattle Breeding

The inclusion of any trait in an animal breeding programme has to be justified. First the trait must be heritable, in order to be improved by selection practices, and preferably the additive genetic variance should be proportionally large. Secondly the relative economic importance of the trait must be large enough to compensate the costs involved in measuring and analysing it, and to make the programme profitable. Lastly a practical and accurate way to measure the trait is to be used, such that differences among individual phenotypes can be detected, or alternatively have an indirect predictor that could be used.

Not all the traits included in current and past breeding programmes have satisfied these requirements and an explanation, in particular for conformation traits in dairy cattle, can be found in the origins of breeding practices and breeding societies .

Type appraisal programmes have been traditionally used in dairy cattle breeding in several countries. Sire and cow evaluations on type traits have been made available to the farmers by Artificial Insemination organisations and Breed Societies for selection purposes.

The geographical isolation of some regions in Europe caused the formation of local breeds. When communications improved, the free trade of animals and their interchange threatened the existence of stable populations of cattle. To save them artificial barriers were formed, some as herdbook regulations, others as legislation prohibiting the importing of exotic breeds, as was the case in the Island of Jersey, where the importing of cattle was forbidden since 1763 (French 1966).

In the herdbook societies recorded the pedigree information and determined what exterior characteristics animals should have to be eligible for registration in an official herdbook of a particular breed (French 1966).

In 1833 the Royal Jersey Agricultural and Horticultural Society was formed, and one year later a scale of points was drawn for judging Jersey cows. In 1866 the Jersey herdbook was opened. All animals had to be inspected before their registration was approved.

In 1878 the English Jersey Cattle Society and the Ayrshire Cattle Society were formed. One year later the first herdbook for Ayrshire cattle was published.

In 1882 the Netherlands Cattle Herdbook Society opened a separate book for Friesian cattle and selection within the breed started. At the beginning selection was mainly based on milk production but beef production was included later as a breeding objective. This brought changes in the conformation standards in that breed (French 1966).

The objectives of pedigree breeding have been based, since the establishment of herdbooks, on genetic purity and on breed type, and its relation to function, namely beef production, dairying or both (Lerner and Donald 1966). The relative ease of subjectively measuring conformation and the observed response to selection encouraged breeders to select for type, hoping that long productive herd life was related to "correct" type (Lerner and Donald, 1966). This later assumption has been maintained until now. Studies testing the hypothesis that sound conformation is related to a long herd life have been undertaken. Results published recently show a relationship between few conformation traits measured in the cow and her herd life (Sieber et al., 1987, and Foster et al., 1989). On the other hand Freeman and Boldman (cited by Murphy, D., 1991) found no correlation between the predicted breeding value of sires for conformation and their daughters herdlife.

In 1921 the Ayrshire Herdbook Cattle Society held the first of five shows. A cow was judged on a system of scoring that awarded up to 65 points for her appearance and a maximum of 35 points for the milk yield of the cow herself, or of her dam and her paternal grand-dam. To get the 35 points for milk yield a heifer needed to have a lactation recorded with at least 850 gallons of milk, and a cow a lactation of at least 1000 gallons of milk. When the last show was held in 1927 practically all the animals exhibited were awarded full points for production of milk. This method of scoring, if used for selection purposes, would represent an index that would assign relative weights of 2:1 to type and yield respectively.

Until 1929 type assessment was undertaken in the showring only with the use of a score card. Then the Hostein-Friesian Association of America initiated a type classification programme with inspectors visiting herds. They awarded an overall classification only as Excellent, Very Good, Good Plus, Good, Fair and Poor. Later classification for individual scorecard breakdown traits were given. The Unified Dairy Cow Scorecard (UDCS) included traits that were classified into four groups to which a total of 100 points could be awarded. The first breakdown of the card consisted of the General Appearance group of traits (30 points), that included breed characteristics, head, shoulder blades, back, rump, legs and feet. Dairy Character was the second breakdown (20 points) and consisted of neck, withers, ribs, flanks, thighs and skin. Then followed Body Capacity (20 points) which included barrel and heart girth. Finally the group of Mammary System (30 points) was formed by udder overall, fore udder, rear udder, teats and mammary veins. Other breeding societies adopted similar programmes subsequently (Warwick and Legates 1979).

In 1967 the Holstein-Friesian Association in the U.S.A. (HFAA) included 17 descriptive traits in its programme.

In Canada the story was a similar one. In 1925 Holstein Canada started to evaluate the conformation of the cows. In 1927 five classes were used to score cows on a scale for total classification from 1 to 100 points. This was later changed to six classes on the same scale. A "true type" model was developed in 1948 that was taken as a pattern to which evaluated cows were compared . The model was redesigned in 1971. The UDCS was used at that time until 1976, when the Canadian Holstein Cow Score Card which was also based on a descriptive scoring system took its place (Eby et al. 1987).

Yet the breeder and the commercial farmer could not get an approximate picture of the conformation of the cow by reading its classification as it was too general.

A large number of studies to estimate phenotypic and genetic parameters of classification traits were done. For a review see Appendix I.

In 1977 the National Association of Animal Breeders (NAAB) in the U.S.A. appointed an ad hoc type committee to study linear scoring of type. Such a committee proposed a scoring system that was adopted by some breed organizations and bull studs (Thompson et al., 1981). Similar programmes were adopted in several countries in the next few years.

A linear scoring system assigns a subjective score to an underlying continuous trait for which there is no practical way of measurement. Scores from 1 to 100, 1 to 50, 50 to 99, 1 to 9 and 1 to 4 are among those more commonly used. In 1981 the evaluation of type by a linear system was introduced to Canada with the first sire proofs being published in 1985

(Hunt, 1986).

The British Friesian Cattle Society adopted a linear scoring system in 1983, in which 16 type traits are scored using a scale of 9 points (Meyer et al., 1987).

Linear traits and their number included in appraisal programmes vary from country to country and from organisation to organisation but can be classified into five general groups:

1. body characteristics and overall conformation,
2. rump and tail,
3. udder,
4. legs and feet, and
5. management and efficiency traits.

Thompson et al. (1983) mentioned the advantages of scoring linearly over categorical scoring:

1. traits are scored individually,
2. the scores cover the biological range of the trait,
3. a wide range of numerical scores can be used,
4. the degree rather than the desirability is recorded,
5. the biological relationship among traits can be interpreted,and
6. the linear scores can be analysed by using continuous scales and mixed model methology.

To test the assumed advantages of linear scoring, Vinson et al. (1982) related linear scores in Holstein cows to body dimensions. The subjective linear scores used in that work corresponded to those proposed by NAAB and HFAA which consisted of a 50 point scale with scores ranging from 50 to 99 points. They found that for some linear traits there was no obvious relationship with any single physical trait. However the linear system used reflected the true variation among cows for physical measurements with satisfactory accuracy. It was suggested that some improvement could be achieved with more training and experience for the scorers, and by redefining several traits in such a way that more observations occurred in lower point ranges.

Yet the advantage of linear scoring was diluted by the existence of different programmes with different scales and groups of traits used and promoted by artificial breeding organisations, breeding societies and extension services, making it difficult for the farmers to compare sires or cows from different sources.

In 1986 the Purebred Dairy Cattle Association, the National Association of Animal Breeders and the National Dairy Herd Improvement Association of the U.S.A. held a meeting with the intention of unifying the different type scoring systems in the industry. The Uniform Type Evaluation Programme was expected to operate in early 1989. This programme has three features:

1. 15 traits from 5 groups will be evaluated,
2. a linear scale from 1 to 50 will be used, assigning extreme scores to extreme phenotypes, and
3. a standard format will be used by all organizations in the industry to display the sequence of traits on worksheets, sire summaries and artificial insemination advertisements.

The traits included were: stature, strength, body depth, dairy form, rump angle, rump width, legs (side view), foot angle, fore udder attachment, rear udder height, rear udder width, udder support, udder depth, front teat placement, and teat length (American Jersey Cattle Club, 1988).

1.2 Dairy Cattle Breeding and Traits Other Than Production In N.Z.

In 1848 the first purebred dairy cattle were imported into New Zealand. The first registered Jersey cattle to be imported into New Zealand arrived in Wanganui in 1862 and consisted of one bull and two cows from Jersey Island. Some importations of pure Jersey animals followed in 1880, but this time coming from England and Jersey Island (N.Z. Jersey Cattle Breeders Assoc., 1970). It was not until 1886 that the New Zealand Herdbook was published for all breeds, except Shorthorn cattle. This first edition included 11 Jersey bulls.

Specialised breeding societies were established in the early years of this century. By then selection of breeding stock was based mainly on conformation, flow of milk and relationships to valued individuals in the breed (Edey,1966) even though milk recording schemes already existed. As in other countries type classification was undertaken in the show ring. Programmes of type classification by visiting inspectors were implemented in 1928 for the Jersey breed and in 1938 for the Friesian breed.

In 1948 the Jersey Association made classification compulsory for mature cows, and in 1950 for all lactating cows of 21 months of age or older, with an official classification of all mature cows at 45 months of age. In 1952 classification was made compulsory for all breeders as all bulls to be registered were required to come from classified dams (Edey, 1966).

Until December 1980 most of the bulls purchased every year by the New Zealand Dairy Board (NZDB) were required to be registered by a Breed Society (Wickham and Stichbury, 1983).

The NZDB acknowledged that some traits besides milk fat and protein production affected the profitability of the dairy operation. They undertook to determine what traits should be included in selection programmes. During a survey some traits were measured and reported by farmers, whose herds were included in the NZDB's sire proving scheme. Originally the traits included were jaws, feet, mastitis, udder, milking ease, temperament and bloat suceptibility (Wickham, 1979). After some changes the traits studied were cups on, cups stay, mastitis, milk letdown, milking speed, stripping, temperament and bloat. By 1983 the total number of traits recorded by this programme and others from the NZDB and Breed Societies was around 50.

In 1988 a linear classification programme called Traits Other than Production (TOP) was implemented by the NZDB and the Breeding Societies with the purpose of:

1. evaluating bulls for these traits, based on the information on their daughters, and
2. providing an economic indicator of the bulls worth by an overall genetic index, that included yield, type and management traits, among other objectives (New Zealand Dairy Board, 1988).

The relative economic values to be applied in the second objective, were derived by using survival rates from first to second lactation for similar traits (Ahlborn-Breier et al., 1990).

1.3 Genetic and Environmental Factors Affecting Conformation

A rather large number of studies on conformation and management traits in dairy cows have been published. Up to 60 descriptive traits have been considered in a single study (eg. Smith et al., 1985), reflecting the interest in determining the importance of environmental and genetic factors affecting conformation and management traits.

Traits vary from study to study, as well as the way they are measured and analysed. Only information on the traits that are relevant to the present study will be reviewed.

Some of the first estimates of parameters for physical traits reported for dairy cattle were limited to phenotypic means of body measurements (French,1966).

Parameters for classification traits have been obtained for several breeds. White (1973) and Bowden (1982) produced extensive reviews of estimates of phenotypic and genetic parameters for type classification and management traits and of environmental factors that have been found to affect classification scores.

When linear scoring was adopted by dairy cattle breeding organizations, studies on possible environmental and genetic factors affecting linear traits were undertaken. Linear models used to analyse such traits are listed in table I. Environmental factors affecting classification traits were expected to have a similar effect on linear traits. In general effects of herd, inspector, parity or age at classification and stage of lactation have been found to be important in explaining variation in linear scores (eg. Thompson et al., 1981; Thompson et al., 1983; Smith et al., 1985). The relative importance of each factor varied from study to study as the sampling procedure differed among programmes.

Because the concept of heritability refers to measurements of traits and not necessarily to the underlying traits, differences between estimates of linear and classification scores (i.e. degree versus desirability) were expected. Furthermore differences between measurements on the same trait using different scales could also be expected (Foster et al., 1988). Thus as linear scoring systems were implemented new estimates of heritabilities were obtained to be used as parameters in selection programmes, some are summarised in table II.

TABLE I. Scales and fixed effects in various analyses of Linear Type and Management Traits.

Author	Scale	Major effects
Thompson et al.(1981)	1 - 50, 1-3, 1-4	Inspector, Herd (Inspector), Parity, Parity x Inspector, Days in milk (1).
Thompson et al.(1983)	50 - 99	Inspector, Herd (Inspector), Age, Inspector x Age, Stage of Lactation.
Smith et al.(1985)	1-3, 1-4	Inspector, Herd-year, Month, Stage of Lactation
Meyer et al.(1985)	1-6, 1-3	Herd-Round-Classifier, Age at Classification (1).
Smith (1987)	1 - 9	Herd-Round-Classifier, Age at Classification (1), Stage of Lactation (1).
Foster et al.(1988)	1 - 50	Herd-Year, Inspector (Herd-Year), Stage of Lactation, Age at First Calving (1).
Klei et al.(1988)	1 - 50	Herd-Year, Age at Calving(1), Stage of Lactation (1), Maternal Grand-Sire Group.

(1) Fitted in the model as linear and quadratic covariables.

TABLE II. Heritabilities for Linear Type and Management Traits for Holstein-Friesian cows found in the literature and their mean.

	AUTHOR (a)								
TRAIT	1	2	3	4	5	6	7	8	av.
Temperament/disposition	0.07		0.04	0.08					0.06
Milking speed	0.10		0.11						0.11
Stature/height	0.59	0.32	0.15	0.36	0.46	0.32	0.44	0.35	0.37
Capacity/body depth		0.48		0.30	0.34	0.15	0.42	0.35	0.34
Rump angle/pin setting	0.27	0.17	0.13	0.25	0.25	0.25	0.33	0.23	0.23
Rump/pin width	0.25	0.26	0.12	0.17	0.22	0.13	0.21	0.27	0.20
Rear legs (side)	0.24	0.15	0.10	0.17	0.18	0.12	0.25	0.16	0.17
Udder support	0.20			0.12	0.26	0.10	0.20	0.11	0.16
Fore udder	0.28	0.15		0.18	0.24	0.19	0.31	0.15	0.21
Rear udder	0.27	0.22	0.12	0.19	0.24	0.24		0.15	0.20
Front teat placement	0.19	0.23	0.22	0.18	0.32	0.21	0.44	0.18	0.25
Rear teat placement	0.19	0.23	0.08	0.18	0.29	0.21		0.18	0.19
Mammary system					0.30				0.30
Dairy char./dairyness	0.28			0.25	0.24	0.13			0.22

a. References:

1.- Thompson et al.(1981).
2.- Thompson et al.(1983).
3.- Smith et al.(1985).
4.- Foster et al.(1988).
5.- Smith (1987).
6.- Klei et al.(1988).
7.- Meyer et al. (1987).
8.- Lawstuen et al.(1987).
av. = average.

Thompson et al.(1981) reported some of the first estimates of heritabilities of linear type and management traits for Holstein cows. Studies on linear traits in other programmes followed later (Thompson et al.,1983; Smith et al., 1985; Smith, 1987; Meyer et al., 1987; Foster et al., 1988; Klei et al. 1988). Within each study the largest heritability estimates have been found for stature (0.15 to 0.59), and lowest for temperament and disposition (0.04 to 0.08). Estimates for udder traits were found to be between 0.10 (udder support) and 0.32 (front teat placement). However values fluctuated between studies.

Milking speed was another management trait studied for which estimates of heritability were between 0.10 and 0.12 . Meyer and Burnside (1986) obtained heritabilities for subjective measurements of milking speed in Canadian dairy cows. The trait was measured using a linear scale from 1 to 5 (very fast to very slow). Estimates for Holstein-Friesian cows were 0.21 for up to 101 days in milk and 0.18 for the whole lactation period.

1.4 Relationship Among Management and Conformation Traits

For the efficient use of the information provided from measurement on traits different to production in selection programmes their correlations, phenotypic and genetic, have to be considered. In a selection programme a genetic correlation between two traits can be utilised in three forms:

1. including the two traits in both the breeding objective and the selection criteria,
2. one trait in the breeding objective and the other as a selection criterion, and
3. having both traits included in the breeding objective but just one in the selection criteria.

One example for the first case is when selection is applied to improve both milk yield and fat yield by means of a selection index that includes both traits. The second case would apply when first lactation milk yield is the selection criteria but this and longevity are both breeding objectives. The third case is exemplified by a selection programme to decrease heifer age at puberty using the same trait in heifers and scrotal circumference in young bulls.

If an undesirable genetic correlation between two traits is not considered, improvement in one trait will be accompanied by a decline in the other trait for single trait selection. If both traits are selected for, progress in total economic value will be improved.

For the case of multivariate estimation of breeding values Henderson (1984) points out that accuracy in selection may be reduced drastically if errors in estimates of phenotypic and genetic correlations exist. Phenotypic and genetic correlations have been estimated for several traits in both the linear and classification scales with most of the estimates published applying to the Holstein breed.

In the reviews by White (1973) and Bowden (1984) summaries of different estimates of phenotypic correlations published in the literature for descriptive management and conformation traits in cows in North America can be found.Phenotypic correlations among linear traits were estimated as soon as sets of data were available. Thompson et al. (1981) obtained estimates of phenotypic correlations between linear type and management traits. They found both positive and negative correlations, but most of them of small to medium magnitude. The largest phenotypic correlations estimated were between rear udder height and rear udder width (0.72) and between centre support and teat placement (0.67). The largest negative correlations were between strength and side view of rear legs (-0.21) and those of rump slope with rump width, rear udder height and rear udder width (all -0.18). Correlations of zero magnitude were observed between rear legs and teat placement, and of disposition with stature, teat placement and rear udder height. The range of estimates of phenotypic correlations reported in the mentioned study and in others are presented in table III. In general relatively large positive correlations among udder traits were reported, as between stature and capacity. Most correlations involving rump angle and side view of rear legs with other traits were negative and small.

Most of the linear type traits are positively correlated with dairyness or dairy chararacter. Other estimates varied in sign or magnitude.

Few phenotypic correlations including management traits have been published. Thompson et al (1981) found that all the phenotypic correlations of disposition and milkout with most conformation traits were very small and negative. However, the correlation between disposition and milkout was 0.11. Smith et al. (1985) studied milking speed besides type traits. They found correlations of milking speed with udder oedema and udder depth of .19 and .12 respectively. Correlations of milking speed with the rest of type traits ranged between -.05 and .06.

The components of the phenotypic covariance between two traits are the additive genetic covariance, the non-additive genetic covariance and the environmental covariance. Of these the additive genetic covariance is the important component for the selection process, as selection of individuals based on one trait will bring changes in genetically correlated traits (Falconer, 1981).

TABLE III. Ranges(1) for phenotypic correlations between linear type traits reported in the literature(2).

TRAITS	ST	CA	RA	RW	LE	US	FU	RU	FT	RT	MS	DA
Stature (ST)	**	0.64	0.07	0.39	-.01	0.17	0.21	0.23	0.11	0.08	0.27	0.40
Capacity (CA)	0.31	**	-.05	0.41	-.11	0.26	0.34	0.34	0.10	0.17	0.41	0.47
Rump angle (RA)	-.02	-.06	**	0.02	0.05	-.04	0.02	-.07	-.02	-.02	-.12	-.07
Rump width (RW)	0.16	0.25	-.18	**	-.01	0.18	0.21	0.26	0.12	0.11	0.27	0.34
Rear legs (LE)	-.12	-.14	-.01	-.09	**	-.01	-.01	-.04	0.00	0.00	-.11	0.06
Udder sup.(US)	-.04	0.11	-.10	-.10	-.08	**	0.56	0.58	0.67	0.67	0.69	0.41
Fore udder (FU)	0.01	0.19	-.13	-.03	-.11	0.19	**	0.59	0.46	0.41	0.71	0.40
Rear udder (RU)	-.03	0.17	-.18	0.07	-.12	0.04	-.02	**	0.43	0.43	0.69	0.43
Front teat (FT)	-.02	0.06	-.09	-.05	-.05	0.15	0.01	0.14	**	0.56	0.53	0.28
Rear teat (RT)	-.02	0.13	-.09	0.01	-.03	0.13	0.02	0.04	0.24	**	0.44	0.24
Mammary s.(MS)	0.23	0.33	-.12	0.21	-.13	0.46	0.34	0.41	0.35	0.30	**	0.52
Dairyness (DA)	0.34	0.28	-.10	0.20	-.08	0.32	0.23	0.29	0.23	0.13	0.43	**

(1) Lower limit = closest value to -1.0, below diagonal,
upper limit = closest value to +1.0, above diagonal.

(2) Sources as for table II.

In table IV ranges of estimates for genetic correlations between linear traits found in the literature are shown. High positive genetic correlations between stature and capacity are reported in the literature, this being consistent with the respective phenotypic correlations. Some negative or zero genetic correlations were found between teat placement or rear udder and other udder traits. The remaining genetic correlations for udder traits were large and positive (0.40 to 0.93). An important result is that the mammary system has been shown to have medium to large positive genetic correlations with all the linear type traits (0.20 to 0.93), with the exception of rump angle with which correlations ranged from -.26 to -.40.

The remaining correlations reported for linear traits fell within a wide range of values. However some tendencies are clear, like a large proportion of high positive estimates for correlations between udder traits, a large proportion of negative correlations involving rump angle as well as side view of rear legs, and a positive correlation between these two traits.

The genetic correlation between disposition and type traits and between milkout and type were estimated by Thompson et al.(1981). They found larger values than the corresponding phenotypic correlations for most, and a change in sign for some relationships. Positive values were observed between disposition and rump angle, side view of rear legs, milkout, stature, strength and teat placement; although very small with the last three traits.

For milkout more positive and larger correlations were found, like those with dairy character (0.39), fore udder attachment, udder depth (0.48) and teat placement (0.54). The genetic correlation between disposition and milkout was estimated to be 0.51.

1.5 Analysis of Type and Management Data

The subjective and rather complex way of scoring conformation and management characteristics made it difficult to analyse the sets of data generated from type assessment programmes, until linear scoring came into use. Also the scarcity of statistical methods, other than those developed to analyse linear models of normally distributed variables, complicated the estimation of parameters for classification traits, their interpretation and their use in selection programmes. Most studies on classification type used linear models to estimate fixed effects. For the estimation of genetic parameters different strategies have been used:

1. fixed effects have been ignored,
2. data have been pre-adjusted for fixed effects, or
3. intra-class analysis of data, often using daughter-dam regression or a sire model (White, 1973; Norman et al.,1978; Wickham,1979).

In some of the more recent studies using categorical data, numerical scores were assigned to the different classes, then a transformation to an objective scale, as suggested by Snell (1964), was undertaken. This normalised the data, and linear methods were applied to the transformed scores (Schaeffer et al., 1978; Schaeffer, 1983). A similar procedure was undertaken in the case of Meyer et al.(1985) where a linear score was assigned to each class in eight scorecard traits and scorecard breakdown traits, then the objective score transformation was applied.

TABLE IV. Ranges(1) for genetic correlations between linear type traits reported in the literature(2).

TRAITS	ST	CA	RA	RW	LE	US	FU	RU	FT	RT	MS	DA
Stature (ST)	**	0.86	0.40	0.73	0.21	0.40	0.53	0.49	0.26	0.21	0.56	0.75
Capacity (CA)	0.52	**	-.10	0.76	0.06	0.47	0.59	0.55	0.32	0.22	0.62	0.73
Rump angle (RA)	-.19	-.26	**	0.0	0.27	0.30	0.57	-.12	0.01	0.13	-.26	0.18
Rump width (RW)	-.20	0.46	-.51	**	0.12	0.36	0.49	0.59	0.19	0.19	0.52	0.67
Rear legs (LE)	-.28	-.37	0.08	-.43	**	-.04	-.10	0.14	0.0	0.08	0.23	-.12
Udder sup.(US)	-.15	0.20	-.34	-.17	-.29	**	0.79	0.77	0.92	0.92	0.89	0.65
Fore udder (FU)	-.08	0.28	-.25	-.14	-.52	0.40	**	0.77	0.71	0.65	0.93	0.73
Rear udder (RU)	-.20	-.01	-.77	-.09	-.52	-.17	-.43	**	0.61	0.61	0.88	0.74
Front teat (FT)	-.06	-.04	-.23	-.24	-.19	0.0	-.07	-.24	**	0.76	0.79	0.51
Rear teat (RT)	-.06	-.04	-.24	-.24	-.14	0.0	-.04	-.24	0.48	**	0.67	0.45
Mammary s.(MS)	0.27	0.59	-.40	0.38	0.20	0.63	0.63	0.64	0.44	0.40	**	0.80
Dairyness (DA)	-.20	0.31	-.32	0.14	-.28	-.30	0.17	-.19	-.01	-.01	0.68	**

(1) Lower limit = closest value to -1.0, below diagonal,
upper limit = closest value to +1.0, above diagonal.

(2) Sources as for table II.

A univariate Restricted Maximium Likelihood (REML) procedure was used for the estimation of variance components, with covariance components being estimated by summing the scores of two traits, computing the variance components for the composite trait and then subtracting the respective single trait variances.

The development and implementation of linear scoring coincided with the development of more sophisticated statistical methods to estimate variance components and breeding values. Thus different approaches to the description and analysis of linear type traits have been used in more recent reports. Some authors have analysed linear conformation data using linear methods, others have used transformations and then applied linear methods to the transformed scores, and others have used recently developed methods for categorical data. Thompson et al (1981) and Thompson et al.(1983) used Henderson's Method 3, also known as the method of fitting constants, to estimate variance and covariance components. Smith et al. (1985) applied mixed-model analysis on 60 type traits using a linear method (Henderson's Method 3) and a non-linear method (assuming a threshold model). Jensen (1986) in obtaining predictors of breeding values for sires of the Red Danish breed on some categorical type traits, compared the BLUP technique with that proposed by Gianola and Foulley (1983) which is based on a threshold model, obtaining a correlation of 0.99 between the estimates from the two techniques.

Meyer and Burnside (1986) estimated parameters for linear scores of milking speed in Canadian cows, with milking speed at early lactation and test day milk yield considered simultaneously in multivariate analysis, using REML in the estimation of variance and covariance components. Smith (1987) applied the objective score transformation to linear scores for type before using a multivariate REML procedure on the transformed vector of observations. The genetic and environmental parameters estimated by Klei et al. (1988) for Holstein cows were obtained by a similar method used by Smith (1987) but without applying a transformation to the vector of observations.

The more frequent use of mixed models and linear methods to analyse linear type data reflects a consensus on the technique preferred by scientists. The appropriateness of this methodology will be examined in the discussion section of this chapter.

2. OBJECTIVE

In New Zealand, cows must be able to move around the farm easily and graze without difficulty with the ability to choose and consume roughage, also they must have a good disposition for an efficient milking operation releasing milk on demand (Wickham and Stichbury, 1983; Holmes and Wilson, 1987). Thus some differences between phenotypic and genetic parameters found in the New Zealand cow population compared to estimates from populations under more intense management could be expected.

In this report results are presented from a preliminary study on the first evaluation for TOP in New Zealand Holstein-Friesian heifers to determine which are the important factors affecting linear scores of TOP in New Zealand Holstein-Friesian heifers, thereby obtaining the appropriate model for the multitrait estimation of variance and covariance components and genetic parameters.

3. MATERIALS AND METHODS

The data analysed corresponds to the first available scores obtained during the 1987/88 season for 17 traits from the TOP programme recently implemented by the NZDB. Included were 2320 records of first calving daughters of 245 Holstein-Friesian sires, distributed in 283 sire proving scheme herds. The traits were scored based on a linear scale of 9 points, with extreme scores assigned to extreme phenotypes. With the exception of three traits (overall opinion, udder overall and dairy conformation) the degree of the corresponding phenotype, rather than the desirability, was scored. The 17 traits include 4 management and 13 conformation characteristics, two of which (stature and weight) are also considered efficiency traits. In table V the traits are detailed with their biological extremes and abbreviations.

The management traits (AD, ST, MS,and OP) were scored by the farmer, and the rest by a visiting inspector, with all lactating heifers in the herd being scored on the same day by the same inspector. About 90% of the inspections were carried out during the months of October and November. As milk production in New Zealand is seasonal 77% of the cows calved during August and September and hence average differences in stage of lactation at a given moment were small.

One of the assumed advantages of scoring linearly over descriptive classifications is that the records can be analysed using continuous scales and mixed model methodology (Thompson et al., 1983). Accordingly no transformation to normalise the data was performed. Furthermore a Kolmogorov-Smirnov test was applied to the vector of observations of each trait and no significant departure from normality was found in the data.

The effects of inspector, herd nested within inspector, age at calving and stage of lactation were tested for significance.

About 15% of the heifers included in the study came from matings of Holstein-Friesian sires with Jersey or Ayrshire cows and thus the effect of breed of dam on all the traits was tested. The information on traits scored by farmers was analysed separatedly from that of traits scored by inspectors.

TABLE V. List of traits, abbreviations and phenotipic values corresponding to extreme scores.

TRAITS		SCORE	
		LOWEST (1)	HIGHEST (9)
Adaptability to milking	(AD)	slowly	quickly
Shed temperament	(ST)	vicious	placid
Milking speed	(MS)	slow	fast
Overall opinion	(OP)	undesirable	desirable
Weight	(WH)	<250 kg	>600 kg
Stature	(STA)	<105 cm	>140 cm
Capacity	(CA)	frail	robust
Rump angle	(RA)	pins high	pins low
Rump width	(RW)	narrow	wide
Legs	(LE)	straight	sickled
Udder support	(US)	weak	strong
Fore udder	(FU)	loose	strong
Rear udder	(RU)	low	high
Front teat placement	(FT)	wide	close
Rear teat placement	(RT)	wide	close
Udder overall	(UO)	undesirable	desirable
Dairy conformation	(DC)	undesirable	desirable

For a two trait analysis the mixed model can be expressed as follows:

$$\begin{bmatrix} y_1 \\ y_2 \end{bmatrix} = \begin{bmatrix} x_1 & 0 \\ 0 & x_2 \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \end{bmatrix} + \begin{bmatrix} z_1 & 0 \\ 0 & z_2 \end{bmatrix} \begin{bmatrix} u_1 \\ u_2 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \end{bmatrix}$$

Variance and covariance components were estimated by fitting the following multivariate mixed model:

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

where:

y is the vector of observations on the t traits sharing the same model,

X is a design matrix that assigns fixed effects to observations,

b is a vector containing fixed effects,

Z is a design matrix that assigns random effects to observations,

u is a vector containing random effects, and

e is a vector of random variables.

Assumptions for the model are:

$E(\mathbf{y}) = \mathbf{Xb}$,

$E(\mathbf{u}) = 0$,

$E(\mathbf{e}) = 0$,

$Var(\mathbf{u}) = \mathbf{G}$, with $4(G)$ = additive variance-covariance matrix,

$Var(\mathbf{e}) = R$ = residual variance-covariance matrix,

$Var(\mathbf{y}) = \mathbf{ZGZ'} + \mathbf{R}$, and

$Cov(\mathbf{u},\mathbf{e}) = 0$.

which in the case of same model affecting both traits in the same individuals then X_1 = X_2 and Z_1 = Z_2, this can be extended to several traits.

Records on daughters of all sires were used to estimate fixed effects, but only daughters of young sires sampled under the NZDB sire proving scheme were used for the estimation of additive sire variance and covariance components (Meyer, 1986). In this part of the study sires were assumed unrelated. The effect of including relationships will be examined in chapter II.

Henderson's Method 3 estimates (Henderson, 1953) of variance and covariance components were obtained. An algorithm described by Harville and Callanan (1990) was extended to assist with generating solutions to the multivariate case. Large sample standard errors were approximated (Falconer, 1981).

Herd effects, and therefore inspector effects, were absorbed to obtain solutions for sires equations. The form of the absorption matrix M (where $M = I - X(X'X)^{-}X'$, with $(X'X)^{-}$ a generalised inverse of X'X) was determined to be block diagonal for herds, so absorption was undertaken herd by herd.

These Method 3 estimates were tested as initial values for a multitrait REML procedure. An EM algorithm (Dempster et al., 1977) for the multivariate case (Henderson, 1984) was used after a canonical transformation (Thompson, 1973; Schaeffer, 1986). Convergence was achieved after 15 iterations. The criterion for convergence was a difference between estimates of two consecutive rounds of $\leq 1\%$.

Heritabilities and genetic correlations were estimated for the management and conformation traits based on the estimates of variance and covariance components.

4. RESULTS AND DISCUSSION

4.1 Means, Standard Deviations and Coefficients of Variation

The distribution of records per sire and herd are shown in table VI where it can be appreciated that 25 herds and that 53 sires had only one heifer recorded and therefore could not be used for the estimation of sire effects. There were on the average 8.2 daughters per sire in the whole sample and 13.2 daughters per sire in the data set used for estimation of variance components.

Phenotypic means, standard deviations (SD) and coefficients of variation (CV) were obtained for all the traits in the sample (Table VII). Mean (± SD) age at calving was 24.2 (±.09) months and the mean (± SD) stage of lactation at time of inspection was 10 (±3.73) weeks.

The linear scoring system implemented by the British Friesian Cattle Society was designed to use a scale of 1 to 9 points and to have the population means near the midpoint (5), and a standard deviation equal to 1.5 (Meyer et al., 1987). In contrast the TOP programme in New Zealand only attempted to have the midpoint close to the expected population mean with extreme values of the scale representing extreme phenotypes (G. Ahlborn-Breier, personal communication). The ways in which each of these two programmes were designed were reflected in the results of the respective analyses.

Estimated means for TOP were very similar to those reported by Ahlborn-Breier et al.(1990) for the same population. Values ranged from 4.27 to 5.75. Traits scored by farmers had similar means (5.45 to 5.70). Means for traits scored by inspectors ranged from 4.27 (FT) to 5.46 (RA). Meyer et al.(1987) observed that for some traits estimated means were smaller, eg. stature (3.76), or larger eg. udder depth (6.93), than the expected value of 5. By comparison, averages for TOP in this study did not differ much from the expected mean (see table VII).

Thompson et al.(1981), Sieber et al. (1987) and Foster et al.(1988) studying the same population of cows at different times, and Klei et al.(1988) reported means of scores of linear traits in a scale from 1 to 50. In the four studies means were larger than the midpoint, with udder depth and center support showing the highest mean consistently. On the other hand Lawstuen et al.(1987) estimated means of linear scores from registered Northamerican Holstein cows, using the same scale of 1 to 50, that were closer to the midpoint, and some were even lower. They observed that the averages for udder depth and udder support in two year olds had the largest means.

Standard deviations for management traits were similar, (1.58 to 1.76), but conformation traits had standard deviations ranging from 0.60 to (LE) to 1.15 (UA). Meyer et al. (1987) obtained standard deviations for linear traits of 1.01 (LE) to 1.75 (udder depth), most of them smaller than the expected SD of 1.5. This was attributed to the scale being perhaps too wide or to classifiers being reluctant to assign extreme scores. A similar situation was observed by Smith et al.(1985) who examined type traits in Northamerican Holstein cows during their first lactation. The same could be said for the distribution of scores of conformation traits in this study, but not for management traits, thus suggesting that farmers were more likely to use extreme scores than were inspectors. In this study, as in Meyer et al.(1987), the distributions of traits were skewed, with 7 of the traits being positively skewed, but no significant departure from normality was found.

TABLE VI. Distribution of TOP Records by herd or sire.

	Number of			Number of	
Records	Herds	Sires	Records	Herds	Sires
1	25	53	21	4	4
2	25	16	22	1	0
3	24	9	23	4	2
4	30	14	24	1	2
5	21	6	26	4	0
6	20	10	27	1	3
7	15	7	28	2	0
8	20	10	29	0	2
9	15	8	30	1	0
10	17	6	31	1	1
11	12	10	34	0	1
12	6	9	38	0	1
13	4	8	46	0	1
14	8	10	47	1	1
15	4	12	50	0	1
16	0	3	61	0	1
17	4	9	73	1	0
18	2	6			
19	3	3			
20	3	4			

TABLE VII.Unadjusted means, standard deviations and coefficients of variation for Traits Other than Production in New Zealand Holstein-Friesian Heifers and from the study by Meyer et al.(1987).

	This study (N=2320)			Meyer et al.(1987)		
TRAIT	Mean	Standard Deviation	C.V.%	Mean	Standard Deviation	C.V.%
AD	5.46	1.76	32.3			
ST	5.54	1.63	29.4			
MS	5.75	1.58	27.6			
OP	5.70	1.75	30.8			
WH	4.43	1.05	23.7			
STA	5.12	1.08	21.1	3.76	1.37	36.4
CA	5.31	1.08	20.5	5.79	1.31	22.6
RA	5.46	0.71	13.1	4.34	1.20	27.6
RW	5.22	0.73	14.1	5.40	1.25	23.1
LE	5.20	0.60	11.6	5.78	1.01	17.4
US	5.32	1.02	19.2	5.78	1.43	25.0
FU	4.93	1.09	22.2	6.13	1.67	27.3
RU	4.94	1.02	20.7	5.66	1.34	23.7
FT	4.27	0.76	17.8	4.86	1.39	28.6
RT	5.23	0.85	16.2			
UA	4.86	1.15	23.7			
DC	5.30	1.11	21.0			

The CV as a measurement of relative variation allows comparisons with other populations scored linearly but not necessarily on the same scale. Standard deviations for TOP in New Zealand cows were reported by Wickham and Stichbury (1983) from a previous programme, where 3 to 5 point scales were used. When CV's were computed from their standard deviations they were observed to be larger than those found for the same traits in this study (ST, MS, FT, UA and DC) in particular for FT and ST. Coefficients of variation obtained from standard deviations published by Meyer et al.(1987) were larger than those of the 9 conformation traits common to the present report, in particular for RA, RW, STA and FT. Similar CV's were found for CA (body depth in their study) and RU. In both sudies STA showed a large CV and LE had the smallest CV. The small CV for LE may indicate some difficulty in observing differences between phenotypes for that trait. When comparing CV's of conformation traits from the current study to those computed from reports on linear traits scored with a scale of 50 points, (eg. Sieber et al., 1987) similar magnitudes were observed, with the exception of RA, RW, LE, FT and RT, for which phenotypic variation was considerably smaller in the present study. It can be concluded that the scores of the traits in the TOP programme closely follow a normal distribution, in accordance with the design of the linear scoring scale. But for some traits (RA, RW, LE, FT and RT) differences between phenotypes are not clearly detected or the true phenotypic variation is less than expected, the former concurring with findings in other studies (Thompson et al.,1981; Meyer et al.,1987).

4.2 Factors affecting TOP

Management traits were significantly affected by herd, which as mentioned above includes environmental effects as well as differences in criteria among farmers when scoring the traits. If the management level of a herd is defined as a set of environmental factors peculiar to a herd that depends on the farmer decisions (eg. design of facilities, stocking rate, feeding and rearing practices, etc.), then some consideration should be given to a possible interaction between management level and scores of management traits. Disposition is related to the temperament of the cow and to the farmer's ability to manage the herd (Sieber et al. 1987). Management practices which stress the cows could enhance the manifestation of undesirable behaviour. The size of the herd and the design of the milking shed could influence the relative importance that the farmer assigns to milking speed (Blake and McDaniel, 1978) and the expression of phenotypes. Thus a study on the effect of size of herd and design of facilities may help to account for unexplained variation, to determine if variances within herd are homogeneous at all management groups and if the relative economic importance of traits changes with herd management level.

The effect of inspector was highly significant (p <.01) on all conformation and efficiency traits, which means that scoring is not yet uniform. The effect of herd, nested within inspector, was highly significant (p<.01) on all the conformation traits as found in other studies (Thompson et al.,1981, Thompson et al., 1983, and others).

No significant effect of breed of heifers' dam was observed on MS or OP. For AD and ST it was significant (p<0.05) but explained less than 1% of the variation. Consequently breed of heifer's dam was dropped from the model to analyse management traits.

Stature was the only type trait affected by breed of dam. The effect was large enough to justify the inclusion of this factor in the model or to adjust the observations before the final analysis was done. As there were relatively few heifers with Ayrshire or Jersey dams the second option was adopted enabling an analysis with the same model for all conformation traits. Heifer daughters of Ayrshire cows had an average score for stature 0.22 units lower than Holstein-Friesians, while heifers from Jersey cows were on the average 0.72 of a point smaller than Holstein-Friesians.

No effect of stage of lactation on management traits was found, due perhaps to most of the farmers scoring the heifers at early lactation as they became adapted to the milking routine.

Stage of lactation has an obvious effect on the weight and on the udder traits of a lactating cow. Thus even though stage of lactation was confounded with herd effect, it was fitted in a model to be tested for its effect on CA, WH, FU, RU and UO. No significant effect of days in milk was found on UO, CA or WH. A significant effect ($p<.05$) was found on FU and RU but the model R-squared only increased by 0.9% with the inclusion of days in milk. The quadratic effect of stage of lactation was not found to be significant for any trait.

To simplify the analysis it was decided not to include stage of lactation as just three traits were slightly affected. In countries where milk is produced during all the year and the cows in a herd are not necessarily scored at the same time, the linear and quadratic effects of stage of lactation have been found to be significant (Thompson et al., 1983, Foster et al. 1988).

From the analytical point of view the method of inspection in the TOP programme in New Zealand is desirable since there is no need of correction factors for stage of lactation, age at inspection, season or round of scoring. However as the programme progresses and more herds will be scored later in the season, more information on conformation at late lactation will be available and then the need for adjustment factors for stage of lactation will arise. On the other hand the effect of inspector, which was significant for all conformation traits, will be less important with time as inspectors become more experienced with the new system of scoring.

R-squared values for the models used to analyse TOP are detailed in Table VIII. The fixed effects in the models explained between 20% to 59% of the variation in conformation traits, and between 30% and 34% in management traits. In White's (1973) review herd effects were found to explain between 8 and 18% of the variation, while pooled effects of year, age, stage of lactation and time trends accounted for 4 to 24% of variation in conformation traits in North American cows. Bowden (1982) reported the herd effect as reducing the sums of squares by 2 to 8% . Meyer et al. (1985) found for Australian cows that 22% to 32 % of variation in type scores could be attributed to herd-round-classifier effects. Hence the proportion of variation explained by the fixed effects for all traits in this study was larger than those reported in the literature for North American cows but similar to that reported for Australian cows, due perhaps to more similar environmental conditions between New Zealand and the latter country.

It would be desirable to increase the R-squared values of the models thus reducing residual variation. However in this case environmental differences between herds that can explain some variation in conformation (eg.level of feeding and rearing practices), are confounded with other variables (eg.stage of lactation and age at calving). This pool of effects could have a more important effect on some traits (eg. weight), as herds inspected early in the season would have a larger proportion of cows with fewer days in milk, better physical condition and less variation between them. Herds inspected later in the season would have cows in a more advanced stage of lactation. Hence heterogeneous intra-herd variances could exist for some factors. To increase the R-squared other factors not considered in the sampling procedure must be included. In evaluating dairy sires for linear type of their daughters in Great Britain the records are corrected for the number of hours between last milking and inspection, within parity and month of calving (Bellamy, unpublished notes, MMB, 1989). Wildman (1981) found that body condition is related to frame size and moderately correlated to weight and the ratio of weight to withers height. Thus physical condition score at the time of scoring conformation could be included to correct for effects not related to efficient conversion of feed. Alternatively a more appropriate time during the lactation could be chosen to score weight, for example a heifer that does not efficiently convert her body reserves to milk, will be heavier than the average heifer after the peak of lactation.

The LIC should give consideration to examining the value of recording these effects to assist with improving the precision with which TOP are assesed.

4.3 Phenotypic Correlations

Moderate to large phenotypic correlations were found amongst management traits (Table VIII). The large correlation between AD and ST may indicate that they are measurements of the same trait. If so a redefinition of the traits or more training of farmers is required, otherwise AD or ST may be redundant in the TOP system. The larger correlation between OP and AD or ST than with MS reflects that farmers opinion is strongly based on AD or ST rather than on MS.

Only two-thirds of the possible phenotypic correlations between management and conformation traits were significant (Table VIII). Most were of small magnitude (-.09 to .12), with the exception of those of OP with UO and DC (.18 and .15 respectively). This may indicate that farmers take into consideration udder and dairy conformation when assesing the desirability of a cow. The results in this study were consistent with those found in the literature (Table III). Although milking speed and disposition are included in most dairy cattle evaluation programmes, very few studies have reported correlations between these two management traits and conformation traits. Thompson et al. (1981) found very small correlations (from -.09 to .07) between disposition or milkout and 16 conformation traits. The largest were with basic form and udder depth. Foster et al.(1988) obtained similar results for disposition and milkout. Smith et al.(1985) estimated phenotypic correlations between milking speed and 35 conformation traits. All values were of small magnitude (-.05 to .06), except that with udder depth which was 0.12.

Correlations amongst conformation traits (table IX) ranged from large and positive to moderately negative. As expected WH and STA were positively correlated (0.66) as were udder traits. Other large positive correlations were those between CA and DC (0.60) and UO (0.48). Most phenotypic correlations involving RA were negative, with the largest with DC (-0.33), and most phenotypic correlations with LE were zero or very small. Most of the estimated phenotypic correlations fell within the range of estimates in the literature (see Table III). Some estimates differed in magnitude with a trend towards smaller absolute values. Correlations between WH with TOP were not found in the literature reviewed. In this study WH was highly correlated with STA, as expected, and CA and moderately correlated with RW and DC, while the rest of the estimates were small or zero. The correlations with CA and RW suggest that wider and more capacious cows look or are heavier than cows with shallow bodies or cows with narrow hips. It would be desirable that cows be scored in their physical condition at the same time as WH to see if the relationships described are due to the optical influence of frame of the heifer or not.

The estimated correlations between CA and other traits tended to be closer to zero than values previously reported, with the exception of the correlation with DC which was large at 0.60.

4.4 Mixed Model and the Estimation of Variances and Covariances

After determining the fixed effects affecting the traits being analysed, a mixed model for the estimation of variance components was decided upon.

For the estimation of variances and covariances by iterative methods a set of initial values is required, but such that the matrix of the initial values for the residuals is positive definite and the matrix for the initial values for random effects is at least positive semi-definite. The method of fitting constants (Method 3) uses information from the sample to yield estimates that can be utilised as starting values. Thus multivariate Method 3 estimates were obtained separatedly for management and conformation traits.

TABLE VIII. Percentage of variation explained by the linear model(1), and phenotypic correlations(2) between management and conformation traits in New Zealand Holstein heifers.

	R^2	Adaptability to Milking	Shed Temperament	Milking Speed	Overall Opinion
AD	0.32	------	0.74	0.47	0.69
ST	0.32		------	0.44	0.71
MS	0.34			------	0.56
OP	0.31				------
WH	0.59		0.06		0.06
STA	0.49				-.09
CA	0.30	0.05	0.07		0.11
RA	0.23				
RW	0.35				0.06
LE	0.28			0.05	
US	0.28	0.10	0.08	0.11	0.13
FU	0.25	0.08	0.07	0.11	0.13
RU	0.30	0.10	0.07	0.10	0.15
FT	0.25	0.08	0.07	0.12	0.13
RT	0.20				0.04
UO	0.26	0.11	0.08	0.11	0.18
DC	0.24	0.07	0.07		0.15

(1) Linear model includes inspector and herd nested within inspector.

(2) Only significant correlations ($p\{r = 0\} < .05$) are shown.

TABLE IX. Phenotypic correlations(a) between conformation traits in New Zealand Holstein-Friesian heifers.

	STA	CA	RA	RW	LE	US	FU	RU	FT	RT	UO	DC
WH	.66	.42	-.09	.26		.06		.08	-.05		.06	.27
STA		.24		.25	-.04		-.04		-.07			.15
CA			.15	.32		.15	.16	.19	.05		.20	.60
RA				-.16		-.16	-.13	-.18	-.10	-.05	-.20	-.33
RW							.11	.07	.13		.10	.29
LE								.06				-.07
US							.65	.60	.27	.16	.70	.37
FU								.52	.27	.10	.70	.38
RU									.24	.16	.69	.40
FT										.38	.47	.15
RT											.12	
UO												.48

(a) Only correlations significantly different from zero (p<.05) are shown.

Heritabilities derived from Method 3 estimates of (co)variances for management traits are shown in table X. These estimates were used as initial values for an iterative procedure, the EM-algorithm, to obtain the respective REML estimates of (co)variance components. Corresponding heritabilities can be compared to Method 3 estimates in table X. Except for MS, larger estimates of sire variances were obtained by Method 3, yielding larger heritabilities as a consequence, especially for AD. Larger sire covariances were obtained by REML estimation. Genetic correlations were derived from estimates by the two methods and are shown in table XI for comparison. With the exception of the genetic correlation between AD and ST, estimates by REML were larger than those by Method 3.

The analysis of conformation traits was complicated by the Method 3 estimated (co)variances being non-positive definite and by some estimates being outside the allowable parameter space. This can be explained since although the residual sums of sqares and random effects sums of squares are positive definite or positive semi-definite, a linear function of the two based on their difference is not necessarily non-negative definite. Hence methods of estimation that make use of this function (e.g. Method 3) have a probability of yielding a variance-covariance matrix that is not positive definite or positive semidefinite (Hill and Thompson, 1978). As a consequence estimates of heritabilities and genetic correlations derived under this condition can fall outside the permissible bounds. The case can worsen through unbalancedness of the data and by the inclusion of a large number of traits. Hill and Thompson (1978) derived probabilities of obtaining a non-positive definite variance-covariance matrix for a one-way balanced multivariate ANOVA model with different sizes of classes and numbers of random levels. They found that if the roots of the characteristic equation $|\sigma^2_e + n\sigma^2_s - \delta\sigma^2_e|$ were unequal, the probability of obtaining a non-positive definite random effects covariance matrix is at least 80% when the size of the class was less than 20, the number of random levels was 40 or less and when the number of traits was 4. The probability increased with a decrease in the intraclass correlation, the number of levels and size of the classes, and with an increase in the number of traits.

To circumvent this problem, Method 3 bivariate estimates were then computed, but covariances were still very high. Method 3 estimates are known to be dependent on the set of equations chosen to find corresponding reductions of sums of squares for submodels (Anderson, 1978; Searle ,1989). Hence although they are unbiased, Method 3 estimates can take extreme values. This appeared to have occurred in this part of the study. Therefore a word of caution is required when using Method 3 estimates as initial values in an iterative procedure for the estimation of variance components. Method 3 bivariate estimates or those from the multitrait analysis considered to be within the defined parameter space (ie. yielded $0\leq h^2\leq 1$, and $-1\leq r_g \leq 1$) were used as initial values in a multivariate REML procedure. From the sire and residual components at assumed convergence (round 15), heritabilities and genetic correlations were computed and are shown in table XII. No previous estimates of heritability for linear scores of WH in Holstein- Friesian cows were found in the literature. Heritabilities for STA, LE, RU, RW and FT were around the upper bound of values previously reported, while DC, FU, US and CA had heritabilities which were markedly larger than those reported previously (see table II).A large number of genetic correlations among conformation traits were very high, eg. those among udder traits and between some of these and DC. Upper bounds for genetic correlations between udder traits found in the literature ranged between .61 and .93, while between dairyness and udder traits they ranged from .67 to .89 (see Table IV). There were some large correlations involving RA, which were not typical of results previously published and are biologically difficult to explain. These correlations and heritabilities will be compared and discussed with those in chapter II.

TABLE X. Residual and sire variance components, and heritabilities for management traits estimated by multivariate Method 3 and REML, in New Zealand Holstein-Friesian heifers.

Trait		AD	ST	MS	OP
	Residual	2.057	1.909	1.973	2.347
METHOD 3	Sire	0.467	0.059	0.064	0.120
	Heritability	0.74	0.11	0.13	0.19
	Std. error	.06	.03	.03	.04
	Residual	2.650	2.089	2.025	2.401
REML	Sire	0.149	0.021	0.075	0.096
	Heritability	0.22	0.04	0.15	0.15
	Std. error	.04	.02	.04	.03

TABLE XI. Genetic correlations for management traits in New Zealand Holstein-Friesian heifers, computed from multivariate Method 3 and REML sire covariance components (1).

	AD	ST	MS	OP
AD		0.19	0.18	0.46
ST	0.11		0.12	0.40
MS	0.49	0.43		0.69
OP	0.55	0.69	0.85	

(1) Method 3 estimates above diagonal and REML estimates below the diagonal.

TABLE XII. Heritabilities and genetic correlations for linear type traits in New Zealand Holstein-Friesian heifers(1).

	WH	STA	CA	RA	RW	LE	US	FU	RU	FT	RT	UA	DC
WH	**.21**												
STA	.29	**.48**											
CA	.37	.01	**.68**										
RA	-.25	-.21	.65	**.13**									
RW	-.30	-.65	.16	.75	**.29**								
LE	.19	.03	.90	.92	.66	**.25**							
US	-.02	.11	.94	.92	.43	.48	**.57**						
FU	.08	.04	.62	.96	.36	.43	.81	**.77**					
RU	.07	.04	.90	.92	.27	.86	.80	.43	**.27**				
FT	-.09	-.16	.12	.06	.18	.15	-.36	-.15	-.05	**.44**			
RT	-.13	-.05	.66	.85	.45	.54	.96	.92	.98	-.08	**.20**		
UO	.01	.07	.73	.95	.42	.35	.99	.92	-.10	-.32	.59	**.32**	
DC	.37	-.11	.59	.95	.22	.47	.81	.91	.19	-.01	.82	.80	**.87**

(1) Heritabilities on the diagonal and genetic correlations below the diagonal. Values obtained from multitrait REML estimates of (co)variance components.

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CHAPTER II

CHAPTER II

MULTIVARIATE ESTIMATION OF VARIANCE AND COVARIANCE COMPONENTS OF TRAITS OTHER THAN PRODUCTION IN NEW ZEALAND HOLSTEIN-FRIESIAN HEIFERS

1. INTRODUCTION

1.1. Multitrait Selection and Estimation of (Co)Variance Components

In dairy cattle as in other economically important domestic species, selection of breeding stock is based on more than one trait. In New Zealand the dairy industry has adopted a new payment system that includes milkfat, milk protein and milk volume (Jackson et al., 1990). Besides these, traits other than production (TOP) have been recognised as important to the dairy farmer, as they influence indirectly the economics of the dairy enterprise (Wickham and Stichbury, 1983). Thus TOP can be part of the selection criterion although they are not breeding objectives themselves.

A set of TOP have been chosen to be included in a economic index for the selection of sires (Ahlborn-Breier et al., 1990). These traits include management and conformation characteristics related to the functionality of the cow as a production unit. A linear method of subjective scoring is used to record the phenotype of the cows. A more detailed description of the TOP programme can be found in chapter I.

For the design of selection programmes use is made of variance and covariance components. The evaluation of families or individuals, the choice of a method of selection and the prediction of selection response are all based on the proportion of the genetic relative to environmental variance components and on the sign and magnitude of estimated covariances.

The relative importance of a trait and all the traits as a group will be determined by the relationships among them. These traits may differ in their heritability and may be favorably or unfavorably correlated in their additive genetic component (Berger, 1976).

To obtain linear minimum variance unbiased predictors of breeding values (BLUPs), Henderson (1973) has shown that it is necessary to know precisely the true parameters of the variance components for the population. But the true parameters are seldom known, so instead best estimates are substituted. The 'best' estimate is one which has minimum sampling variance and is an unbiased quadratic function of the observations. When the best estimate is not used the resulting predictors are biased and do not have minimum variance. However the ranking of individuals based on these predictors is positively correlated with the ranking based on BLUPs. Unfortunately this does not apply for the case of multitrait prediction of breeding values or computation of selection indices. Large standard errors, biased estimates, and incorrect ranking of individuals will result as a consequence (Henderson, 1984).

1.2. Appropriateness of Model and REML

It is necessary to ensure that the assumptions made when constructing a model for the estimation of variance components will not be violated. Absence of selection in one or several traits, normality, independence of random error and random effects, and homogeneous variances within and between blocks are some of the assumptions generally made.

If selection has occurred, biased prediction of random effects (breeding values) will result as a consequence of the reduction in the variance among them, errors becoming correlated and a covariance arising between errors and random effects (Henderson, 1984). Changes in genetic variance result from both changes in gene frequency and the establishment of covariances between genotypic values at different loci, or linkage disequilibrium. ANOVA related methods can not take into account such effects and hence a different approach should be taken in the estimation of parameters.

The use of records of young sire's daughters for the estimation of (co)variance components has the purpose of avoiding the bias due to selection on either the cows (based on their ancestors breeding values) or on the sires to be used extensively in a population. However if due to a small population or very intensive family selection, large average relationships exist among individuals in the sample then covariances between genotypic values of different loci and among individuals will arise. The inclusion of the numerator relationship matrix (NRM) accounts for changes in genetic (co)variances due to these circumstances (Kennedy and Sorensen, 1988). When relationships are taken into account by including the numerator relationship matrix (NRM) in the model, the evaluation of individuals (i.e. predictions of random effects) are adjusted for those of their mates and their progeny, accomodating assortative and disassortative mating (Kennedy and Sorensen, 1988) and thus the parameters relevant to the base population are estimated.

Three methods can be used to estimate variance and covariance components, eliminating the bias due to selection, Maximum Likelihood (ML), Restricted Maximum Likelihood (REML) and Minimum Variance Quadratic Unbiased Estimation (MIVQUE) (Henderson, 1984). REML and ML can take account of two types of selection. When sequential culling is practised then information used to take breeding decisions must be included in the REML analysis (Thompson, 1973). If selection has been operating in the population for several generations then the parameters of the base population are those needed for evaluation.

Bias may result from assuming that single trait selection does not affect correlated traits. Johansson and Sorensen (1990) have shown that multitrait REML corrects for bias due to multitrait selection.

Skewness observed in data assumed to be normally distributed can be the result of sampling; subjective measurements of underlying continuous normal variables with large variation in class frequencies, or due to selection (Banks et al, 1985). This asymmetry of the distribution may be a reflection of skewness of errors, sire effects or both. Thus applying estimators that assume normality may yield biased estimates of parameters. In a simulation study Banks et al. (1985) determined the effect of skewness in the sample on REML estimates of heritability. For discrete observations on an underlying normally distributed variable they determined that the estimates of heritability approached normality asymptotically, when the number of classes was 4 or more. It was observed, however that if one of the classes had a high proportion of the observations, then the addition of classes to the scale did not help to increase the accuracy in the estimation of heritabilities. They concluded that although estimates of variances have larger dispersion as a result of skewness in the sample, as compared to estimates from normally distributed data, REML estimation is robust to skewed distribution of observations.

The method of ML consists of finding the particular set of parameters which maximises the likelihood function of the data vector. Whereas the related procedure of REML consists of finding the particular set of estimates that maximises the likelihood of a linear function of the observations that have expectation zero, or so-called error contrasts. In other words REML maximises that portion of the likelihood function of the vector of observations that is independent of the fixed effects in the model.

The distribution of REML estimates is unknown (Garrick, 1988), but although they are not necessarily unbiased (Searle, 1989), they are consistent, asymptotically normal and efficient (Harville, 1977). One computational advantage of REML is the relationship among the likelihood equations, the Mixed Model Equations (MME) and the information matrix (Harville, 1977; Searle, 1979). Their asymptotic variance-covariance matrix equals the inverse of the information matrix associated with the likelihood of error contrasts (Harville, 1977; Garrick, 1988). This information matrix is obtained when the REML equations are solved using method of Scoring or Newton-Rapson algorithms. Harville and Callanan (1990) suggest that a 100(1-α)% confidence interval for the ratio of REML estimates of variance components can be obtained by exploiting the distribution of the difference between the log likelihood associated with the REML estimates and the log likelihood of estimates corresponding to values at the extreme of the interval (twice this difference approximates a chi-squared distribution with one degree of freedom). An alternative suggestion was to use a function of the elements of the inverse of the information matrix.

As Harville and Callanan (1990) show, the limits of the confidence interval based on standard errors may yield results difficult to interpret if non-linear functions of the estimates of variances (heritabilities) and covariances (residual and genetic correlations) are generated from the analysis.

Extensive computation effort and computer capacity are required to obtain REML estimates, and hence it is only recently that this method has become more popular (Meyer, 1990).

1.3. Multitrait Estimation of (Co)Variance Components

The Mixed Model Equations (Henderson,1973) for the multitrait case are:

$$\begin{bmatrix} R^{-1} * X'X & R^{-1} * X'Z \\ R^{-1} * Z'X & R^{-1} * Z'Z + G^{-1} * I \end{bmatrix} \begin{bmatrix} \beta \\ u \end{bmatrix} = \begin{bmatrix} (R^{-1} * X')\,y \\ (R^{-1} * Z')\,y \end{bmatrix}$$

Where:

X and Z are design matrices for fixed and random effects respectively,

R = residual variance-covariance matrix,

G = random effects variance-covarinace matrix,

β = vector of fixed effects,

u = vector of random effects,

y = vector of observations,

`I` = identity matrix of order equal to the number of random levels,

and * denotes the direct product operator.

The solutions for these equations are Best Linear Unbiased Estimates (BLUE) of the fixed effects and Best Linear Unbiased Predictors (BLUP) of the random effects when R and G are known with precision. For a clear derivation of these equations see Thompson (1973) or Quaas (1984). These MME were reparameterised by Thompson(1973) as:

$$\begin{bmatrix} \mathrm{I} * X'X & \mathrm{I} * X'Z \\ \mathrm{I} * Z'X & \mathrm{I} * Z'Z + RG^{-1} * \mathrm{I} \end{bmatrix} \begin{bmatrix} \beta \\ u \end{bmatrix} = \begin{bmatrix} (\mathrm{I} * X')\, y \\ (\mathrm{I} * Z')\, y \end{bmatrix}$$

With I the identity matrix of appropriate dimensions. Thompson (1973) observed that in these equations the off-diagonal elements of $RG^{-1} = \Gamma$ keep the MME from being block-diagonal and hence can not be solved as t separarate sets of MME of reduced size.

Henderson(1984) presented an Expectation Maximization (EM) algorithm to obtain REML estimates by exploiting the properties of the MME in a multivariate analysis. However for a vector of solutions for the random effects (u) of size s and for t traits, the order of the MME after absorbing fixed effects is (s x t) x (s x t), which normally represents a large number of equations making computations extensive and cumbersome. Thompson (1977) suggested the use of a transformation on the vector of observations such that the parameter Γ is diagonal. A canonical decomposition of Γ provides a transformation matrix that does this (Thomson,1977). Actually the orthonormal eigenvectors of Γ form the matrix of transformations (T) to be used, resulting in $T R T' = D$ and $T G T = \mathrm{I}$. The residual variance-covariance matrix is the matrix of eigenvalues of Γ and the random effects variance-covariance matrix is equal to the identity matrix after the transformation. Other transformations with similar properties have been proposed. Quaas (1981, unpublished notes) presents a transformation based on the factorisation of R^{-1} in two lower triangular matrices as:

$$R^{-1} = L'L,$$

and the canonical decomposition of $L^{-t} G^{-1} L^{-1} = V'D\,V$ so

$$VL^{-t} G^{-1} L^{-1} V' = D,$$

and

$$VL^{-t} R^{-1} L^{-1} V' = \mathrm{I}.$$

The transformation matrix is then: $T^{-t} = VL$, with -t indicating the transpose of the inverse, V the matrix of orthonormal eigenvectors, and D the diagonal matrix of eigenvalues.

An alternative is a lower triangular decomposition of R as LL' and the canonical decomposition (Quaas,1984):

$$L^{-1} G L^{-t} = V'D V,$$

so

$$VL^{-1} G L^{-t} V' = D,$$

and

$$VL^{-1} R L^{-t} V' = I.$$

Meyer (1985) applies a variation of the transformation suggested by Thompson (1977) in which the random effects variance-covariance matrix reduces to a diagonal matrix and the residual variance-covariance matrix to the identity matrix. Schaeffer (1986) proposes the canonical decomposition of R as V D V' so:

$$R^{-1} = V D^{-1} V',$$

and then to pre- and post-multiply G by $D^{-½} V'$ to form:

$$D^{-½} V'G V D^{-½} = M,$$

and then to obtain the eigenvalues and eigenvectors of M as P Dg P'. The transformation matrix is then:

$$T = P D^{-½} V'.$$

The vector of transformed observations (canonical variables) is $\tilde{y} = y\,T'$.

After transformation the residual variance-covariance matrix of the canonical variates is the identity matrix and the random effects variance-covariance matrix is Dg, a diagonal matrix of eigenvalues. This method results in the same transformation matrix as in Quaas (1984) but requires more computations to be obtained (see Appendix II).

The use of canonical variates is a common procedure in multitrait analysis (Harris, 1975). The idea is to obtain a set of new variables that are linear combinations of original variables, but with the attribute of being uncorrelated. Each canonical variable accounts for some proportion of the covariance of the original observations and variance among original variables (Harris, 1975). The i_th canonical variable has the i_{th} largest variance. This property of the canonical variables has been applied in selection index theory (Rouvier,1966). Meyer (1985) gives an example in the interpretation of canonical variables when applied to animal breeding data, for the computation of linear functions of traits for selection purposes (eg selection indices).

When sires are related, and hence covariance exist between some individuals in different levels of random (sires) effects, the lower right sub-matrix of the coefficient matrix of the MME has the form:

$$R^{-1} * Z'Z + G^{-1} * A^{-1}$$

or if reparameterised

$$I * Z'Z + RG^{-1} * A^{-1}$$

If the estimation of variance and covariance components is the single purpose of the analysis (i.e. no estimate of β is needed) the absorption of fixed effects simplifies the construction and solution of the MME. After absorption the MME become:

$$[R^{-1} * Z'MZ + G^{-1} * A^{-1}]\, u = [R^{-1} * Z'M]\, y,$$

or $$[I * Z'MZ + RG^{-1} * A^{-1}]\, u = [I * Z'M]\, y,$$

with $M = I - X(X'X)^{-}X'$, the absorption matrix.

1.4. The Performance of Multitrait vs Single Trait Analysis

Accuracy in the estimation of genetic parameters and in the prediction of breeding values is the most important reason when chosing a method of estimation, as increased accuracy increases the response to selection. It has been argued that estimates of parameters from multivariate studies are more accurate than single trait estimates (Henderson, 1984). These multivariate estimates need to be used to reduce the bias in evaluation by selection on correlated traits (Pollak et al., 1984).

Variance and covariance components have been estimated using univariate, bivariate and multivariate analyses.

A single trait approach to compute covariances is based on the distribution of the sum (Z) of two random variables, say X and Y. The variance of such a sum is equal to Var(X) + Var (Y) + 2 Cov(XY) . Hence by applying a univariate analysis to z = x + y, Cov(xy) can be derived as:

$$Cov(xy) = [Var(z) - Var(x) - Var(y)] / 2.$$

This approach has been used, for example, in the estimation of covariance components for conformation traits in Australian dairy cows (Meyer et al, 1985).

Lin and Lee (1986) studied the effect of adding traits to a univariate analysis on the estimates of genetic parameters. They observed changes in the estimates of heritabilities as more traits were included in the study. However no particular trend was detected. No increase in accuracy of estimation of heritability resulted from the inclusion of more traits, in a simulation study by Jensen et al. (1990). That was not the case for genetic correlations as standard errors decreased when more traits were included. The use of a single trait model yields biased estimates of genetic parameters when multitrait selection has been operating (Johansson and Sorensen, 1990) so the inclusion of correlated traits increases the accuracy in the estimation. Absolute values of estimated genetic and phenotypic correlations derived from single trait analyses, were generally smaller than estimates from 5-trait and 19-trait analyses as observed by Lin and Lee (1986). These authors also determined that genetic and phenotypic correlations can change not only in magnitude but also in sign, depending upon whether the analysis is single-trait or multi-trait and upon the traits included in the multitrait model. A similar result was observed by Schaeffer and Wilton (1981) for changes in sign of correlations between breeding values depending on the type of analysis.On the other hand when Moore et al.(1989) compared REML estimates of heritabilities and genetic correlations from single and multitrait models by simulation, they found that standard errors of estimates decreased as the number of traits decreased, when traits had different heritabilities. When traits had equally low heritabilities the genetic correlations were biased, but this bias increased as the number of traits decreased.

1.5. Selection Intensity and Relationships of Dairy Cattle in New Zealand

The dairy cattle genetic improvement scheme in New Zealand is characterised by its high selection intensity, as just a small proportion (5 to 10%) of young sires sampled every year are selected for extensive use in artificial breeding. Also an even smaller number of bulls (3 to 4 per breed) are selected to sire the young bulls to be tested every year (Wickham and Bishop, 1988). This same selection intensity will result in some young sires sharing maternal grand-sires. Thus covariances among some young bull's breeding values will exist. The more bulls that are related the larger will be the average additive genetic covariance in the group within a year.

2. OBJECTIVE

Two general characteristics of the early stages of a breeding programme are worth mentioning. One is that previous estimates of the population parameters may not exist. The second is the relatively small number of levels of random effects obtained initially, in relation to the population size, with unbalancedness and empty subclasses. These problems must be dealt with.

The objectives of this study are to determine whether the inclusion of relationships among bulls is necessary to account for the covariances between their additive breeding values which are required for the estimation of variance and covariance components. Finally aspects of multitrait evaluation with no previous estimates of (co)variance components will be considered. These aspects will be studied while estimating variance and covariance components for traits other than production (TOP) in New Zealand Holstein-Friesian heifers.

3. MATERIALS AND METHODS

The variance and covariance components were derived taking advantage of absorption of fixed effects and a canonical transformation, but in doing so the form of the absorption matrix was obtained. Its form was block diagonal so the absorption of fixed effects was undertaken herd by herd. In the present study the methods suggested by Schaeffer (1986) and Quaas (1984) for the canonical transformation were used.

The absorbed MME after the canonical transformation are:

$$[I * Z'MZ + D^{-1} * A^{-1}] \ddot{u} = [I * Z'M] \ddot{y},$$

with $\ddot{u}$ being the solutions for random effects affecting the vector of canonical variables $\ddot{y}$, and with A being the NRM (that in the case of sires being unrelated is the identity matrix). The coefficient matrix and the right-hand-sides are block diagonal and therefore the solution of the MME is equivalent to obtaining t univariate solutions.

The corresponding EM-REML estimates of the sire and residual variance-covariance matrices for the canonical variables at each round of iteration are:

$$G_C = (\ddot{u}'A^{-1} \ddot{u} + Tr) / s \text{ , and}$$

$$R_C = (\ddot{e}'\ddot{e} + PQ - (D^{-1} Tr)) / N.$$

where:

A^{-1} is the inverse of the NRM,

s is the number of sires,

N is the number of observations,

$\ddot{e}$ is the vector of residuals,

PQ is a diagonal matrix with non-zero elements equal to s + r(X), and

Tr a diagonal matrix whose (i,i) element (i = 1, ... ,t) is:

$$tr (A^{-1} (Z'MZ + d_i A^{-1})^{-1}).$$

with d_i^{-1} the i_{th} diagonal element of D^{-1}, the inverse of the sire variance-covarince matrix for the canonical variables.

Estimates of (co)variance components in the original scale are computed by back-transformation as:

$$G = T^{-t} G_C T^{-t},$$

and

$$R = T^{-1} R_C T^{-t}.$$

Variance components for management traits were estimated including and ignoring relationships between young sires.

Different approaches to obtain initial values for iterative methods of estimation of variance components have been published. The sets of starting values used include Henderson's Method 3 estimates (Taylor et al.,1985), guessed values (Meyer,1985), variances from preliminary univariate analyses and zero covariances (Meyer, 1983), gradually increasing the number of traits in the analysis (Meyer,1986), and values calculated using the phenotypic variance adjusted by fixed effects (V) and a diagonal G with guessed values, where R is obtained by the difference V - G (Schaeffer, 1986). However initial values for R and G have to result in positive definite matrices.

Two sets of starting values were used in this study. One set (A) of starting values was obtained by using univariate Henderson's Method 3 estimates while maintaining the covariances from Chapter I. The other set (B) was obtained as suggested by Schaeffer (1986) assuming zero genetic covariances (i.e. diagonal G in the original scale).

When relationships were considered in the multitrait analysis of the four management characteristics the algorithm failed to converge with either set of starting values. One very large eigenvalue resulted after several iterations. After back-transformation a very large sire variance component was observed for AD in both cases. A known consequence of including highly correlated variables in a multitrait analysis, when using a relatively small sample of blocks is that the corresponding variance-covariance matrix may become non-positive definite, due to sampling (Meyer, 1985). Alternatives to solve this problem are the use of bending (Hayes and Hill, 1981) or to impose constraints on the parameter space while iterating (Meyer, 1985).

For the multitrait analysis with the four management traits it was decided to obtain different starting values that, if closer to values at convergence would not drift outside the allowable parameter space. One set (C) was obtained by performing a series of three bivariate analyses with OP and the other traits and using the values obtained at convergence as starting values. The other two sets (D and E) were formed by the estimates at convergence of two trivariate analyses excluding OP and AD respectively. In chapter I it was mentioned that multitrait estimates for the sire variance-covariance components for the 13 conformation traits, obtained by the Method 3 were outside of the allowable parameter space, thus a new set of starting values was used for this study. The method suggested by Schaeffer (1986) to obtain a set of initial values was used for the analysis including and ignoring relationships. The 'guessed' values for the sire variances were obtained by using average values of heritabilities for similar traits published in the literature. As no previous estimate of heritability for a linear score on weight was found, then the heritability obtained in chapter I was used.

As in the case for the analysis of management traits, when the NRM was included in the equations the algorithm for the full set of linear conformation traits failed to converge. Thus based on the experience with the analysis of management traits when relationships were included, a set of starting values for the analysis of type traits was obtained from iterating on subsets of traits. Sieber et al.(1987) evaluated linear type traits by means of factor analysis. They obtained eight groups of highly correlated traits, representing the so-called factors. Based on their findings, the traits to be analysed were chosen to form each subset such that each belonged to different factor. For example in Sieber et al.(1987) , factor 1 included stature, strength and rump width, and hence STA and RW were not allocated to the same subset. A total of 6 subsets of 3 traits each were formed. After convergence in each subset, the (co)variances obtained were used as starting values for the a final multitrait run.

However sire (co)variances for CA,US and FU failed to converge. Thus a multivariate analysis excluding these traits was undertaken and, after convergence the three remaining traits were succesfully included in the analysis one after the other.

Convergence criteria was the statistic C which is computed as follows (Schaeffer, 1986):

$$C = 1 - [tr((G_j-G_i)'(G_j-G_i))^{½} / tr(G_j'G_j)^{½}]$$

With G_i the sire variance-covariance matrix in the i_{th} iteration ($j = i + 1$). Convergence is reached when C => 1. Schaeffer (1986) suggests that when C does not approach 1 with additional iterations then convergence will not be achieved and that the values obtained when C reaches a maximum could be used as estimates.

4. RESULTS AND DISCUSSION

4.1. Relationships

Relationships among young bulls included in the study were obtained considering only links through sires and maternal grand-sires. There were 10 sires and 28 grand-sires appearing in the pedigrees with up to 34 young bulls being sired by the same bull and up to 7 young bulls with common maternal grand-sire. The additive relationship matrix was thus built assuming that there were no common dams for young sires and hence the coefficients of relationship could take only four possible values: 0.3125 for bulls with common sire and maternal grand-sire, 0.25 with common sire only, 0.0625 with common maternal grand-sire only and 0.0 for bulls with no common ancestors.

Because of the size of the relationship matrix, and of the known coefficients for the three types of possible relationships, its construction and inversion was relatively simple.

4.2. Variance and Covariance Components for Management Traits

4.2.1. Additive Relationships Between Young Sires Ignored

The same estimates were obtained for management traits when using two different sets of starting values, but convergence was reached more quickly when using set A than B (66 and 71 iterations respectively). The convergence behaviour of the sire and residual variance component estimates for shed temperament are shown in figure 1 and figure 2 respectively, similar convergence patterns were observed for the other traits.

Heritabilities and genetic correlations were obtained from the (co)variances estimated at convergence and are presented in table I.

Under the model ignoring relationships all heritabilities were estimated to be low (.09 to .13). Genetic correlations ranged from low and negative (-.19 between AD and ST) to high and positive (.89 between MS and OP).

4.2.2. Additive Relationships Considered.

All bivariate and trivariate analyses converged providing variances and covariances that were used to compute heritabilities and genetic correlations, and two sets of initial values for two multivariate analysis with the four management traits. Variances for OP differed among the three bivariate analyses, so their average was used as a starting value (set C). The multivariate analyses utilising sets C and D converged after 32 and 30 iterations respectively, although different heritabilities resulted from the two sets. The analysis using set E of initial values failed to converge, generating one very large eigenvalue as in the case with initial values from the mutivariate Method 3 study.

For comparison with the analysis ignoring relationships, heritabilities and genetic correlations from the 2-trait, 3-trait and 4-trait studies are summarised in table I.

When relationships were taken into account the resulting heritabilities were on the average, larger than when relationships were excluded. However the trivariate study excluding AD yielded heritabilites and genetic correlations similar to those for the same traits in the part of the study ignoring the NRM. The greatest differences were found with estimates from the algorithm using set C of initial values compared with the other estimates. Important differences, in sign and magnitude, were found for genetic correlations from the two models, ignoring and including relationships. When incorporating the NRM in the model, the genetic correlations of AD with MS and OP changed in sign, and that between AD and ST increased in magnitude. The correlation between MS and OP was larger when sires were assumed unrelated, but in both cases, was consistently large (.66 to .89). The correlation between ST and MS was intermediate for sires assumed unrelated when compared with the two results including relationships.

Figure 1: Estimate of sire variance component for shed temperament, from two initial values

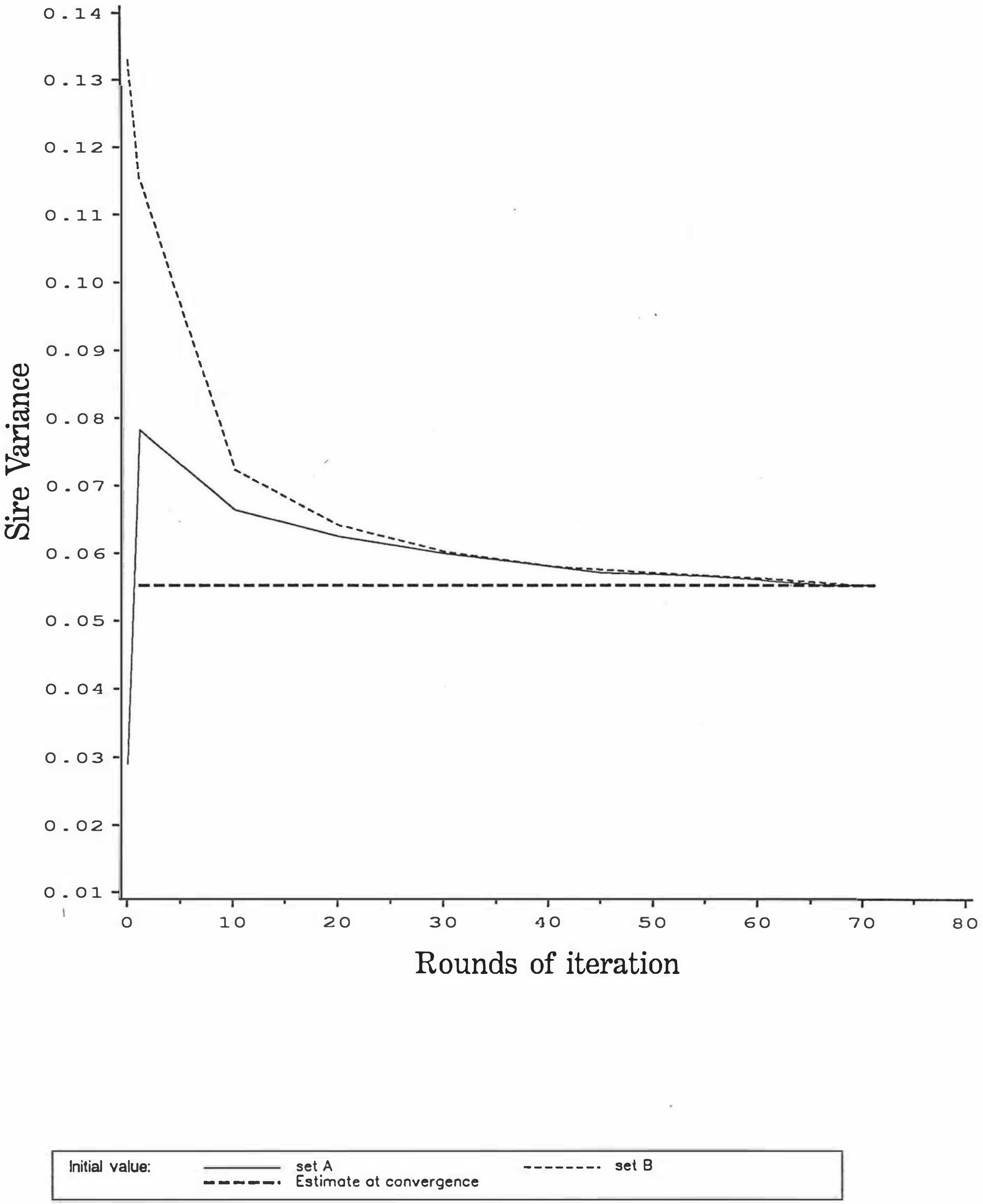

Figure 2: Estimate of residual variance component for shed temperament, from two initial values

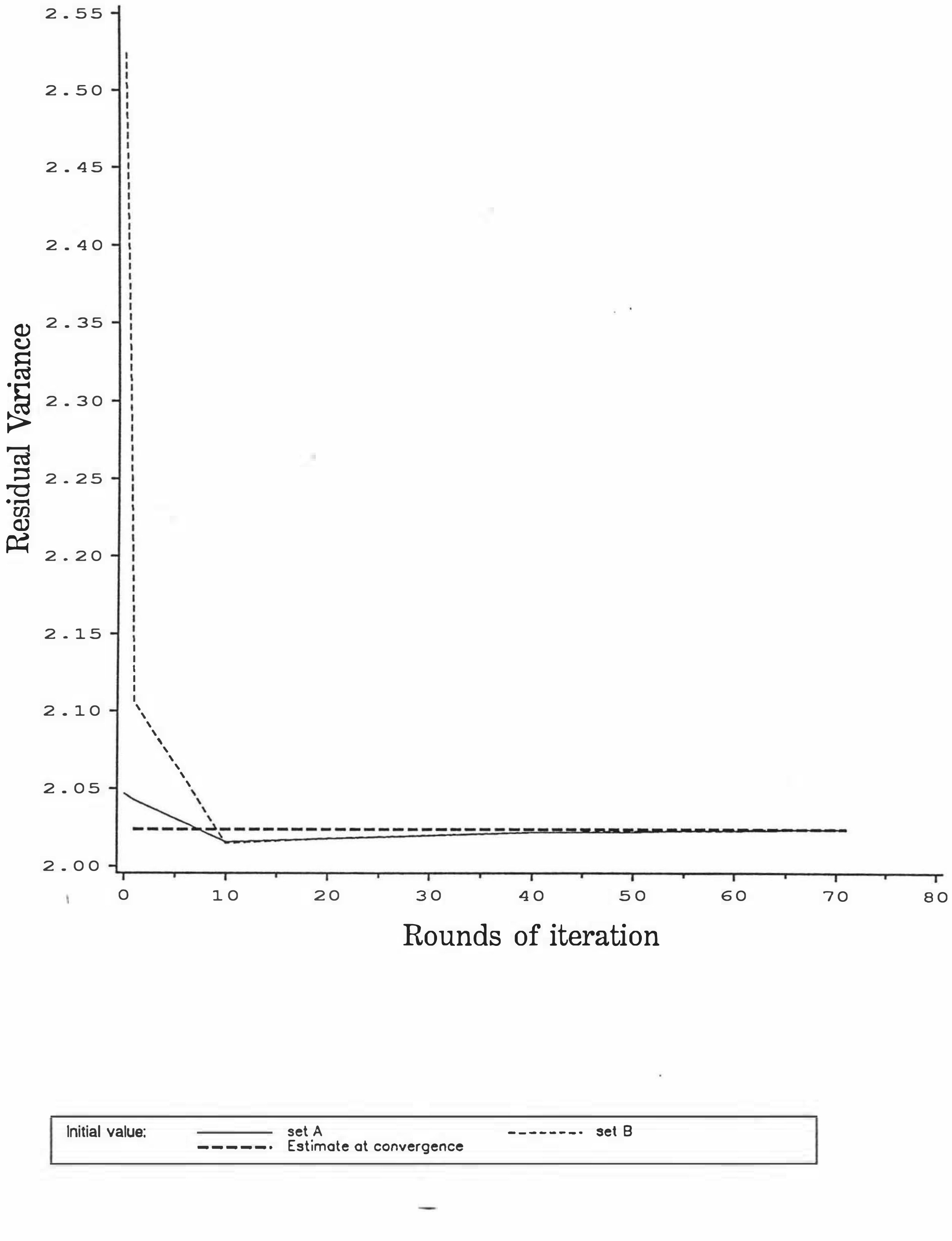

Table I. REML estimates of heritabilities and genetic correlations for linear management traits, from bivariate, trivariate and multivariate analyses, using a model including the NRM.

		MODELS (1)					
	TRAITS	1	2	3	4	5	6
HERITABILITIES	AD	.09	.13	.20	N/A	.28	.30
	ST	.11	.11	.16	.12	.18	.11
	MS	.10	.11	.13	.11	.11	.07
	OP	.13	.10* .13 .14	N/A	.14	.20	.10
GENETIC CORRELATIONS	AD-ST	-.19	N/A	-.17	N/A	-.68	-.49
	AD-MS	.27	N/A	-.10	N/A	-.38	-.20
	AD-OP	.26	-.46	N/A	N/A	-.68	-.48
	ST-MS	.27	N/A	.27	.20	.34	.19
	ST-OP	.50	.27	N/A	.40	.66	.46
	MS-OP	.89	.54	N/A	.64	.78	.66

(1) Models:
1.- Ignoring relationships,
2.- bivariate, to generate set C,
3.- trivariate excluding OP, to generate set D
4.- trivariate excluding AD, to generate set E
5.- multivariate with set C, and
6.- multivariate with set D.
* from bivariate analyses with MS, ST and AD, respectively.
N/A = not applicable.

4.3. Variance and Covariance Components for Linear Conformation

4.3.1. Relationships Ignored.

The algorithm for the model with 13 conformation traits converged at 45 iterations. Fewer rounds of iteration were needed than for the analysis of management traits, due perhaps to initial values for the conformation traits being, on the average, closer to values at convergence.

Lin and Lee (1986) observed that multitrait REML analysis, by canonical transformation, converged faster than the corresponding single trait analysis. By increasing the number of traits more restrictions are imposed on the variance-covariance matrix of the sample to keep it positive definite, and therefore EM-REML (Jensen et al., 1990). Thus the search for a global maximum is simplified as the allowable parameter space is reduced. So it is possible that an increase in the number of traits may increase the rate of convergence, depending on the covariance structure.

Sire and residual variances and covariances at convergence are shown in table II, with the respective initial values. Proportionately DC, RU, CA and STA had the largest sire variance component.

4.3.2. Relationships Included.

As observed in the analysis of management traits, some variances changed in magnitude and covariances changed in magnitude and / or sign, depending on the traits and their number fitted into the model. For example the sire covariance between WH and CA changed from .0032 to -.0081 when RA was added to the model including ST, WH and CA only. When a trait strongly correlated with others was included in the analysis (eg. US or CA), the sire variances changed by either increasing or decreasing, and the covariances tended to increase.

Lack of convergence was observed for subsets of traits that included CA, or US or FU, except when fitted in subgroups including WH, STA and RT or RW. This confirmed the assumption that if traits in the same factor (as defined in Sieber et al., 1987), were allocated to the same subset of traits in the search for initial values, extreme eigenvalues could be obtained and hence very extreme estimates would result. Variance components for sire effects and error for the 13 conformation traits are shown in table III.

To compare these results to those computed by assuming sires unrelated, heritabilities and genetic correlations for both models are presented in table IV. In general larger heritabilities were obtained when including the NRM in the analysis. Four traits, RW, RU, FT and DC had lower heritabilities when relationships were considered, but when correlated traits were excluded from the analysis their heritabilities were similar or larger than those computed under the assumption of sires being unrelated. As an example the heritability of RU increased when US and FU were removed from the analysis. Largest differences in heritabilities were observed for US and FU.

The main difference between the two models (including or ignoring relationships) was the magnitude and sign of some of the corresponding genetic correlations, as was also observed when management traits were analysed.

Three major changes were observed in the correlations, between WH and CA (from .27 to -.18), between RU and RA (from .39 to -.19), and between RU and LE (from .44 to -.08) when the NRM was included in the MME.

TABLE II. Multitrait REML estimates of residual and sire variances and covariance components by assuming sires are unrelated(1).

TRAITS	WH	STA	CA	RA	RW	LE	US	FU	RU	FT	RT	UO	DC
WH	**.485**	.303	.267	.011	.079	.024	.024	.001	-.045	-.057	-.002	-.030	.196
	.016												
STA		**.567**	.142	.037	.079	-.031	.043	-.046	-.014	-.018	-.013	-.045	.108
	.020	**.051**											
CA			**.848**	-.084	.144	.013	.079	.159	.086	.029	.024	.187	.566
	.009	-.015	**.076**										
RA				**.390**	-.012	.020	-.053	-.068	-.084	-.051	-.018	-.090	-.189
	-.004	-.009	.004	**.016**									
RW					**.337**	-.022	.004	-.017	-.007	-.038	-.013	-.012	.173
	-.007	-.015	.001	.001	**.013**								
LE						**.223**	-.007	.142	-.005	-.020	-.016	-.024	-.016
	-.001	-.003	.005	-.003	.003	**.015**							
US							**.738**	.493	.440	.103	.074	.555	.306
	-.015	-.005	-.002	-.001	.009	.001	**.068**						
FU								**.935**	.411	.140	.061	.666	.376
	-.015	-.021	-.015	.007	.019	.008	.017	**.079**					
RU									**.780**	.131	.122	.616	.324
	-.001	-.006	.021	.014	.005	.015	.006	.019	**.076**				
FT										**.444**	.146	.311	.099
	-.005	-.010	-.016	.001	.006	.008	.001	.022	.016	**.030**			
RT											**.518**	.145	.086
	-.007	-.010	-.001	.002	.010	-.001	.008	.021	.017	.002	**.030**		
UO												**1.03**	.477
	-.006	-.006	.001	-.001	.011	.025	.014	.054	.048	.021	.012	**.088**	
DC													**.911**
	.015	-.014	.034	-.001	-.005	.001	.066	-.020	-.006	-.004	-.009	-.009	**.105**
Res.	1.06	.980	1.15	.470	.613	.345	.966	1.12	.922	.542	.666	1.18	.666
Sire	.055	.095	.093	.025	.025	.015	.050	.054	.052	.054	.052	.102	.060

(1) Residual (co)variances above main diagonal and sire (co)variances below main diagonal. Initial values at the two bottom rows.

TABLE III. Multitrait REML estimates of residual and sire variance and covariance components by including additive relationships between sires.

TRAITS	WH	STA	CA	RA	RW	LE	US	FU	RU	FT	RT	UO	DC
WH	**.479**	.292	.293	.019	.077	-.013	.057	.028	-.033	-.050	.006	-.006	.204
	.017												
STA		**.564**	.158	.043	.074	-.027	.056	.029	-.010	-.022	-.012	-.041	.107
	.016	**.058**											
CA			**.844**	-.087	.130	.015	.054	-.084	-.082	.016	.059	.147	.579
	.007	-.036	**.095**										
RA				**.393**	-.012	.015	.060	-.082	-.082	-.052	-.019	-.093	-.189
	.008	-.015	.011	**.016**									
RW					**.468**	-.021	.029	-.012	.003	-.028	-.007	.001	.166
	-.003	-.009	.002	.002	**.010**								
LE						**.215**	-.053	.109	-.006	-.027	-.026	-.043	-.019
	-.020	-.005	.005	.001	.004	**.020**							
US							**.627**	.411	.453	.085	.042	.548	.220
	-.031	-.018	-.010	.001	.021	.020	**.116**						
FU								**.850**	.425	.130	.034	.671	.330
	-.029	-.040	-.016	.015	.030	.021	.044	**.116**					
RU									**.787**	.113	.102	.598	.326
	-.004	.001	.007	-.007	-.001	-.003	-.019	.030	**.071**				
FT										**.427**	.130	.275	.086
	-.002	-.004	-.002	.001	.002	.008	-.001	.016	.021	**.024**			
RT											**.516**	.130	.075
	-.004	-.003	.011	.002	.003	.003	.017	.024	.029	.003	**.029**		
UO												**.998**	.470
	-.002	.007	.030	-.002	.005	.028	-.001	.044	.055	.031	.018	**.117**	
DC													**.926**
	.004	-.023	.026	-.001	.004	-.001	.056	.001	-.015	.001	-.002	-.004	**.082**

Residual (co)variances above diagonal.
Sire (co)variances below diagonal.

Changes in magnitude but not in sign involved correlations of RW with US (from .31 to .61), with FU (from .57 to .88) and with RT (from .52 to .20). Other changes were observed in correlations between CA and FT (-.34 to -.04), between US and LE (.07 to .42), and between RT and UO (.24 to .56).

While about 25% of the correlations changed in sign the estimates were always of small absolute value. Among all the conformation traits RU and DC had correlations that changed most frequently.

In general the most obvious changes in correlations in the present study involved an increase from relationships excluded to relationships included, but changes in sign followed the opposite case.

Changes in magnitude of genetic estimates can be explained by the inclusion of the NRM in the MME equations, as account is taken for the establishment of covariances sires, as shown, among others, by Kennedy and Sorensen (1988), and Henderson (1990). Werf et al. (1989) based on a simulation study, concluded that when relationships are included in a REML analysis some correction for selection bias can be achieved. Using simulated data, Jensen et al.(1990) found that, for an animal model and in a population undergoing selection, unbiased estimates were derived if complete relationships were considered. The same was observed for a sire model but with the inclusion of records of sires on a correlated trait. In this last study estimates obtained by ignoring relationships were biased downwards.

Results obtained in studies with simulated data are not consistent with those observed in the present study, except that changes occur when relationships are included in the analysis.

Table IV. Heritabilities and genetic correlations for linear type traits obtained when the additive relationship matrix for sires is ignored and included in the analysis(1).

TRAITS	WH	STA	CA	RA	RW	LE	US	FU	RU	FT	RT	UO	DC
WH	**.14**	.51	-.18	-.48	-.24	-.11	-.65	-.65	-.10	-.10	-.19	-.04	.10
	.13												
STA		**.37**	-.49	-.47	-.38	-.15	-.22	-.49	.01	-.12	-.07	.08	-.34
	.68	**.33**											
CA			**.40**	.28	.06	.11	-.10	-.15	.08	-.04	.21	.28	.30
	.27	-.23	**.33**										
RA				**.16**	.16	.02	.01	.35	-.19	.04	.08	-.05	-.01
	-.23	-.31	.12	**.16**									
RW					**.08**	.30	.61	.88	-.04	.13	.20	.15	.15
	-.51	-.58	.03	.07	**.14**								
LE						**.34**	.42	.42	-.08	.35	.14	.58	-.01
	-.01	-.11	.14	-.19	.23	**.25**							
US							**.63**	.38	-.22	-.02	.29	-.01	.58
	-.44	-.09	-.03	-.02	.31	.07	**.37**						
FU								**.48**	.33	.30	.41	.37	.01
	-.42	-.33	-.19	.18	.57	.22	.23	**.31**					
RU									**.33**	.50	.65	.61	-.20
	-.04	-.10	.28	.39	.15	.44	.08	.25	**.35**				
FT										**.22**	.13	.58	.01
	-.23	-.26	-.34	.03	.32	.37	.01	.45	.34	**.25**			
RT											**.22**	.56	.17
	-.33	-.25	-.05	.09	.52	-.05	.18	.44	.37	.07	**.21**		
UO												**.42**	-.04
	-.16	-.09	.02	-.02	.33	.69	.18	.65	.59	.41	.24	**.31**	
DC													**.32**
	.38	-.19	.38	-.03	-.15	.02	.78	-.22	-.07	-.07	-.16	-.09	**.41**

1) Heritability estimates are on the main diagonal. Estimates from model with NRM above main diagonal, and estimates from model ignoring NRM below main diagonal.

No large differences were observed by Klei et al.(1988), between estimated variance and covariance components for linear type traits from including and excluding relationships. The same was observed by Smith (1987) in genetic parameters for linear traits in Australian Holstein cows. These two studies included larger samples of cows and bulls than in the present study. On the other hand,Lawlor et al.(1984) observed a small increase in the estimates of genetic parameters for milk and fat yield , two intensively selected traits, with the inclusion of the NRM, when analysing 154,762 records of daughters from 493 sires by multitrait REML. Thus it is possible that the size of the sample and the intensity of selection in the population determine the size of the difference, and hence the bias, in genetic estimates by excluding the NRM from the analysis.

Differences between Method 3 and REML estimates in this study are due to different assumptions in the model, as Method 3 assumes that sires are unknown parameters (fixed effects) and only when equating their summ of squares to the respective expectations are assumed random, while by REML only young sires were assumed to be random and old sires to be fixed, yielding basically a different model to that analysed by Method 3.

Changes in sign of genetic estimates from the two analyses in the present study are not necessarily attributable only to the addition of the NRM into the model. These can also be due to the traits, their number and the order in which they were added into the algorithm during the analysis. For example when a subset of traits including RU, FT, RT, UO and DC was analysed by REML, with the NRM in the MME, the genetic correlation between RT and DC was estimated at -.03, while from the full set of 13 traits the genetic correlation was estimated to be .17. A similar result was observed by Lin and Lee (1986) when analysing milk production and body weight related traits in Canadian Holstein cows. The estimated genetic correlation between milk yield at 308 days and body weight gain (112 to 168 days) of .59 from a bivariate model changed to -.47 and -.59 in 5-trait and 19-trait analyses, respectively. In all the cases the relationships among sires were considered.

In the present study the inclusion of the NRM in the model resulted in changes in the covariance structure of the multivariate distribution in such a way that the effect of some traits on this covariance structure was made evident.

Some linear traits have been found playing a major role in the genetic covariance of other traits. In the study by Smith (1987), 13 traits were found to explain most of the common genetic variation in a full set of 31 linear type traits. Height of cow had a very important effect on the rest of the linear traits, as their average heritability dropped from .26 to .17 after removing the genetic variation due to height.

There is no available information on the genetic correlations between yield traits and conformation or management traits based on New Zealand data. Therefore it is not known whether selection based on production traits could induce linkage disequilibrium between loci affecting TOP. Since the genetic covariances with the traits under selection have not been included in the analysis the inclusion of the NRM will have accounted only for the covariances between additive genetic values of sires. Furthermore, in the present analysis a sire model rather than an animal model was used and therefore only the relationships between maternal grandsire, sire and dam are accounted for. Thus there will be some correction for assortative mating.

For the case of management traits there are two sets of estimates that could be used in the prediction of breeding values. The difference between the two seems to be caused by the simultaneous presence of AD and OP, and as mentioned before the strong relationship between AD and ST. In both sets of estimates the genetic correlations of AD with ST and OP were of equal magnitude (see table I). This supports the suggestion made in Chapter I of redefining the traits and retraining farmers, or to exclude AD from the set of traits.

The possibility that sampling has an important influence on the results can not be ignored. A study with a larger sample size is required to examine this possibility.

If AD were to be dropped from the set of traits then the set of estimates to be used are those from the respective 3-trait analysis (column 4 from table I).

For the case of conformation traits the relatively small difference between heritabilities from the two analyses, may have a small impact on the estimation of breeding values, with the exception of US and FU. On the other hand, the observed differences in sign and magnitude for genetic correlations indicate that, under intensive selection, estimates of (co)variance components by REML are biased if the NRM is excluded from the analysis. Hence the estimation of breeding values could be greatly affected.

4.4. The Effect of Initial Values on an EM Algorithm

4.4.1 The Effect of Initial Values on Estimates

Several differences in estimates were found in this part of the study from those obtained by Method 3 and multivariate REML with Method 3 estimates as initial values (Chapter I). The heritability estimates for management traits in Chapter I tended to be of the same magnitude as in those found by multivariate REML with different initial values (Chapter II). The estimate for AD by Method 3 was the exception; it was very large.

The algorithm using set C of initial values resulted in larger sire variances and covariances than that using set D. The main difference between these two sets of initial values was a relatively larger sire variance for AD in set D (.12 vs .07). This caused the sire variances for the rest of the traits to drop during iterations, along with small increases in covariances. In the algorithm with set C all the variances and covariances increased steadily. Consequently, estimates of heritabilities from set C were larger than those from set D, except for AD for which there was only a small difference, and also larger genetic correlation estimates.

Some estimates for conformation traits (Table IV) showed a tendency for heritabilities to be larger than those obtained by using Method 3 estimates as initial values and no relationships. There were similar trends, however, such as the ranking of traits by the magnitude of the heritabilities. For both methods US, FU, STA, CA, UO and DC had the largest heritabilities. While RA and RT had the lowest. The exceptions were RW and FT for which larger heritabilities were found by using Method 3 initial values and relationships ignored (Chapter 1).

Estimates of genetic correlations for management traits in Chapter 1 were always positive. The genetic correlations of OP with MS and ST were within the range of estimates of Chapter II, but correlations with AD were different in sign and magnitude.

Some genetic correlations among linear conformation traits estimated in the first part of the study were similar in sign and size to estimates in Chapter II (including and excluding relationships). This was especially true for correlations involving WH, STA, FT, RT and DC. But estimates for other traits were larger and of different sign in Chapter I than corresponding estimates from Chapter II.

REML estimates obtained by using Method 3 estimates as initial values, were in general very extreme (i.e. near the boundaries of the parameter space). These large initial values and the fewer iterations needed to achieve convergence, supports the argument that a local maximum may be arrived at when using Method 3 estimates as initial values. Although the possibility of finding a local maximum in single trait analyses is apparently nonexistent (Meyer, 1990), it has been reported for the multivariate case. Kovac and Groenveld (1989) proved the existance of a local maximum, after they found two sets of estimates at convergence when using different sets of initial values. In the present work a larger likelihood at convergence was computed for set C than that for set D, in the two 4-trait analyses, and thus a global maximum was assumed to be estimated from set C. Meyer (1990) mentioned that when large negative sampling correlations exist, then a ridge in the topography of the likelihood will make convergence difficult. Thus, it is possible that the use of set D of initial values made climbing the surface of the likelihood more difficult.

4.4.2. Effect on the Convergence Rate of Algorithms

It is known that, generally, the EM algorithm converges slowly. Under certain conditions, however convergence is reached with fewer rounds.

A reparameterization of the model may speed convergence (Meyer and Thompson, 1986). Taylor et al.(1983) observed a rapid convergence to a global maximum with only small changes of (co)variances after the 10th iteration, when using a multitrait EM algorithm. Similarly Lin and Lee (1986) detected relatively smaller changes in estimates from the 9th to the 10th round of iteration, for a multitrait EM-REML. This was also the case in the present study. Where convergence occurred, larger changes in estimates occurred before the 10th iteration (see Figures I and II). However covariances tended to be slower to converge and in some cases went from zero to negative in initial iterations, then to zero and then to positive values at convergence. This was observed, for example, for the covariance between ST and MS in a 3-trait analysis with an EM algorithm, with relationships considered and initial values for covariances as zero. Also when some initial values for covariances were assumed to be positive, they increased for a few rounds, stabilised, and then shifted to a negative value at convergence.

With the choice of zero covariances as initial values, an EM algorithm always converged. Furthermore when two different sets of initial values for variances and zero covarinces were used the algorithms converged to the same estimates, and thus the probability of having found a local maximum was assumed to be reduced.

4.5. Comparisons of Estimates with Findings in Other Studies

4.5.1. Management Traits

The low heritabilities estimated for management traits suggest that they will respond only slowly to selection, furthermore they will be poor indicator traits for economically important traits, even if large genetic correlations were to exist.

Estimates for ST are, however, larger than those found in the other studies (Thompson et al., 1981, and Foster et al.,1988). The estimated heritability for MS is similar to that reported for milkout by Thompson et al.(1983) and Foster et al.(1988), but smaller to that found by Meyer and Burnside (1986) for MS. No estimate of heritability for the farmer's overall opinion on workability of cows was found in the literature. The heritability obtained for this trait in the present study suggests that selection for this character will bring improvement in the average desirability of cows as members of the herd, or a lower frequency of undesirable cows. No reports were found in the literature reviewed on AD or any trait with similar definition.

The large positive phenotypic correlation between OP and MS suggests that fast milkers tend to get higher scores by the dairy farmers. Furthermore their genetic correlation is also positive and large which would assist in the simultaneous improvement of both traits if included together in a multitrait selection programme or by indirect selection, by having OP as selection criteria only. The same can be said for the genetic correlations of ST with MS and OP, but to a lesser extent, as the expected correlated response for such a trait will be smaller due to smaller genetic correlations and heritability.

The intermediate size of the genetic correlation between ST and MS contrasts with that found by Thompson et al.(1981) of .51 for disposition and milkout, but is similar to that reported by Foster et al.(1988) of .24. The inclusion of AD in a selection programme, on the other hand, as it is currently defined and scored would slow the rate of improvement in the other management traits, as all the genetic correlations with this trait were typically negative and often large.

4.5.2. Conformation Traits.

The linear type programmes for which results have been published include different numbers of traits, with some traits being defined in a different fashion. For example in Foster et al.(1988) dairyness is defined as desirable dairy conformation while in Klei et al.(1988) it is defined as angularity of the body of the cow. Some studies name the same trait differently, for example angularity in Meyer et al.(1987) is dairy character in Thompson et al.(1983). Some programmes condense two traits into one, like front and rear teat placement, or use two traits to describe one condition, like udder depth and suspensory ligament for udder support. So, although similar results to previously reported were generally obtained, direct comparisons of results are difficult. This is further complicated by conflicting results from analyses of the same or separated populations. For example Thompson et al.(1981) and Foster et al.(1988) both used large samples (9,500 and 43,000 records respectively) of the same population, scored with the same scale on the same traits, and obtained different estimates of the various parameters. In general Foster et al.(1988) estimated lower heritabilities and genetic correlations than Thompson et al.(1981).

There are also consistencies with the literature, such as those reported by Smith (1987) with respect to a previous study by Meyer et al.(1985) on Australian Holstein cows , but scored by a classification scale.

As mentioned before no previous estimate of heritability for a linear score on weight of dairy cows was found in the literature, although Lin et al. (1985) estimated heritabilities for pre and post-calving body weights in Canadian Holstein heifers. Values for heritabilities ranged from .22 to .33, which are substantially higher than the estimate for WH found in the present study (.14).

The heritability estimates for most of the conformation traits were within the range of values found in the literature, with values for RA and RW closer to the lower bound and the rest of the estimates towards the upper bound. Estimates for FU, RU and US and DC were somewhat larger than those found in the literature. Most heritabilities indicated that genetic improvement could be achieved through direct selection.

The estimated genetic correlations did not have consistent similarities with any particular study, but tended to be close to the bounds of the range of values reported in other studies.

As linear scores of body weight have not been adopted in other programmes no correlations including this trait have been reported.

Correlations involving STA and WH have a similar trend, being negative with most of the traits, but a high positive between them.

One important difference found here compared with other studies was that the estimates of the correlations of STA with CA and RA were large and negative in contrast to large positive or moderately negative estimates found in the literature.

As in all the reviewed reports there was a tendency for udder traits to be positively correlated amongst each other. The exceptions being correlations of US with RU, FT, and UO. This difference can be attributed to the large number of udder traits and to the way these have been defined. There are two udder traits (US and UO) that could explain an important proportion of the covariation in that group of characteristics.

Dairy conformation (DC) was defined to complement the rest of the linear traits in describing the conformation of the cows. In other reports the range of correlations of DC with other traits (except for LE) ranges from moderately negative to large and positive, with a consistently high and positive correlation with mammary system. When analysing TOP in this study, dairy conformation was positively correlated to CA, US, WH, RW and RT. The genetic correlation between DC and US was large and positive (.58), however that with UO was low and negative (-.04). DC is defined as excluding udder traits in the New Zealand TOP programme (Ahlborn-Breier et al.1990), so the negligible correlation with UO is not surprising, but that with US implies that selection on DC will bring an important correlated improvement on US. The negative and moderate correlation of DC with RU coincides with the lower bound found in the literature but that with STA falls outside of the lower bound of previously reported estimates.

Given the differences just described, it cannot be recommended to use estimates of genetic correlations found in the literature for use in the multivariate estimation of breeding values in the New Zealand Holstein-Friesian population. These parameters not only describe the biological relationship between traits, but also the covariance structure, and thus the joint distribution of breeding values, which is likely to be peculiar to each population.

4.6 The Use of Estimated Parameters

The integration of the estimated parameters into a selection scheme in New Zealand will depend on the role the traits will play in such a programme. Relative economic values are to be assigned if the characters are included in the selection objective. These relative economic values should reflect the importance of management traits on the costs of the dairy operation. The economic relevance of linear type traits is more difficult to relate to specific aspects of milk production. The stature and weight of a cow have been used to determine the efficiency of the animal under the assumption that bigger cows have higher maintenance requirements (Ahlborn-Breier et al., 1990).

A long, efficient and productive herdlife is considered an important economic component so as to reduce the costs of replacement needed after involuntary culling, and conformation traits have been thought to be related to herdlife. The justification of selecting on conformation rather than on the actual herdlife has been that the generation interval would increase considerably if individual selection on this trait was practised. However not until recently the correlation between type and longevity has been studied.

Heritabilities for survival estimated at .05 in Jersey cows (Rogers et al., 1990), and of .03 for true and functional stayability of Holstein cows (Boldman et al., 1990) would support the alternative of applying indirect selection if linear type traits with larger heritabilities and genetically correlated with herdlife were available. However there is not a consensus in this respect. Rogers et al. (1990) found in Jersey cows that only udder traits had genetic correlations with survival large enough to justify including them as selection criteria. While Boldman et al. (1990) determined that the accuracy of predicting breeding values of sires for herdlife based on estimated breeding values for linear type traits was low at 0.58, but higher than the selection accuracy on herdlife alone if the effective progeny number was less than 100. On the other hand research undertaken by a North American artificial insemination cooperative (cited by Murphy, 1991) showed that the current evaluation for linear type in the U.S.A. has a low correlation with longevity. They derived a selection index including herdlife and yield traits, with a larger expected economic gain than the index currently used by the U.S.A. Association of Holstein breeders, based on linear type and yield.

A reduction in the number of characters, by discarding those that are redundant, such as adaptability to milking and linear score on weight in this study, or the use of composite or canonical traits explaining most of the covariance in conformation as done in North-America by the Holstein breeders, could simplify the problem of multivariate selection. A further study on these alternatives would be advisable.

5. CONCLUSIONS

The importance of using the correct parameters in the prediction of breeding values and response to selection has been widely discused in the literature. Where correct parameters are not known the best estimates will be used instead. Where no previous estimates of the population parameters exist, experimental or field data can be used to obtain estimates of the parameters. Large and balanced samples are ideal for the estimation of genetic parameters, but these are difficult to obtain.

Multiple trait REML can be used to estimate variances and covariances from unbalanced data. For the estimation of the base population parameters relationships need to be included. Although in some reports only small differences between estimates obtained from either including or excluding relationships were found, significant differences between estimates were detected in the present study where the population was under intensive selection .

When a multiple trait selection programme is designed, all important traits contributing to revenue and costs should be included, so as to maximise economic response to selection. The same group of traits should be included in the estimation of variance and covariance components. The inclusion of different measures of the same trait (e.g. STA and WH for cow size, and ST and AD for cow behaviour) can affect the rate of convergence of an iterative procedure. The exclusion of an important trait or the inclusion of an unimportant trait will generate a different set of estimates and this will bias the prediction of selection response. The presence of one or a few traits highly correlated to other traits will have an effect on the estimates obtained and their computation. Thus when a set of traits is to be analysed for their inclusion in a selection program, linear functions of subsets of traits can be analysed, in the form of a factor analysis, to determine how much of the variation of the full set of traits is explained by each subset of traits. This can help in deciding which traits to include in the programme.

In this study it was observed that Method 3 produced a negative definite variance covariance matrix. After correction for this condition, the estimates were used as initial values for an EM algorithm, but a local maximum was obtained at convergence. This was possibly due to the covariance structure of the sample. A practical strategy to obtain initial values for use in an iterative multivariate REML with canonical variables, is to use subsets of lowly correlated traits assuming zero covariances and guessed heritabilities. The estimates at convergence can be used as starting values for an analysis with the full set of traits. This strategy will also help to detect strongly correlated traits that may affect the estimation procedure. This approach, although practical, may result in slow convergence for the covariances, particularly for the first 10 to 15 iterations, but as the number of traits increases so does the speed of convergence. If the Common Intercept Approach (Schaeffer, 1979) is used to increase the rate of convergence, it is suggested to apply it after the 10th round of iteration to avoid finding inaccurate predicted convergence values, as changes in sign may be observed after adding traits to the algorithm.

To increase the probability of finding the global maximum, rather than a local, at convergence, two distinct sets of starting values can be used. The estimates at convergence with a larger likelihood can be taken as the true REML estimates, or if the two sets of estimates converge to the same values these can be assumed as the set corresponding to the global maximum.

Changes in estimates of heritabilities and genetic correlations will result from the addition of traits to the model when using canonical EM-REML, due to some traits explaining (co)variation in other traits.

The simultaneous inclusion of AD and OP, as with STA and WH, in a multitrait analysis complicated the estimation of parameters in this study. Based on the results obtained it is suggested to redefine AD , to train farmers to ensure a clear distinction among traits, or to eliminate AD from the system.

Low heritabilities were found for shed temperament and milking speed, but their high, desirably positive genetic correlation with OP, may make their inclusion in a multitrait selection programme worthwhile. A more accurate measurement of weight would probably improve the behaviour of the variable in a multivariate analysis involving STA, RW and CA.

Genetic parameters for conformation traits are in general close to those reported in the literature, with a trend towards the upper bound. However, a peculiar covariance structure was found for the traits in this study, and therefore these estimates should be used in a multitrait selection programme involving New Zealand Holstein-Friesian dairy cattle. In can be suggested that when more information becomes available the variance-covariance components should be re-estimatimated. Also the effect of ignoring covariances between traits in the evaluation of sires for TOP, as currently done in New Zealand, should be studied.

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CHAPTER III

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COMPARISON OF TWO ALGORITHMS FOR THE ESTIMATION OF VARIANCE AND COVARIANCE COMPONENTS OF TRAITS WITH EQUAL DESIGN MATRICES.

1. INTRODUCTION

The desirable properties of Restricted Maximum Likelihood (REML) estimates described for the univariate normal distribution (Patterson and Thompson, 1971; Harville, 1977) can be exploited in the multivarate case, making this method an important research tool. The derivation of multivariate REML (M-REML) for the general multivariate normal case by Thompson (1973) has been extended to different models arising in animal breeding.

The natural extension of REML to a multivariate distribution consists of setting a model in which several traits have the same model, ie. they are affected by the same fixed and random effects, and therefore have the same design matrices. Thompson (1973) applied M-REML on a set of traits recorded in pairs of parents-offspring and extended it to the case of sequential culling. Although in these two instances traits were assumed to have equal design matrices not all parents had progeny with records. Also the probability of not having progeny recorded was a function of the record on the parent. Schaeffer et al.(1978), based on Thompson's (1973) work, described M-REML for a model where no residual covariances between traits exist, and no crossproducts or sums of variates can be obtained, due to the structure of the data. Such a model arises in the situation when one trait is recorded in one group of progeny and a different trait in another group.

Meyer (1983) described M-REML estimation of parameters for traits recorded on the same animal but where different models applied to each trait. Furthermore the method was adapted for the case of sequential culling to provide estimates free of bias due to selection.

The above mentioned models are a sample of different data structures that animal breeders have to deal with. These cases can be classified as:

- estimation of parameters for certain known underlying distributions, and

- estimation of parameters from data for which particular assumptions need to be made due to the structure of the vector of observations.

1.1 The Multivariate Mixed Model

The general linear mixed model is:

$$y = Xb + Zu + e \, , \qquad (1.1)$$

where:

y is a vector of observations on t variables,

b is a vector of fixed effects,

u is a vector of random effects,

X and Z are design matrices,and

e is a vector of independent random variables.

Assumptions are:

$E(y) = Xb$,

$E(u) = 0$,

$E(e) = 0$,

$Cov(u,e) = 0$,

$Var(u) = G = \sigma^2_u I_s$, with s being the number of random levels,

$Var(e) = R = \sigma^2_e I_N$, with N being the number of observations,

and $Var(y) = V = ZGZ' + R$.

Differences in the variance-covariance structure of the various models can be easily described if the bivariate distribution is used to illustrate such differences. The model for a bivariate distribution is:

$$\begin{bmatrix} y_1 \\ y_2 \end{bmatrix} = \begin{bmatrix} X_1 & 0 \\ 0 & X_2 \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \end{bmatrix} + \begin{bmatrix} Z_1 & 0 \\ 0 & Z_2 \end{bmatrix} \begin{bmatrix} u_1 \\ u_2 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \end{bmatrix} \qquad (1.2)$$

with:

y_i a vector of observations on the i_{th} trait ($i = 1, 2$),

b_i a vector of fixed effects on the i_{th} trait,

u_i a vector of random effects on i_{th} trait,

X_i and Z_i are the corresponding design matrices, and

e_i a vector of independent random variables in trait i.

Assumptions are:

$E(y_i) = X_i b_i$

$Var(u_i) = G_{ii}$,

$Cov(u_i, u_j) = G_{ij}$,

$\mathrm{Var}(e_i) = R_{ii}$,

$\mathrm{Cov}(e_i, e_j) = R_{ij}$, and

$\mathrm{Cov}(u_i, e_i) = 0$.

With $\mathbf{G} = G * I_S$ the matrix of variances and covariances among traits due to random effects and $R = R * I_N$ the matrix of residual variances and covariances, with '*' denoting the direct product operator. The corresponding Mixed Model Equations (MME) are (Quaas, 1981):

$$\begin{bmatrix} R^{-1} * \mathbf{X}'\mathbf{X} & R^{-1} * \mathbf{X}'\mathbf{Z} \\ R^{-1} * \mathbf{Z}'\mathbf{X} & R^{-1} * \mathbf{Z}'\mathbf{Z} + G^{-1} * I \end{bmatrix} \begin{bmatrix} \mathbf{b} \\ \mathbf{u} \end{bmatrix} = \begin{bmatrix} (R^{-1} * I)\mathbf{X}'\mathbf{y} \\ (R^{-1} * I)\mathbf{Z}'\mathbf{y} \end{bmatrix} \quad (1.3)$$

where

$$\mathbf{X} = \begin{bmatrix} X_1 & 0 \\ 0 & X_2 \end{bmatrix}, \quad \mathbf{Z} = \begin{bmatrix} Z_1 & 0 \\ 0 & Z_2 \end{bmatrix}, \quad \mathbf{b} = \begin{bmatrix} b_1 \\ b_2 \end{bmatrix} \text{ and } \mathbf{u} = \begin{bmatrix} u_1 \\ u_2 \end{bmatrix}.$$

The covariance structure will depend on the specific model and assumptions. For example with all traits having equal design matrices:

$Z_1 = Z_2 = Z$,

$X_1 = X_2 = X$,

$\mathrm{Cov}(u_1, u_2) = G_{12}$,

$\mathrm{Cov}(e_1, e_2) = R_{12}$,

$\mathrm{Cov}(u_1, e_2) = 0 = \mathrm{cov}(u_2, e_1)$, and

$\mathrm{Cov}(y_1, y_2) = V_{12} = ZG_{12}Z' + R_{12}$.

Thus the covariance structure is:

$$\mathrm{Var}\begin{bmatrix} u_1 \\ u_2 \\ e_1 \\ e_2 \end{bmatrix} = \begin{bmatrix} G_{11} & G_{12} & 0 & 0 \\ G_{21} & G_{22} & 0 & 0 \\ 0 & 0 & R_{11} & R_{12} \\ 0 & 0 & R_{12} & R_{22} \end{bmatrix} = \begin{bmatrix} \mathbf{G} & 0 \\ 0 & \mathbf{R} \end{bmatrix} \qquad (1.4)$$

A detailed description of the left hand side (LHS) of the MME in this case is:

$$\begin{bmatrix} r^{11}(X'X) & r^{12}(X'X) & r^{11}(X'Z) & r^{12}(X'Z) \\ r^{21}(X'X) & r^{22}(X'X) & r^{21}(X'Z) & r^{22}(X'Z) \\ r^{11}(Z'X) & r^{12}(Z'X) & r^{11}(Z'Z)+g^{11}I & r^{12}(Z'Z)+g^{12}I \\ r^{21}(Z'X) & r^{22}(Z'X) & r^{21}(Z'Z)+g^{21}I & r^{22}(Z'Z)+g^{22}I \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \\ u_1 \\ u_2 \end{bmatrix} \qquad (1.5)$$

While the right hand side (RHS) of the MME can be expressed as:

$$\begin{bmatrix} X'(r^{11}y_1 + r^{12}y_2) \\ X'(r^{21}y_1 + r^{22}y_2) \\ Z'(r^{11}y_1 + r^{12}y_2) \\ Z'(r^{21}y_1 + r^{22}y_2) \end{bmatrix} = \begin{bmatrix} (\mathbf{R}^{-1} * X')y \\ \\ (\mathbf{R}^{-1} * Z')y \end{bmatrix} \qquad (1.6)$$

With r^{ij} and g^{ij} the ij_{th} elements of the respective inverses of R and G.

For the situations in which there are no residual covariances between traits, the variance-covariance structure in the model is as follows:

$$\mathrm{Var}\begin{bmatrix} u_1 \\ u_2 \\ e_1 \\ e_2 \end{bmatrix} = \begin{bmatrix} G_{11} & G_{12} & 0 & 0 \\ G_{21} & G_{22} & 0 & 0 \\ 0 & 0 & R_{11} & 0 \\ 0 & 0 & 0 & R_{22} \end{bmatrix} \qquad (1.7)$$

Consequently the corresponding MME have the following form (Schaeffer et al.,1978):

$$\begin{bmatrix} r^{11}(X_1'X_1) & 0 & r^{11}(X_1'Z_1) & 0 \\ 0 & r^{22}(X_2'X_2) & 0 & r^{22}(X_2'Z_2) \\ r^{11}(Z_1'X_1) & 0 & r^{11}(Z_1'Z_1) + g^{11}I & g^{12}I \\ 0 & r^{22}(Z_2'X_2) & g^{21}I & r^{22}(Z_2'Z_2) + g^{22}I \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \\ u_1 \\ u_2 \end{bmatrix}$$

$$= \begin{bmatrix} r^{11}(X_1'y_1) \\ r^{22}(X_2'y_2) \\ r^{11}(Z_1'y_1) \\ r^{22}(Z_2'y_2) \end{bmatrix}$$

In this case the coefficient matrix is more sparse than in the previous case and the RHS have a more simple structure.

1.2 Estimation by REML

The different algorithms used for obtaining REML estimates of dispersion parameters make use of solutions for random effects and traces of the inverse of the coefficient matrix of the MME. Hence estimation of variance components by REML requires the simultaneous solution of the MME for both fixed and random effects, or alternatively for the random effects after absorbing the fixed effects.

REML estimation consists of maximising the likelihood or log-likelihood function of error contrasts. A set of error contrasts is a set of linear functions of the observations that have zero expectation (Searle, 1979). First derivatives of the log-likelihood function with respect to the parameters need to be obtained. Thus some of the first-used algorithms for univariate REML made use of first derivatives, for example Patterson and Thompson (1971) and Thompson (1973).

Different approaches to differentiate the log-likelihood of error contrasts have been described (Patterson and Thompson, 1971; Harville, 1977; Searle, 1979). In general the functon has the form:

$$L(Sy) = L^\circ = k - \tfrac{1}{2}\log |SVS| - \tfrac{1}{2}\log y'S(SVS)^{-}Sy, \qquad (1.8)$$

Where Sy is a linear function of a vector of observations, with expectation zero and variance SVS, k a constant that disappears upon differentiation, and $(SVS)^{-}$ a generalized inverse of SVS. With S a matrix independent of the parameters of the model, the differentiable part of the likelihood will be the same for all S with the mentioned properties. One set of error contrasts is given by Sy, with $S = R^{-1} - R^{-1}X(X'X)^{-}X'R^{-1}$. Searle (1979) showed that an equivalent expression to 1.8, invariant to any S, is:

$$L^\circ = \tfrac{1}{2}\log |V| - \tfrac{1}{2}\log |X^\circ V^{-1} X^\circ| - \tfrac{1}{2}(y - Xb)V^{-1}(y - Xb), \qquad (1.9)$$

where X° is an N-r(X) full column rank submatrix of X. Differentiating L(Sy) with respect to Θ_i, which is the i_{th} (co)variance component to be estimated, yields (Harville, 1977; Searle, 1979):

$$\begin{aligned} \delta L^\circ/\delta\Theta_i &= -\tfrac{1}{2}\operatorname{tr}(P\delta V/\delta\Theta_i) + \tfrac{1}{2}y'P(\delta V/\delta\Theta_i)Py \\ &= -\tfrac{1}{2}\operatorname{tr}(P\delta V/\delta\Theta_i) + \tfrac{1}{2}(y - Xb)'V^{-1}(\delta V/\delta\Theta_i)V^{-1}(y - Xb) \quad (1.10) \end{aligned}$$

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

As Meyer (1983) shows by equating this derivative to zero, the REML equations:

$$tr(P\delta V/\delta\Theta_i) = y'P(\delta V/\delta\Theta_i)Py \qquad (1.11)$$

have equivalent expressions:

$$tr(PVP\ \delta V/\delta\Theta_i) = y'P(\delta V/\delta\Theta_i)Py =$$

$$\Sigma_i\, tr[P\ (\delta V/\delta\Theta_i)P(\delta V/\delta\Theta_j)]\Theta_i = y'P(\delta V/\delta\Theta_i)Py, \qquad (1.12)$$

in terms of second derivatives (Meyer, 1986b).

For the univariate case $\delta V/\delta\Theta_i = Z_iZ_i'$, and thus the REML equations are (Searle, 1979):

$$tr\{[PZ_iZ_i'PZ_jZ_j']\}\ \Theta_i = \{y'PZ_iZ_i'P\}. \qquad (1.13)$$

Garrick (1988) describes with detail the derivatives of the log-likelihood for the multivariate case of a sire model. For Θ_{ij} an element in G the respective first order-derivative of the likelihood is:

$$\delta V\ /\ \delta\Theta_{ij} = \delta(ZGZ' + R)\ /\ \delta\Theta_{ij} = Z\ (\delta G\ /\ \delta\Theta_{ij})\ Z',$$

and hence

$$tr\ [Z'PZ\ (\delta G\ /\ \delta\Theta_{ij})] = y'PZ\ (\delta G\ /\ \delta\Theta_{ij})\ Z'Py, \qquad (1.14)$$

and for Θ_{ij} an element of R the derivative takes the form:

$$\delta V\ /\ \delta\Theta_{ij} = \delta(ZGZ' + R)\ /\ \delta\Theta_{ij} = \delta R\ /\ \delta\Theta_{ij},$$

so the respective equation is:

$$tr\ [P(\delta R\ /\ \delta\Theta_{ij}) = y'P\ (\delta R\ /\ \delta\Theta_{ij})\ Py. \qquad (1.15)$$

The REML equations can be represented in the form (Harville, 1977):

$$B\,\Theta = d. \qquad (1.16)$$

Where the ij_{th} element of B is equal to $tr[P(\delta V/\delta\Theta_i)P(\delta V/\delta\Theta_j)]$, the i_{th} element of d is equal to $y'P(\delta V/\delta\Theta_i)Py$ and Θ is the matrix of parameters.

The number of parameters to be estimated depends on the model, and so the total number of equations to be solved. For a sire model with t traits having the same design matrix, there are $t(t + 1)$ (co)variance components to be estimated. If no residual covariances exist then the number of parameters to be estimated is reduced to $2t + t(t-1)/2$.

Explicit forms of the REML equations are different for different models, and parameterisations, but in all cases some elements of B will be computed as traces and products of corresponding submatrices of the inverse of the coefficient matrix from the MME. Harville (1977) gives a detailed description of first-order and second-order derivatives of the log-likelihood with respect to the parameters σ^2_e and $\Gamma = \sigma^2_u/\sigma^2_e$, the residual variance and the ratio of the random effects variance to the residual variance respectively.

For the various multivariate cases the corresponding expressions have been derived. In the case of traits with the same model, Thompson(1973) described the REML equations showing an application for when sequential culling was applied.

For models with no residual covariance Schaeffer et al.(1978) derived the respective REML equations. Meyer (1983, 1986b) analysed the case of traits with different models and missing records, obtaining the corresponding equations.

REML theory is well developed, and first-order and second-order derivatives of the likelihood for different models are well documented (eg. Harville, 1977; Searle, 1979; Meyer, 1983; Garrick, 1988). However, the REML equations can not be solved explicitly and therefore iterative algorithms need to be used for the computation of estimates. The problem consists then of finding a numerical solution of a constrained non-linear optimisation problem, as emphasised by Harville (1977) and Meyer (1990). Unfortunately, no single numerical procedure can be used for all models and all sets of data, so specific approaches have been taken for particular cases, through the adaption of general algorithms. Harville numerical procedure can be used for all models and all sets of data, so specific approaches have been taken for particular cases, through the adaption of general algorithms. Harville (1977), Searle (1979), Harville and Callanan (1990) and Meyer(1990) describe the algorithms that can be used to solve these equations iteratively. The algorithms can be grouped into two categories. One group includes the methods that make use of first-order and second-order derivatives of L°, and the other the so-called derivative-free methods. In the first group, it is common to find forms of Fisher's Method of Scoring (FMS), the Newton-Rapson (N-R) algorithm and Expectation Maximisation (EM) algorithms. Methods using first-order and second-order partial derivatives are called mathematical methods, and EM algorithms, statistical methods (Garrick, 1988). Derivative-free methods used include the Simplex method, which is a direct search procedure, and a simple grid search as described by Smith (1987). What all methods have in common is the large number of computations required to construct the MME and the use of specialised numerical routines to solve them.

Harville and Callanan (1990) describe the N-R algorithm as a method for finding stationary points of a function by equating its first-order partial derivatives to zero. When applying an N-R algorithm to the REML equations one round of iteration can be represented by:

$$\hat{\Theta}_{(k+1)} = \hat{\Theta}_{(k)} - B^{-1}_{(\Theta k)} d_{(\Theta k)} . \qquad 1.17$$

For a sire model this is:

$$\hat{\Theta}_{(k+1)} = \hat{\Theta}_{(k)} - \begin{bmatrix} \delta^2 L^\circ / \delta(\sigma^2_u)^2 & \delta^2 L^\circ / \delta\sigma^2_u \, \delta\sigma^2_e \\ \delta^2 L^\circ / \delta\sigma^2_u \, \delta\sigma^2_e & \delta^2 L^\circ / \delta(\sigma^2_e)^2 \end{bmatrix}^{-1} \begin{bmatrix} \delta L^\circ / \delta\sigma^2_u \\ \delta L^\circ / \delta\sigma^2_e \end{bmatrix}$$

An alternative to the N-R algorithms is Fisher's Method of Scoring, in which use is made of the expectation of the second-order partial derivatives instead of the derivatives themselves. Thus B is replaced by $B_e = E[B_{(\Theta)}]$.

One round of iteration of this algorithm is equivalent to the solution:

$$\hat{\Theta}_{(k+1)} = \hat{\Theta}_{(k)} - B^{-1}_{e(\Theta k)}\ d_{(\Theta k)}. \qquad (1.18)$$

A related algorithm that has been used consists of expressing the REML equation in terms of the information matrix associated with the likelihood function of error contrasts, so they have the form:

$$B\hat{\imath}_{(\Theta k)}\ \hat{\Theta}_{(k+1)} = d_{(\Theta k)}, \qquad (1.19)$$

with solutions

$$\hat{\Theta}_{(k+1)} = B\hat{\imath}^{-1}_{(\Theta k)}\ d_{(\Theta k)}.$$

The ij_{th} element of $B_{\hat{\imath}}$ is:

$$\tfrac{1}{2}\mathrm{tr}[P\ (\delta V/\delta\Theta_i)\ P\ (\delta V/\delta\Theta_j)].$$

Expectation Maximisation algorithms (Dempster et al., 1977) have been favoured in the estimation of variance components in animal breeding research. In general, this method consists of estimating parameters by applying successive approximations in a two-step process. First, the conditional expectation of the random effects is computed, at the current value of the dispersion estimates and given the error contrasts. The second step consists of maximising the likelihood function for the computed conditioned expected random effects and residuals. So for the general model in (1.1):

$$\hat{u} = E[\ u|k'y,\ G_{(\Theta k)},\ R_{(\Theta k)}],\ \text{and}$$

$$\hat{e} = E[\ e|k'y,\ G_{(\Theta k)},\ R_{(\Theta k)}],\ \text{so then}$$

$$\hat{\Theta}_{(k+1)} = \mathrm{Var}(\hat{u}|k'y,\ \hat{\Theta}_{(k)}).$$

For a sire model the equations to solve for Θ in G° and for Θ in R° are:

$$\hat{\Theta}_{ij} = (\{\hat{u}_i'\hat{u}_j\} + \mathrm{tr}\ [C^{ij}])\ /\ n,$$

$$\hat{\Theta}_{ij} = (\{\hat{e}_i'\hat{e}_j\} + \mathrm{tr}\ [H_{ij}])\ /\ N,$$

where C^{ij} is a submatrix of C^{-1}, the inverse of the mixed model coefficient matrix, and H_{ij} is a submatrix of $H = [X:Z]\ C^{-1}\ [X:Z]'$, both pertaining to the i_{th} and j_{th} traits (Henderson, 1984).

Thompson (1973) applied a FMS algorithm to estimate variances and covariances from data consisting of pairs of parent-offspring records, with sequential culling. For a case in which there were no residual covariances, Schaeffer et al.(1978) obtained REML estimates by a modification of the method presented by Thompson(1973). A similar application was described by Meyer (1983 and 1986b) for models with residual covariances but with sequential culling and missing observations.

1.3 General Properties of the Described Methods

Properties of the methods described above have been reviewed by Harville (1977), Garrick (1988), Harville and Callanan (1990) and Meyer (1990). Mathematical methods have the desirable property of fast convergence, however, no restriction with respect to parameter space and the condition of the variance-covariance matrix at each round is implicitly imposed, and hence solutions at convergence are not necessarily REML estimates. An additional disadvantage is that the log-likelihood is not guaranteed to increase at each round. In contrast EM algorithms impose implicit restrictions on the estimates so they fall within the allowable parameter space, increasing the log-likelihood with each round of iteration and the variance-covariance matrix stays positive-definite as long as its initial value is positive-definite. The slow rate of convergence of EM algorithms is well known and is the consequence of it being a method of first-order successive approximations with linear convergence (Meyer, 1990). The speed of convergence can be affected by the ratio of the variance of random effects to the residual variance (Meyer, 1990), by the choice of the model (Thompson and Meyer, 1986) or by an inappropriate selection of complete data

(Garrick, 1988).

1.4 Simplification of Computations for Multivariate Models

As mentioned above, extensive computations are required to obtain REML estimates by any method. This is the cause of the limited use of REML. Computing time is increased when fitting multivariate models to large sets of data. Jensen and Mao (1988) reviewed transformations to simplify computations of algorithms for the univariate and multivariate REML estimation of (co)variances by EM algorithms, for models with one random effect and equal design matrices. There are in general two approaches to reduce the burden of computing. One is the transformation of the vector of observations or reparameterisation of the model, and the other the transformation of the coefficient matrix in the MME to simplify the computation of inverses, products and traces required at each step of the algorithms.

The use of a linear transformation of the vector of observations on t traits, such that the analysis is done on t genetically and phenotypically uncorrelated traits, as suggested by Thompson (1973, 1977), considerably simplifies the computations. A canonical decomposition of the variance-covariance matrix provides a transformation matrix that when applied to the vector of observations yields a new set of variables for which the corresponding variance-covariance matrix for the random effects is diagonal, and hence the corresponding inverse (G^{-1}) is diagonal with elements τ^i, and the residual variance-covariance matrix is the identity matrix. However such a transformation is restricted to models with one random effect with same fixed effects affecting all the traits (Meyer, 1985). One approach that can be utilised in the case of traits with different design matrices for fixed effects is to use a transformation such that the residual variance-covariance matrix becomes the identity matrix. This reduces the number of parameters to be estimated on the transformed scale, as if no residual covariances existed.

The second approach, consists of a transformation of the MME in such a way that computations of inverses, traces and hence of solutions of random effects are reduced. One natural transformation is given by the absorption of the fixed effects, this reduces the order of the coefficient matrix of the MME to the total number of levels in the random effects (number of sires in a sire model) times the number of traits so the MME become:

$$[R^{-1} * Z'MZ + G^{-1} * I_s]\, u = [R^{-1} * Z'M]\, y, \qquad (1.20a)$$

where $M = I_N - X(X'X)^{-}X'$ and s the number of random levels. This approach can be combined with the use of canonical variables in which case the absorbed MME are:

$$[I_t * Z'MZ + G^{-1} * I_s]\, \ddot{u} = [I_t * Z'M]\, \ddot{y}, \qquad (1.20b)$$

where M has the same form as above and the subindices N, s and t represent the order of the identity matrices (the number of observations, sires and traits respectively), G^{-1} is diagonal and $\ddot{u}$ and $\ddot{y}$ are solutions and observations on the canonical scale, respectively. In 1.15b the coefficient matrix is block diagonal, and can be expressed as:

$$\Sigma^{+}_{i}\, (Z'MZ + \tau^{i} I_s). \qquad (1.21)$$

With Σ^{+} denoting the direct sum operator.

Quaas (1981) proposes two further transformations of the coefficient matrix after absorption of the fixed effects, that are related and applicable after the canonical transformation of the vector of observations. The general form of the transformation is $Z'MZ = H'FH$, with H an orthogonal matrix, so HZ'MZH'= F. The transformation of the coefficient matrix is achieved by first premultiplying both sides of the MME by H, then:

$$H(Z'MZ + \tau^{i}I)\ \ddot{u} = HZ'M\ddot{y}, \qquad (1.22)$$

by inserting H'H=I in the LHS, and leaving the RHS unchanged,

$$H(Z'MZ + \tau^{i}I)H'H\ddot{u} = HZ'M\ddot{y}, \qquad (1.23)$$

thus $$(HZ'MZH' + H\tau^{i}IH')H\ddot{u} = HZ'M\ddot{y}, \qquad (1.24)$$

$$(F + \tau^{i}HIH')H\ddot{u} = HZ'M\ddot{y},$$

$$(F + \tau^{i}I)H\ddot{u} = HZ'M\ddot{y}, \qquad (1.25)$$

$$u^{\circ} = H\ddot{u} = (F + \tau^{i}I)^{-1}\ HZ'M\ddot{y},$$

$$u^{\circ} = C^{-1}\ HZ'M\ddot{y}, \qquad (1.26)$$

by defining $C = F + \tau^{i}I$.

The limiting factor is therefore the form of F. Two simple structures of F are possible. One is F = T, where T is a tridiagonal matrix, and the other F = D, a diagonal matrix. Quaas (1981) suggests that T can be obtained by Householder transformations using a finite algorithm that requires about the same computing time as the inversion of a full-stored matrix. A series of s-2 Householder matrices pre- and post-multiplying Z'MZ will achieve this (Taylor et al, 1985). Smith and Graser (1986) describe with detail an application of the tridiagonal factorisation of the coefficient matrix on a class of univariate mixed models combined with a grid search. Solutions of the equations can be obtained by gaussian elimination (Smith and Graser, 1986) or by factorising T as LL' with L a lower triangular matrix and applying forward and backward substitution (Quaas, 1981). Determinants and traces are computed under a separate process. The factorisation suggested by Smith and Graser (1986) requires the further transformation of F as T = UDU' with U upper triangular and D diagonal, so obtaining the determinant of the diagonal matrix D is, by a general result, equal to the product of the diagonal entries, hence $\log(\det(D)) = \Sigma_k \log d_k$, where d_k is the k_{th} diagonal entry of D. For F = LL', the corresponding logarithm of the determinant is obtained as:

$$\log(\det(LL')) = \log(\det(L) \det(L')) = 2\ \Sigma_k \log l_k,$$

with l_k the k_{th} diagonal element of L. The computations of log (det(F)) in both cases are trivial. However the evaluation of the trace of C^{-1} requires the inverse of a lower triangular matrix. Although the tridiagonalisation of the coefficient matrix has to be performed only once, evaluations of traces and determinants are required at each round of iteration. This method has been used by Smith and Graser (1986), Taylor et al.(1985) and Klei et al.(1988) with EM algorithms, and by Colleau et al. (1989) with N-R and EM algorithms.

The diagonalisation of F is feasible since Z'MZ is a real and symmetric matrix, and therefore by orthogonal similarity there exists a diagonal matrix such that D = HZ'MZH', with H orthogonal (Hill, p 305, 1988). Thus the diagonalization of a real symmetric matrix is called the similar transformation of that matrix, which is considered a special case of the singular value decomposition of a matrix. This is an iterative process that, from early in the 1950's and until the discovery of the QR algorithm, was based on Jacobi's method which uses plane rotation so two symmetrically located elements are eliminated, converging to a diagonal matrix in quadratic time (Stewart, 1973). For the QR algorithm to be applied to a real matrix, Householder transformations can provide an efficient computation of its similar form. For a small matrix, say A, the similar transformation is achieved by finding the roots of the characteristic equation $\det(A - \phi I) = 0$, corresponding to the eigenvalues. In fact for positive-definite matrices the eigenvalues and singular values are the same. This last form can be applied, for example, in the canonical decomposition of the variance-covariance matrix. The computation of a diagonal F matrix, and hence a diagonal C matrix, requires more computation than for F being tridiagonal. In fact as both computations can use

Householder matrices, the tridiagonal F matrix can be an intermediate step in the computation of the diagonal F matrix.

For an F diagonal matrix solutions to the MME are:

$$H\ddot{u} = u^{\circ} = (D + \tau^{i}I)^{-1}\, HZ'M\ddot{y} = C^{-1}HZ'M\ddot{y}, \qquad (1.27)$$

where D is diagonal with d_k the k_{th} diagonal element, and hence the k_{th} element of C^{-1} is $\{d_k + \tau^{i}\}^{-1}$, the sum of the k_{th} diagonal element of D and τ^{i}, and therefore the inverse of C can be computed easily as $\{1/(d_k + \tau^{i})\}$. Furthermore by the properties of similar matrices the determinant of the coefficient matrix is equal to the product of its singular values:

$$|Z'MZ + \tau^{i}I| = |D + \tau^{i}I| = \Pi_k\,(d_k + \tau^{i})\ ;$$

while the traces are:

$$\mathrm{tr}(Z'MZ + \tau^{i}I)^{-1} = \mathrm{tr}(D + \tau^{i})^{-1} = \Sigma_k\, 1/(d_k + \tau^{i}).$$

Also by the property of orthogonality of H:

$$u^{\circ\prime}u^{\circ} = \ddot{u}'H'H\ddot{u} = \ddot{u}'\ddot{u}, \text{ and} \qquad (1.28)$$

$$u^{\circ\prime}HZ'M\ddot{y} = \ddot{u}'H'HZ'M\ddot{y} = \ddot{u}'Z'M\ddot{y}. \qquad (1.29)$$

So no back-transformation is required to compute quantities needed (det(C), $\mathrm{tr}(C^{-1})$ and u'u) in the estimation of parameters in the canonical scale for each round of iteration. Hence the advantage of F = D over F = T is the reduction of computation required at each round of iteration. However the computation of D requires an undetermined number of iterations, always larger than the number of iterations needed to compute T, but as in the case of T the transformation is performed only once. Applications of the diagonalisation of F have been recently described by Dempster et al.(1984) and Lin (1987) with EM algotrithms. Although the diagonal transformation appears to be a purely numerical solution, Harville and Callanan (1990) show that linear functions of the vector of observations free of fixed effects (contrasts) can be derived naturally by using the similar transformation of Z'MZ in the coefficient matrix of the MME, and by assuming u is a vector of unknown parameters. Let:

$M = I - X(X'X)^{-}X$, so $MX = 0$;

$Z'MZ = K = WDW'$, with $W'W = I$,

that is W is a matrix of orthonormal eigenvectors, and D is a diagonal matrix, then

$Ku = Z'My$.

By premultiplying both sides of the equation by $D^{-\frac{1}{2}}W'$ it becomes

$D^{-\frac{1}{2}}W'Ku = D^{-\frac{1}{2}}W'Z'My =$

$D^{-\frac{1}{2}}W'WDW'u = D^{-\frac{1}{2}}W'Z'My =$

$D^{-\frac{1}{2}}DW'u = D^{-\frac{1}{2}}W'Z'My =$

$D^{\frac{1}{2}}W'u = D^{-\frac{1}{2}}W'Z'My = a$

Where **a** is a linear function of the vector of unknown parameters u. With $\hat{u}$ an estimate of u, and a linear function of the random variable Z'My, then $\hat{a}$ is an estimate of **a**, and also a linear function of Z'My. The expectation of the first and second moments of $\hat{a}$ are thus:

$E(\hat{a}) = E(D^{-\frac{1}{2}}W'Z'My) = 0$, as $E(Z'My) = 0$, and

$$\mathrm{Var}(\hat{a}) = \mathrm{Var}(D^{-½}W'Z'My\,WD^{-½}).$$

For the parameterisation $\mathrm{Var}(y) = \sigma^2_e\,(I + \alpha ZZ')$, with $\alpha = \sigma^2_u/\sigma^2_e$, then

$\mathrm{Var}\,(Z'My) = \sigma^2_e(K + \alpha K^2)$, hence the variance of $\hat{a}$ reduces to $\sigma^2_e(I + \alpha D)$, and hence $\hat{a}$ is a set of error contrasts (Harville and Callanan, 1990).

The use of diagonalization of the coefficient matrix of the MME has been applied for univariate analysis only (Dempster et al., 1984; Harville and Callanan, 1990).

1.5 Inclusion of the Numerator Relationship Matrix

Accuracy in estimation of (co)variance components is one of the reasons REML procedures are preferred (Henderson, 1984). However it has been shown empirically that for REML to account for selection bias, all information available and all known relationships have to be included in the analysis (Jensen et al., 1990; van der Werf and Boer, 1990). If no records on the base population are available, unbiased estimates are obtainable when relationships are traced back to the base population (Jensen et al.,1990). When relationships exist between sires, i.e. there are covariances among levels of the random effects, the component of the variance-covariance matrix of the sample due to sires is $\mathbf{G} = G * A$, where A is the numerator relationship matrix (NRM), instead of $\mathbf{G} = G * I$, and hence the corresponding form of the coefficient matrix in the MME is:

$$(R^{-1} * Z'MZ + G^{-1} * A^{-1}), \qquad (1.30)$$

which after the canonical transformation is:

$$\Sigma^{+}_{i} (Z'MZ + \tau^{i} A^{-1}).$$

For each round of iteration of an EM algorithm after a canonical transformation, the expectation step requires the solution of the MME for each canonical trait, thus the expectation step yields:

$$\hat{u}_i = (Z'MZ + \tau^{i} I)^{-1} Z'M\ddot{y}_i,$$

$$\hat{e}_i = \ddot{y}_i - Xb_i - Z\hat{u}_i,$$

and

$$\hat{e}_i'\hat{e}_i = y_i'My_i - \hat{u}_i'Z'My_i - \tau^{i}\hat{u}_i'\hat{u}_i .$$

The maximisation step consists of solving the following equations (Quaas, 1981):

$$g^{*}_{ii} = [\hat{u}_i'\hat{u}_i + \mathrm{tr}\,(Z'MZ + \tau^{i})^{-1}\,]/\,s,$$

$$g^{*}_{ij} = [\hat{u}_i'\hat{u}_j]\,/\,s, \text{ for i \quad j; and}$$

$$r^{*}_{ii} = \{\hat{e}_i'\hat{e}_i + [s + p - \tau^{i}\,\mathrm{tr}(Z'MZ + \tau^{i})\text{-}1\}/\,N,$$

$$r^{*}_{ij} = \hat{e}_i'\hat{e}_j\,/\,N, \text{ for i \quad j;}$$

where r and g are (co)variance components for sires and residuals respectively, '*' denotes components in the canonical scale and i,j = 1,2, ..., t, the corresponding traits. These equations are modified to account for the covariance between relatives as follows:

$$\{g^{*}_{ij}\} = \{\hat{u}_i'A^{-1}\hat{u}_j\}/\,s + \mathrm{diag}\,\{\mathrm{tr}(A^{-1}\,(Z'MZ + \tau^{i}A^{-1})^{-1})\}/\,s,$$

$$\{r^{*}_{ij}\} = \{\hat{e}_i'\hat{e}_j\}/\,N + \mathrm{diag}\,\{h + s - \tau^{i}\mathrm{tr}(A^{-1}(Z'MZ + \tau^{i}A^{-1})^{-1}\}/\,N,$$

with $\hat{e}_i'\hat{e}_j = \ddot{y}_i'M\ddot{y}_j - \hat{u}_i'Z'M\ddot{y}_j - \tau^i\hat{u}_i'A^{-1}\hat{u}_j$, and h and s the rank of X and Z respectively.

The REML equations for a FMS algorithm on canonical variates is given by Meyer (1985). Here the equations are given after modification when the NRM is included in the model (following the proof of equivalences given by Harville and Callanan, 1990).

$$\begin{bmatrix} s - \alpha^i tr(C_i) - \alpha^j tr(C_j) & \tfrac{1}{2}[tr(C_i) + tr(C_j) \\ + \alpha^i\alpha^j tr(C_iC_j) & - (\alpha^i + \alpha^j) tr(C_iC_j)] \\ & \\ \tfrac{1}{2}[tr(C_i) + tr(C_j) & \alpha_i\alpha_j(N-q-s) + tr(C_iC_j) \\ - (\alpha^i + \alpha^j) tr(C_iC_j)] & \end{bmatrix} \begin{bmatrix} g_{ij} \\ \\ \\ r_{ij} \\ \\ \end{bmatrix}$$

$$= \begin{bmatrix} \hat{u}'A^{-1}\hat{u} \\ \\ \alpha_i\alpha_j\ [y_i'My_j - \hat{u}'Z'My - \alpha^i\hat{u}_i'A^{-1}\hat{u}_j] \end{bmatrix}$$

Lin (1988) proposes an algorithm for the simultaneous diagonalisation of Z'MZ and A^{-1} in the coefficient matrix, by first applying a Cholesky factorisation of A to transform the MME in such a way that A^{-1} vanishes. Let A = LL', then by an operation similar to that of diagonalising the MME premultiply the MME by L:

$$L(Z'MZ + \tau^i A^{-1})\ u = LZ'My,$$

then by inserting $L'L^{-t}$, with $L^{-t} = (L^{-1})'$

$$L(Z'MZ + \tau^i A^{-1})L'L^{-t}u = LZ'My$$

$$(LZ'MZL' + \tau^i LA^{-1}L')L^{-t}u = LZ'My$$

$$(LZ'MZL' + \tau^{i}I)L^{-t}u = L'ZMy. \qquad (1.31)$$

Lin (1988) suggests that equations (1.28) and (1.29) show the equivalence of the transformed and untransformed models, not in terms of solutions (u vs.$L^{-t}u$) , but in terms of quantities required to compute first and second moments and REML estimates, eg.

$$\hat{u}'L^{-1}L^{-t}\hat{u} = \hat{u}'A^{-1}\hat{u}, \text{ and}$$

$$\hat{u}'L^{-1}LZ'My = \hat{u}'IZ'My = \hat{u}'Z'My.$$

Then by applying a similar transformation on LZ'MZL rather than on Z'MZ a simultaneous diagonalisation of Z'MZ and A^{-1} is achieved.

After the simultaneous transformation the new equations have D_i in place of C_i and $\hat{u}^{\circ} = RL^{-t}\hat{u}$ in place of $\hat{u}$, yielding equivalent products as shown above. Harville and Callanan (1990) use equivalent expressions of elements in these equations in terms of sums of the diagonal elements of the transformed coefficient matrix of the MME.

1.6 Including Records of Daughters of Selected Sires

Sometimes the base population is not well defined. For example if selection has operated on one or few traits for some generations and then changes in the selection objective occurs (eg. inclusion of more traits in the objective or changes in prices of components) the 'new' base population will be formed by old sires selected for the previous objective, and young sires being sampled. If an additive genetic correlation between the old and new selection objectives exists, a decrease in the additive genetic variance in the new selection objective may have occurred, the decrease being proportional to the correlation between the objectives. Hence if selected bulls are used contemporaneously to young sires being sampled, the estimation of (co)variances can be biased (Meyer,1986a). By treating proven sires as fixed the problem of bias by this condition is accounted for, and no information on the means and variances within subclasses is lost. Also proven sires are used to improve connectedness when sampling young sires, and hence if only records of daughters of young sires are included in the analysis some connectedness can be lost. Van Vleck (1985) describes in algebraic terms the absorption of old sires equations into the young sires equations in the MME. Forms of equations to estimate variances are derived by partitioning the design matrices into separate sets for records of daughters of old and young sires, respectively. In such a case the factorization of the MME will require the previous absorption of the old sires equations, and the use of the NRM for young sires tracing relationships as far into the past as possible.

1.7 Objective

In this paper an application of simultaneous diagonalisation of the coefficient matrix of the MME on multivarate estimation of (co)variance components using a sire model, after a canonical transformation and absorption of fixed sire effects, is presented. Two algorithms, an EM and a FMS are compared for their computational and convergence attributes.

2. MATERIALS AND METHODS

The comparison between algorithms was carried out analysing data of Ayrshire cattle correponding to the Traits Other than Production (TOP) programme from the Livestock Improvement Corporation (LIC). Three traits were chosen, from the 13 available, so as not to have strong correlations and small heritabilities to avoid obtaining extreme eigenvalues for the transformed variance-covariance matrix, based on experience from a previous analysis on the same set of traits in Holstein-Friesian cows. The traits included in the analysis were stature (STA), udder support (US) and dairy conformation (DC), and represented the three groups of conformation traits (body dimensions, udder traits and dairy conformation). The analysed records were from daughters of bulls used in young sire sampling herds in the two initial years of the programme (1987 and 1988). There were 2165 records from daughters of 319 sires, distributed in 148 herd-year-inspector (HYI) subclasses. From the 319 sires, 148 had one daughter recorded only. Younger sires (47) were taken as random while older bulls were assumed fixed to avoid bias due to selection. HYI effects were absorbed first, followed by the fixed sire effects. For this last step, sires were assigned a chronological identification, then records with subclass effects to be absorbed were sorted by sire identification and then the absorption of fixed sires effects was carried out.

Ancestry information of random bulls included sire and maternal grand-sire. The NRM was sparse and therefore its construction and factorization was simple. Relationships ranged from 0 to .5, with .0625 the most frequent after 0.

Computer programs to build the MME, absorb fixed efffects, and obtain the NRM were written in PASCAL. Factorisation of both, NRM and Z'MZ matrices, was undertaken utilising MATLAB software (Moler et al., 1987). Simultaneous transformation was undertaken only once and transformed matrices were stored on disk.

The computation of the required terms was simplified by using vector operations. Let **Ç** be a matrix of order s x t with the i_{th} column $Ç_i$ ($i = 1, 2, \ldots, t$) which contains the diagonal elements of the square matrix D_i, and **1** a column vector of ones of the same order as $Ç_i$, then:

$$\mathbf{1}'Ç = [\, \mathbf{1}'Ç_1 \;\; \mathbf{1}'Ç_2 \,..\, \mathbf{1}'Ç_t] = [\mathrm{tr}\,(D_1) \;\; \mathrm{tr}(D_2) \,..\, \mathrm{tr}(D_t)],$$

corresponding to a vector containing the required traces. Now let D_i and D_j be diagonal matrices and their product $D_i'D_j = \mathbf{D}$, with k_{th} diagonal element $\{d_{ki}d_{kj}\}$, and zeroes on the off-diagonals. Hence the trace of the product is $tr(D_iD_j) = \Sigma\{d_{ki}d_{kj}\}$, which is equal to the product $Ç_i'Ç_j$. Thus all traces of products between D_i's can be obtained by computing the product $\mathbf{Ç'Ç}$. By developing this approach all computations required for a FMS algorithm to be applied after the similar transformation of Z'MZ became trivial. The form of the equations to solve in the FMS algorithm were derived using the equivalent forms presented by Harville and Callanan (1990), and the equations derived by Meyer(1985) for untransformed Z'MZ.

Two sets of initial values were used (table I), to increase the probability of finding an overall maximum. One set corresponded to variances estimated previously (excluding other traits) in the Holstein-Friesian population for the same traits, and the other to assumed heritabilities in the opposite direction of magnitude, but not extreme. In the two cases genetic covariances were assumed zero. Convergence criteria was $CC = 1 - \{||G_{(k+1)} - G_{(k)}|| \div ||G_{(k)}||\}$ (Jensen and Mao, 1988), for $CC \geq .999$, and where $||\bullet||$ denotes the norm of the enclosed expression. This criteria of convergence coincided with an accuracy of eight significant digits.

3. RESULTS AND DISCUSSION

The FMS algorithm required 7 (set A) or 8 (set B) iterations to reach convergence, while 90 iterations were needed for the EM algorithm to converge with either set of initial values. The two sets of initial values in the EM algorithms reached equal values at 40 iterations. In figure I the convergence behaviour of the sire variance for stature is shown. For residual variances it took 2 iterations to approximate to final values with the FMS algorithms, while 14 to 16 iterations were required with the EM algorithm. For the FMS algorithm the sire variances showed similar rates of convergence to that of residual variances. On the other hand when an EM algorithm was used values for sire variances fluctuated around the true value in the first 20 iterations in some cases. For example the sire variance for US changed from .116

(initial value) to .0172 in round 10, and at round 40 the estimate was 0.02, while the estimate at convergence was .0211. The rate of convergence of covariances appears to be slower than that of variances. For the two sets of initial values and with the two algorithms the sire covariance between STA and US was negative after the first round of iteration, the value then changed to positive. However the absolute value of the estimate was always very small. In figure 2 the rate of convergence of the sire covariance between STA and US is described.

Meyer (1985) suggested that although the FMS algorithm required more computation effort at each round of iteration than EM algorithms, the fewer iterations needed to reach convergence compensated for this. After diagonalisation of the coefficient matrix of the MME this difference in computing was decreased considerably. Thus the faster convergence rate of the FMS algorithm suggested an advantage in using it. However it could be argued that accelerating procedures applied to EM algorithms and the positive-definitive condition of the variance-covariance matrix ensured with these last methods make the choice difficult. But extra computing work involved with accelerating procedures and changes in sign or direction of estimates at first rounds of iteration can eliminate the assumed advantage. Thus keeping the variance-covariance matrix positive-definite during iterations seems to be the only advantage of the EM algorithms.

Dempster et al. (1984) compared an N-R and an EM algorithm in a univariate study, after diagonalisation of the coefficient matrix. They observed convergence at 7 rounds of iteration for the N-R and at 10 rounds for the EM. In comparing 6 algorithms and their modifications, with a univariate model and diagonalisation, Harville and Callanan (1990) found that the N-R type and FMS type algorithms were faster to converge than the EM and successive approximations methods. These differences were more obvious when the initial values for the ratio σ^2_u / σ^2_e were very small. In their study Harville and Callanan (1990) found the FMS converged at 9 to 13 rounds while the EM algorithms converged at 297 and 1203 rounds for the same accuracy. In a multivariate study, Colleau et al.(1989) used N-R, FMS and EM algorithms after tridiagonalistion of the coefficient matrix. Convergence was reached after 4 iterations with the N-R, after 9 rounds with the EM and after 6 rounds with an accelerated EM. However the initial values utilised, obtained by Henderson's Method 3, were very close to the REML estimates at convergence.

Lin (1987) pointed out that the only limitation that the singular value transformation of the absorbed coefficient matrix MME had, was the size of this matrix. The larger the size of C the more computations required to obtain the singular values and vectors. In fact all the results found in the reviewed literature where diagonalisation was used involved less than 100 levels of the random effects. Lin (1987) reported the singular value decomposition of a matrix of order 900.

Jensen et al.(1990) suggested that univariate sire models may yield biased estimates of variance components even if analysed by REML, although the use of all information and all relationships among sires may alleviate this. They observed that the use of animal models with complete relationships yielded unbiased estimates of the population parameters when selection was operating. Hence for some conditions (eg. under a selection model) the use of animal models should be preferred to a sire model. This implies a large size of the coefficient matrix and hence the diagonalisation of the coefficient matrix may not be possible to obtain. On the other hand experimental data has generally a reduced number of levels in the random effects. Also data from some breeding programmes may have a number of levels (sires or dams) that makes the diagonal transformation possible. This can be the case of young sire sampling programmes or nucleus herds. Thus the reduction in complex computations, applicable to these last examples, makes the use of the diagonal transformation, and therefore of REML estimation, more appealing for its use by researchers. This should alleviate the problem of cumbersome and tedious computing which has been blamed as one cause of the limited use of REML estimation (Meyer, 1986a, 1990).

Heritabilities and genetic correlations obtained in the present study are shown in table II. It should be pointed out that these estimates were obtained under a model that assumes independence from other traits, and therefore should only be applied to a selection programme where only STA, US and DC are included, either as selection criteria or in the selection objective, as the inclusion of any other trait could change the estimates.

The heritabilities derived from variances estimated in the present study suggest that a rather large selection response for DC can be obtained, a slower response in STA and little change in US due to selection could be expected. However the moderate positive genetic correlation estimated between DC and US suggests that an improvement in the selection response in US would occur if selected together with DC. The large genetic correlation estimated between STA and DC suggests a common genetic basis to the two traits. This could be due to stature being given a considerable attention when scoring dairy conformation.

The heritability obtained in the present study for STA (.38) is similar to that obtained for Holstein-Friesian cows (.37). On the other hand heritability for US (.16) was considerably lower than that estimated for Holstein-Friesian cows (.63), while the heritability estimated for DC (.52) was larger than that for Holstein-Friesian cows(.32). The estimated genetic correlation of STA with US and DC were different with the corresponding estimates for Holstein-Friesian cows, which were negative in both cases (-.22 and -.34, respectively), with the correlation between US and DC consistent with the correlation estimated from scores on Holstein-Friesian cows (.43 and .58, respectively). It is important to mention that the estimates for Holstein-Friesian cows were obtained under a model that included 10 other traits, some of them highly correlated with either of STA, US or DC, so this could explain some of the differences between the two breeds.

TABLE I. Sets (I and II) of initial values utilised in the multivariate REML estimation of variance components for stature (STA), udder support (US) and dairy conformation (DC) of New Zealand Ayrshire cattle.

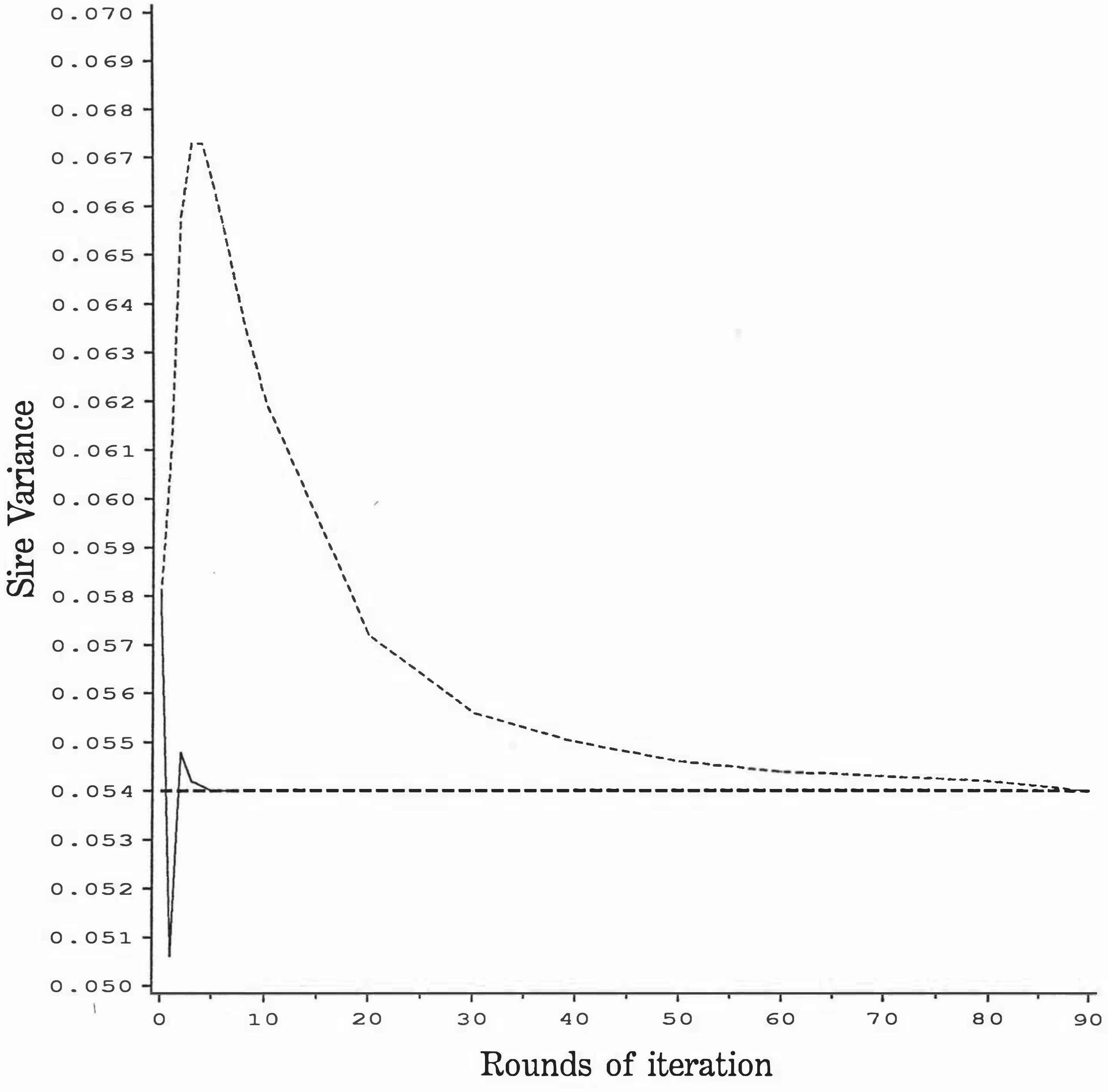
		Residual variances			sire variances		
		TRAITS					
		STA	US	DC	STA	US	DC
SET	I	0.56	0.62	0.92	0.0580	0.1160	0.0800
	II	0.51	0.51	0.63	0.1020	0.0490	0.0600

TABLE II. REML estimates of variances, covariances, heritabilities and genetic correlations for stature (STA), udder support(US), and dairy conformation (DC), in New Zealand dairy cattle1.

	Residual variances and covariances			Sire variances and covariances			Heritabilities and genetic correlations		
Traits	STA	US	DC	STA	US	DC	STA	US	DC
STA	0.5157	0.0144	0.0483	0.0540	0.0007	0.0522	0.38	0.02	0.74
US		0.5085	0.1899		0.0211	0.0190		0.16	0.43
DC			0.6248			0.0925			0.52

1 Variances and covariances rounded to four significant digits. Variances and heritabilities are on the diagonal, and covariances and genetic correlations above the diagonal.

Figure 1. Rate of convergence of estimate of sire variance component for STA of New Zealand Ayrshire cows, by Method of Scoring and EM algorithms



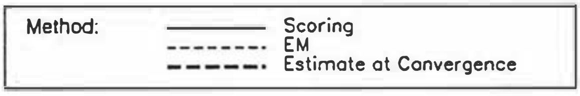
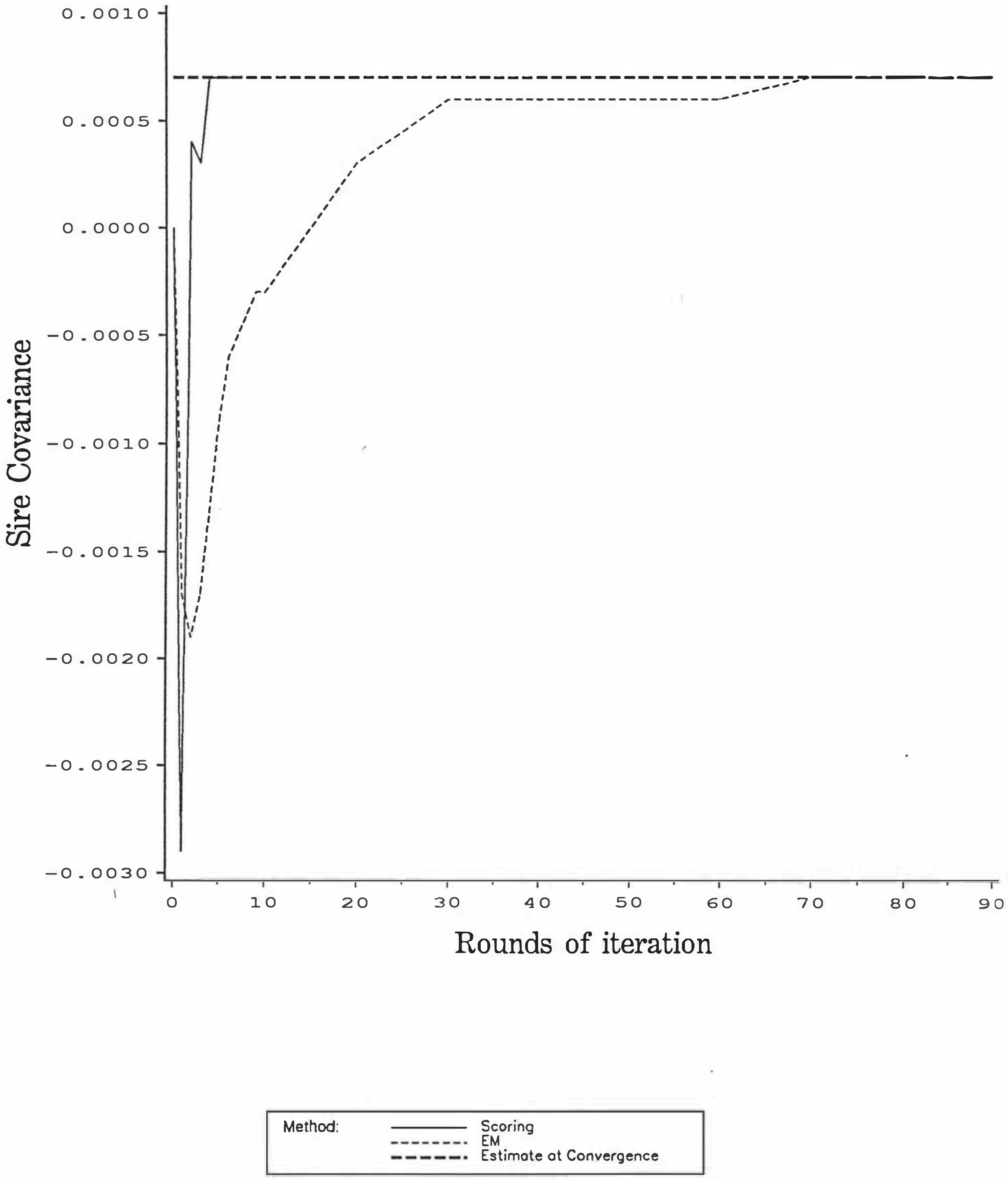


Figure 2. Rate of convergence of estimate of sire covariance component between STA and US of New Zealand Ayrshire cows, by Method of Scoring and EM algorithms



4. CONCLUSIONS

The factorisation of the coefficient matrix to its similar form (a diagonal matrix) simplifies the multitrait estimation of variances and covariances after a canonical transformation. This transformation is restricted to multivariate models with the same design matrix and observations in all traits.

Multivariate models are required to estimate covariances between traits in animal breeding programmes, also the inclusion of correlated traits may increase the accuracy of estimates of breeding values. However the extensive computing required has limited their use. With the canonical transformation and the diagonalisation of the coefficient matrix of the MME this is not a problem. Furthermore fast converging algorithms that without transformation require more computations per round of iteration, are relatively simple to implement with these transformations.

The Method of Scoring algorithm proved to converge much faster than an EM algorithm. Two different sets of starting points were used to decrease the probability of obtaining solutions at convergence that were non-positive definite, however both sets converged to the same value in almost the same number of iterations. The slow convergence of EM algorithms is apparently worsened by 'poor' starting values, but this condition is difficult to predict a-priori. If an EM algorithm is used, with no previous estimates available as initial values, then iterating on two sets of initial values and an accelerating procedure applied after the 10th round of iteration will help to reach convergence more rapidly.

An important limitation in the use of the singular value decomposition of the coefficient matrix is the size of the coefficient matrix to be factorised, thus this transformation is only applicable to sire models, to animal models with relatively few levels or to experimental data with a number of random levels manageable by the available computing capability.

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APPENDICES

APPENDIX I

Classification Type in Dairy Cows

From 1929 until the establishment of linear type programmes, classification scores of body conformation were the only means to describe the type of the cow. Many reports on phenotypic, environmental and genetic parameters have been published since then. White (1973) and Bowden (1982) reviewed the literature available on type classification and management traits. They found that the main factors affecting the phenotypic variation of descriptive classifications in North American cows were: herd, year, classifier, age at classification and the cow by year interaction.

Schaeffer et al. (1978) used a mixed model to study a transformation of subjective classification conformation that included the fixed effects of age at classification, year of classification, and the cow's dam classification. Norman et al. (1978) considered the effects of age and stage of lactation when analysing within herd-year classes for type of Jerseys in the USA. Schaeffer (1983) analysed an expanded form of classification used by Holstein-Canada, using a model that considered the fixed effects of year-round-classifier, parity, age at classification, stage of lactation, and dam's classification as a covariable. In the study by Smith et al. (1985) on North American Holstein cows, type traits were subjectively scored by inspectors using a 1 to 3 and 1 to 4 scale and analysed by a mixed model that included herd-year subclasses, month of classification, stage of lactation and describer as fixed effects. Meyer et al. (1985) found the effect of herd-year-round subclasses and age at classification to significantly affect a transformation on categorical scores on Australian Holstein cows. Therefore in most studies effects of herd, year and classifier were consistently found to be significant. However the amount of variation in the different traits analysed, explained by these effects fluctuated from 1% to about 18%.

The importance of additive genetic effects on categorical type and management traits was the center of many studies (White, 1973), for the Holstein breed mainly and to a lesser extent for other breeds, as knowledge of the heritabilities and correlations allowed the design of selection programmes to improve such traits. In table A1 a summary of heritability estimates for classification type traits based on the review of White (1973) and on other reports is shown. Heritabilities of body dimensions in Holstein cows (eg. stature and body capacity) ranged from 0.12 to 0.66. For degree of desirability in udder traits heritabilities ranged from 0.08 (teat placement) to 0.37 (mammary system). For rump, legs and feet the heritabilities reported ranged from 0.08 to 0.25.

Among other management traits, temperament and milking speed, scored on a subjective scale of three levels of desirability, were included in the study of New Zealand Holstein cows by Wickham (1978). Heritabilities for the two traits varied from 0.11 to 0.12 and 0.08 to 0.15 respectively.

For the Jersey breed Norman et al. (1978) obtained estimates of heritability for descriptive scores, the highest being for stature (0.43) and the lowest for degree of desirability of leg shape (0.09). For New Zealand Jersey cows Wickham (1978) estimated heritabilities of milking speed of 0.09 and 0.13, and for temperament of 0.09 and 0.11.

For Australian registered Holstein cows Meyer et al. (1985) obtained estimates of heritability of classification scores transformed to an objective scale. Heritabilities of transformed body scores varied from 0.32 to 0.41. Udder traits related to those in the present study had estimates between 0.24 and 0.32. The estimate for the composite trait feet and legs was low at 0.09 while estimates for rump traits were between 0.14 and 0.25.

Some phenotypic and genetic correlations have been estimated for several categorical type traits in dairy cows, with most of the published results referring to the Holstein breed. In the reviews by White (1973) and Bowden (1982) summaries of different phenotypic correlations published in the literature for classification type and management traits can be found.

Table A1. **Ranges of heritabilities for descriptive type and management traits for three breeds of dairy cows.**

TRAIT / BREED	HOLSTEIN		JERSEY
	Registered	Grade	
Stature	0.26 - 0.51	0.26 - 0.50	0.46
Capacity	0.12 - 0.66	0.17 - 0.36	0.14
Rump	0.20 - 0.25	0.17 - 0.23	0.23
Feet and legs	0.10 - 0.15	0.08 - 0.33	0.15
Mammary system	0.18 - 0.37		0.26
Fore udder	0.09 - 0.21	0.16 - 0.30	0.22
Rear udder	0.12 - 0.21	0.10 - 0.26	0.21
Teat placement	0.08 - 0.21	0.08 - 0.10	0.19
Temperament		0.11 - 0.12	0.08 - 0.15
Milking speed		0.09 - 0.11	0.09 - 0.13
Disposition			0.11 - 0.40
Milk out			0.09 - 0.24

Sources: White (1973), Norman et al. (1978), Meyer et al. (1985) and Wickham (1978).

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APPENDIX II

Canonical transformation of the variance-covariance matrix.

As mentioned in Chapter II the main idea behind the use of canonical variables in place of variables in the original scale for the estimation of their co-variance components, is to simplify the MME into a block diagonal structure. For this to be achieved the matrix of residual co-variances R has to be transformed into an identity matrix, and the additive genetic co-variance matrix G (or the sire co-variance if a sire model is used) has to be transformed into a diagonal matrix. Quaas (1984) and Schaeffer (1986) suggested two alternative approaches to do this. Both methods have in common that R is factored into two symmetric matrices that are then inverted. These inverses premultiply and postmultiply G, and then the eigenvalues and eigenvectors of this product are obtained, to generate the transformation matrix. The transformation requires R to be positive definite and symmetric, and G non-negative definite and symmetric. The method suggested by Quaas(1984) uses the Cholesky factorisation of R into LL', with L a lower triangular matrix, while Schaeffer (1986) suggested that R could be factored into $VDV' = VD^{1/2} D^{1/2}V'$, with V a matrix of orthonormal eigenvectors and D a diagonal matrix of respective eigenvalues.

It will be shown that the two methods described generate the same set of transformed variables. Let R be:

$$\begin{bmatrix} 2.5470 & 1.4494 & 0.6687 & 1.5759 \\ 1.4494 & 2.0236 & 0.3262 & 1.4136 \\ 0.6687 & 0.3262 & 2.0996 & 0.9514 \\ 1.5759 & 1.4136 & 0.9514 & 2.5128 \end{bmatrix}$$

Then by Cholesky factorisation R = LL', with L equal to:

$$\begin{bmatrix} 1.5959 & 0.0 & 0.0 & 0.0 \\ 0.9082 & 1.0949 & 0.0 & 0.0 \\ 0.4190 & -.0496 & 1.3862 & 0.0 \\ 0.9874 & 0.4720 & 0.4048 & 1.0729 \end{bmatrix}$$

which has L^{-1} as inverse and equal to:

$$\begin{bmatrix} 0.6266 & 0.0 & 0.0 & 0.0 \\ -.5197 & 0.9133 & 0.0 & 0.0 \\ -.2080 & 0.0327 & 0.7214 & 0.0 \\ -.2696 & -.4142 & -.2721 & 0.9321 \end{bmatrix}$$

The second step requires to compute the product $B = L^{-1} G L^{-t}$, so to illustrate this let G be:

$$\begin{bmatrix} 0.0600 & -.0110 & 0.0152 & 0.0190 \\ -.0110 & 0.0552 & 0.0147 & 0.0345 \\ 0.0152 & 0.0147 & 0.0528 & 0.0605 \\ 0.0190 & 0.0345 & 0.0605 & 0.0870 \end{bmatrix}$$

so then the product B is:

$$\begin{bmatrix} 0.0236 & -.0258 & -.0012 & 0.0012 \\ -.0258 & 0.0727 & 0.0144 & 0.0065 \\ -.0012 & 0.0144 & 0.0264 & 0.0228 \\ 0.0012 & 0.0065 & 0.0228 & 0.0295 \end{bmatrix}.$$

The respective matrices of eigenvalues(D) and eigenvectors (V) are:

$$\begin{bmatrix} 0.0890 & 0.0 & 0.0 & 0.0 \\ 0.0 & 0.0117 & 0.0 & 0.0 \\ 0.0 & 0.0 & 0.0471 & 0.0 \\ 0.0 & 0.0 & 0.0 & 0.0044 \end{bmatrix}$$

$$\begin{bmatrix} 0.3464 & -.8929 & 0.2737 & 0.0883 \\ -.8739 & -.4005 & -.2427 & 0.1299 \\ -.2790 & 0.0018 & 0.6008 & -.7491 \\ -.1959 & 0.2055 & 0.7108 & 0.6436 \end{bmatrix}$$

The transformation matrix $Q_1 = V'L^{-1}$ is

$$\begin{bmatrix} 0.7821 & -.7262 & -.1480 & -.1826 \\ -.4071 & -.4509 & -.0546 & 0.1915 \\ -.0189 & -.4964 & 0.2400 & 0.6625 \\ -.0298 & -.1724 & -.7155 & 0.5998 \end{bmatrix}$$

So for a vector of observations, say **y**, with variance R + G, there exists a set of transformed variables $Q_1\mathbf{y}$ with variance $Q_1 Var(\mathbf{y}) Q_1' = Q_1(R + G)Q_1'$. Thus with R and G as defined above.

$$Q_1RQ_1' = \begin{bmatrix} 1.0 & 0.0 & 0.0 & 0.0 \\ 0.0 & 1.0 & 0.0 & 0.0 \\ 0.0 & 0.0 & 1.0 & 0.0 \\ 0.0 & 0.0 & 0.0 & 1.0 \end{bmatrix}$$

and

$$Q_1GQ_1' = \begin{bmatrix} 0.0890 & 0.0 & 0.0 & 0.0 \\ 0.0 & 0.0117 & 0.0 & 0.0 \\ 0.0 & 0.0 & 0.0471 & 0.0 \\ 0.0 & 0.0 & 0.0 & 0.0044 \end{bmatrix}$$

Now by factorising R into its corresponding matrices of eigenvectors (V) and eigenvalues(D) as suggested by Schaeffer(1986), we have $R = V\,D\,V'$, where V is equal to:

$$\begin{bmatrix} 0.2266 & 0.7420 & 0.2558 & 0.5768 \\ 0.3806 & -.2276 & -.7575 & 0.4791 \\ -.8939 & 0.1386 & -.2979 & 0.3050 \\ -.0689 & -.6152 & 0.5216 & 0.5871 \end{bmatrix}$$

and D is:

$$\begin{bmatrix} 1.8645 & 0.0 & 0.0 & 0.0 \\ 0.0 & 0.9207 & 0.0 & 0.0 \\ 0.0 & 0.0 & 0.6892 & 0.0 \\ 0.0 & 0.0 & 0.0 & 5.7086 \end{bmatrix}$$

and hence $D^{-\frac{1}{2}}$ has the form:

$$\begin{bmatrix} 0.7323 & 0.0 & 0.0 & 0.0 \\ 0.0 & 1.0422 & 0.0 & 0.0 \\ 0.0 & 0.0 & 1.2046 & 0.0 \\ 0.0 & 0.0 & 0.0 & 0.4185 \end{bmatrix}$$

Let $P = D^{-\frac{1}{2}}V' =$

$$\begin{bmatrix} 0.1659 & 0.2787 & -.6546 & -.0504 \\ 0.7733 & -.2372 & 0.1444 & -.6411 \\ 0.3081 & -.9125 & -.3588 & 0.6283 \\ 0.2414 & 0.2005 & 0.1276 & 0.2457 \end{bmatrix}$$

Compute B as P G P' =

$$\begin{bmatrix} 0.0218 & 0.0119 & -.0117 & -.0122 \\ 0.0119 & 0.0627 & 0.0327 & -.0118 \\ -.0117 & 0.0327 & 0.0458 & 0.0041 \\ -.0122 & -.0118 & 0.0041 & 0.0219 \end{bmatrix}$$

Let W be the corresponding matrix of eigenvectors of B:

$$\begin{bmatrix} 0.6191 & 0.7181 & -.0624 & 0.3116 \\ 0.2643 & -.4329 & -.8035 & 0.3117 \\ -.5356 & 0.5387 & -.5803 & -.2935 \\ -.5099 & 0.0816 & 0.1174 & 0.8483 \end{bmatrix}$$

So the matrix of transformations is Q_2 = W'P =

$$\begin{bmatrix} 0.0189 & 0.4964 & -.2400 & -.6625 \\ -.0298 & -.1724 & -.7125 & 0.5998 \\ -.7821 & 0.7262 & 0.1480 & 0.1826 \\ 0.4071 & 0.4509 & 0.0546 & -.1915 \end{bmatrix}$$

The transformed variables have (co)variance components Q_2RQ_2'=

$$\begin{bmatrix} 1.0 & 0.0 & 0.0 & 0.0 \\ 0.0 & 1.0 & 0.0 & 0.0 \\ 0.0 & 0.0 & 1.0 & 0.0 \\ 0.0 & 0.0 & 0.0 & 1.0 \end{bmatrix}$$

and Q_2GQ_2' =

$$\begin{bmatrix} 0.0471 & 0.0 & 0.0 & 0.0 \\ 0.0 & 0.0044 & 0.0 & 0.0 \\ 0.0 & 0.0 & 0.0890 & 0.0 \\ 0.0 & 0.0 & 0.0 & 0.0117 \end{bmatrix}$$

And hence the same set of variance components are derived. It is important to observe that the rows and columns of Q_1 are a permutation of rows and columns of $-Q_2$. The total number of floating point operations required to compute Q_1 for this example were 1155, while 1718 floating point operations were needed to obtain Q_2.

APPENDIX 111

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MULTIVARIATE ESTIMATES OF GENETIC PARAMETERS FOR TRAITS OTHER THAN PRODUCTION IN NEW ZEALAND DAIRY COWS.

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INTRODUCTION

In New Zealand a linear classification programme for traits other than production (TOP) in dairy cows was started in 1987 (New Zealand Dairy Board 1988). Two of the objectives of this programme were:

- The evaluation of bulls for TOP based on the information on their daughters, and
- to provide an economic indication of a bulls total worth, by a selection index that includes yield, type and management traits.

These two objectives require the estimation of unknown genetic and environmental variances and covariances. Such parameters may differ from those obtained in other countries where milk is produced under intensive systems.In New Zealand, cows must be able to move around the farm easily and graze without difficulty, also they must have a good disposition for an efficient milking operation (Holmes and Wilson, 1987).

In this report results are presented from a preliminary study on the first evaluations for TOP in New Zealand friesian cows.

MATERIAL AND METHODS

The traits incuded in the analysis are : adaptability to milking (AM), shed temperament (ST), milking speed (MS), overall opinion (OP), capacity (CA), rump angle (RA), rump width (RW), legs (LE), udder support (US), fore udder (FU), rear udder (RU), front teat placement (FT), rear teat placement (RT), udder overall (UO) and dairy conformation (DC). The first four traits are assesed by the farmer and the remainder by an inspector. All traits are scored using a scale from 1 to 9, with extreme values corresponding to extreme phenotypes (Ahlborn-Brier et al. 1990).

Evaluations for TOP were made during the 1987-1988 season. There were 2320 records of first calving daughters of 245 Holstein-Friesian sires distributed in 283 herds. A sire model was used, where herds, inspectors and old and proven sires were treated as being fixed. Only young sires were treated as being random for the estimation of additive variances and covariances (Meyer 1986). Young sires were assumed unrelated for comparison with a further study where relationships will be included.

One of the assumed advantages of scoring linearly over descriptive classification is that the records can be analysed using continuous scales and mixed model methology (Thompson et al.1983). Accordingly no transformation to normalise the data was performed. Furthermore, a Kolmogorov - Smirnov test was applied to each trait and no significant departure from normality was found in the data.

A multitrait REML procedure was used to estimate the variances and covariances, applying an Expectation Maximization algorithm (Henderson 1984) after a canonical transformation (Thompson 1977; Shaeffer 1986). Initial values for the REML component of the analysis were obtained by the method of fitting constants, extending the algorithm described by Harville (1987) to the multivariate case. Traits scored by farmers were analysed separately from those scored by visiting inspectors.

RESULTS AND DISCUSSION

Phenotypic means and standard deviations are shown in Table 1, where it can be observed that means ranged between 4.27 to 5.75 , and standard deviations ranged from 0.60 to 1.76. Estimates of variance for legs, rump angle, rump width and front teat placement were the smallest. These estimates could reflect the true variation in the population or could indicate that there is a tendency by the scorers to regress their assessment towards the mean.

Table 1 Phenotypic Means and Standard Deviations*, Heritabilities Genetic and Phenotypic Correlations for Traits Other than Production in New Zealand Dairy Heifers.

	AD	ST	MS	OP	CA	RA	RW	LE	US	FU	RU	FT	RT	UA	DC
MN	5.4	5.5	5.7	5.7	5.3	5.4	5.2	5.2	5.3	4.9	4.9	4.2	5.2	4.8	5.3
SD	1.7	1.6	1.5	1.7	1.08	0.71	0.73	0.6	1.02	1.1	1.02	0.76	0.84	1.15	1.1
AD	.225	.743	.473	.688											
ST	.113	.039	.443	.711											
MS	.493	.435	.146	.562											
OP	.553	.688	.853	.155											
CA					.687	-.15	.326		.159	.166	.193			.203	.603
RA					.652	.133	-.16		-.16		-.18			-.20	-.337
RW					.162	.755	.287								.295
LE					.90	.917	.661	.25							
US					.944	.917	.427	.477	.567	.657	.609	.278	.159	.703	.376
FU					.622	.96	.359	.427	.815	.767	.521	.269		.705	.384
RU					.901	.92	.275	.862	.798	.427	.276	.241	.16	.692	.402
FT					.119	.057	.176	.151	-.36	-.15	-.05	.443	.386	.469	.153
RT					.659	.851	.451	.543	.965	.925	.978	-.08	.204	.214	
UA					.733	.95	.422	.354	.993	.918	-.10	-.32	.593	.319	.488
DC					.589	.95	.216	.475	.815	.909	.187	-.01	.825	.805	.869

* Means and standard deviations in first two rows.

**Phenotypic correlations above the diagonal, heritabilities on the diagonal and genetic correlations below the diagonal.

Heritabilities, genetic and phenotypic correlations are presented in Table 1. Heritabilities ranged from 0.039 for shed temperament, to 0.86 for dairy conformation. Wickham (1979) found estimates for temperament (0.11 and 0.12) and milking speed (0.08 and 0.15) for Friesian cows in New Zealand fitting the effect of sire in a simple random linear model. However the scale of measurement in that study included three categories only with 93% to 97% of the observations occuring in two of them. Some of the estimated heritabilities for the rest of the traits are similar to those found for Australian Holstein-Friesian cows (Meyer et al. 1985; Smith 1987), for the same trait scored on a different scale or for an alternative measurement of the trait (eg. mammary system and udder overall), while the values for dairy conformation, capacity and fore udder were considerably larger than for those reported for the same or related traits.

Most of the initial values obtained for the genetic correlations involving rump angle had values outside the defined parameter space and after re-estimation, by means of bivariate analysis with the rest of the traits, were close to one. This could be explained by the small estimated variance for rump angle, while the covariances were relatively large. Excluding rump angle the traits that had a higher genetic correlation with dairy conformation were udder traits which means that improvement in these traits will result in cows with more desirable dairy conformation.

The phenotypic correlations were calculated using all the observations, and only those found to be significantly different from zero are considered in Table 1. Phenotypic correlations had values between -0.33 (for dairy conformation and rump angle) and 0.705 (for udder overall and fore udder). The large positive phenotypic correlation between adaptability to milking and shed temperament, their small genetic correlation and the small heritability of shed temperament would suggest that there is an important environmental factor affecting both traits in the same direction, being stronger on shed temperament.

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