Copyright is owned by the Author of the thesis. Permission is given for a copy to be downloaded by an individual for the purpose of research and private study only. The thesis may not be reproduced elsewhere without the permission of the Author.

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

A thesis presented in partial fulfilment
of the requirements for the degree of
Doctor of Philosophy
at Massey University

Goluhewage Sirimathie Wewala

1984

ABSTRACT

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

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

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

ACKNOWLEDGEMENTS

The author is especially grateful to Professor R.D. Anderson and Professor A.L. Rae for the invaluable guidance and supervision given to her during this study.

Sincere thanks are due to Dr. R.J. Brook and Professor B.I. Hayman for their advice and encouragement.

Particular thanks are due to Dr. G.A. Wickham for his suggestions in certain aspects of the thesis, Dr. S.J. Byrne for her advice in using the optimization routines and Dr. W.C. Smith and Mr. R. Laird for providing the pig data.

The author appreciates the financial assistance given to her through the Helen E. Akers Scholarship, the Farmers Union Scholarship and G.O. Anstiss Scholarship.

Finally, very special thanks are due to her husband and her parents for their support and encouragement.

TABLE OF CONTENTS

			page
ABSTRACT	Γ		ii
ACKNOWLE	EDG EM EN TS		iv
TABLE OF	F CONTENTS	3	V
LIST OF	TABLES		х
CHAPTER	1.	INTRODUCTION	1
CHAPTER	2.	LITERATURE REVIEW	4
22	2.1.1. 2.1.2. 2.1.2.1. 2.1.2.2.	Estimation of variance components Balanced data Unbalanced data Henderson's methods Maximum likelihood and restricted maximum likelihood methods Quadratic estimation of variance components	4 4 5 5 7
		Estimation of variance and covariance	12
	2.2.1.	components : Maternal effects models Equating covariances between relatives to their expected values	12
	2.2.2.	Method of least squares	15
	2.2.3.	Restricted maximum likelihood approach	17
	2.2.4.	Analysis of reciprocal crosses	19

	2.3.	Prediction techniques	22
	2.3.1.	Best prediction	22
	2.3.2.	Best linear prediction (Selection index)	23
	2.3.3.	Best linear unbiased prediction	25
	2.4.	Prediction techniques : Maternal effects models	28
	2.4.1.	Selection index for direct and maternal genetic components	28
	2.4.2.	Best linear unbiased prediction	30
	2.4.3.	Using linear functions of breed means	44
	2.5.	Evidence for the existence of maternal effects	46
	2.5.1.	Swine	48
	2.5.2.	Cattle	49
	2.5.3.	Sheep	52
	2.5.4.	Laboratory species	54
CHADTED	2	MATHEMATICAL AND CTATICTICAL DELIMINADIEC	56
CHAPTER	3.	MATHEMATICAL AND STATISTICAL PRELIMINARIES	56
	3.1.	Maximum likelihood estimation under the assumption of a normal distribution	56
	3.2.	Computing the inverse of a numerator relationship matrix	59
	3.3.	Vec operator and Kronecker product of matrices	64
	3.4.	Inverse and determinant of a partitioned matrix	65

CHAPTER	4.	MAXIMUM LIKELIHOOD METHOD FOR ESTIMATING VARIANCE COMPONENTS WITH UNBALANCED DATA IN A MATERNAL EFFECTS MODEL	69
	4.1.	A maternal effects model	69
	4.2.	Estimation of the parameters : A single-trait setting	71
	4.2.1.	The likelihood function under normality assumptions	73
	4.2.2.	The structure of the variance-covariance matrix	75
	4.2.3.	The inverse of the variance-covariance matrix	78
	4.2.4.	The determinant of the variance-covariance matrix	82
	4.2.5.	Generating the equations	83
	4.2.5.1.	Generating the linear equations (system (4.7))	83
	4.2.5.2.	Generating the nonlinear equations (system (4.8))	90
	4.2.6.	Constrained maximization of the likelihood function	95
	4.2.7.	Large-sample variances for the estimates of fixed effects and variance components	99
	4.3.	Estimation of the parameters: A multiple-trait setting	100
	4.3.1.	The structure of the variance-covariance matrix	103
	4.3.2.	The inverse of the variance-covariance matrix	105
	4.3.3.	Generating the equations	108
	4.3.3.1.	An algorithm to compute the system of	110
		equations used for obtaining solutions for the fixed effects	

	4.3.3.2.	An algorithm to compute the equations used to obtain the ML estimates of variance components	113
CHAPTER	5.	BEST LINEAR UNBIASED PREDICTION OF DIRECT AND MATERNAL GENETIC EFFECTS	119
	5.1.	BLUP equations for predicting direct genetic values for all animals and the maternal genetic values of their corresponding dams	121
	5.2.	The inverse of the variance-covariance matrix of direct and maternal genetic values	124
	5.2.1.	Expressions for D _i	126
	5.2.2.	Generating G_{∞}^{-1}	129
	5.3.	The inverse of the variance-covariance matrix of the residual effects	132
	5.4.	A multiple-trait setting	134
	5.4.1.	Generating the inverse of the	1 36
		variance-covariance matrix of the genetic effects	
	5.4.2.	Inverting the variance-covariance matrix of the residual effects	143
CHAPTER	6.	A STUDY OF MATERNAL EFFECTS IN WEANING WEIGHTS OF SHEEP AND SWINE	146
	6.1.	Sheep	146
	6.2	Suine	158

CHAPTER 7.	DISCUSSION	168
APPENDIX 1	An algorithm for computing A_{i11} for a single-trait setting	173
APPENDIX 2	An algorithm to generate the determinant of the variance-covariance matrix	180
APPENDIX 3	An algorithm for computing $\underset{\sim}{\mathbb{A}}_{i11}$ for a multiple-trait setting	185
APPENDIX 4	Examples to illustrate the inversion of the variance-covariance matrix of direct and maternal genetic effects (single-trait)	187
APPENDIX 5	An example to illustrate the inversion of the variance-covariance matrix of the direct and maternal genetic effects (multiple-trait)	202
BIBLIOGRAPHY		206

LIST OF TABLES

Table 4.1	Expressions for θ_i and U_i in (4.4)	71
Table 4.2	Coefficients (f_{hm}) associated with the variance parameters (θ_m) in the phenotypic variance and the full-sib, paternal half-sib, dam-offspring and sire-offspring covariances	73
Table 4.3	Values of f _{hm}	109
Table 6.1	ML solutions for fixed effects resulting from a constrained optimization using weaning weights of Romney lambs	149
Table 6.2	ML estimates of variance components resulting from a constrained optimization using weaning weights of Romney lambs	150
Table 6.3	Standard errors of the ML solutions for the fixed effects	151
Table 6.4	Standard errors of ML estimates of the variance components	153
Table 6.5	A comparison of estimates obtained from this study and that of Ch'ang and Rae (1970,1972)	154
Table 6.6	A comparison of the estimates of the effects of birth and type of rearing, age of dam, sex and age at weaning on weaning weights of Romney lambs	155
Table 6.7	Adjustment factors for Romney lamb weaning weights	157

Table	6.8	ML estimates of variance components resulting from an unconstrained optimization using 8-week weights of Yorkshire pigs	160
Table	6.9	ML solutions to the equations corresponding to the fixed effects resulting from an unconstrained optimization using 8-week weights of Yorkshire pigs	161
Table	6.10	ML estimates of the variance components resulting from a constrained optimization using 8-week weights of Yorkshire pigs	163
Table	6.11	ML solutions to the equations corresponding to the fixed effects resulting from a constrained optimization using 8-week weights of Yorkshire pigs	164
Table	6.12	A comparison of three sets of variance components for 8-week weights of Yorkshire pigs	166
Table	A1	Pedigree information of the example	187
Table	A2	The exact inverse of $\frac{G}{2}$ for example 1	197
Table	A3	Comparison of the exact and the approximate g^{-1} for example 2	201
Table	A 4	Pedigree information of example 3	202
Table	A5	The inverse of G for example 3	205