GENETIC PARAMETER ESTIMATION OF PRODUCTION AND REPRODUCTION TRAITS OF THE ELSENBURG DORMER STUD

by

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4. **GENETIC PARAMETER ESTIMATES FOR REPRODUCTION AND SURVIVAL**

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1

GENERAL INTRODUCTION

Sheep breeding enterprises have to be dynamic in implementing changes to meet the changing demands of consumers, changing environments and economic realities. Accurate genetic parameter estimates for a breed are needed before changes are made to selection criteria to meet ever changing needs. Continuous advances in computer technology, hard- and software, as well as improved statistical methods allow animal breeders to continually re-evaluate genetic parameters to better define selection strategies for the modern market.

The Elsenburg Dormer stud was started at the Elsenburg college of Agriculture in 1940 by crossing Dorset Horn rams with German Merino ewes and has been evaluated previously by Van der Merwe (1976) and Van Wyk *et al.* (1993a, b, c, d, e). Each evaluation, although done on the same stud is unique in the sense that more data are available each year. The methods of the analysis were also completely different due to vast improvements in methodology during the 17 years separating the first two studies. Inbreeding had increased as no animals were introduced to the flock until after the second study. The initial cross of Dorset Horn rams and German Merino ewes were between totally unrelated breeds. The inbreeding coefficients of the base animals can therefore be considered to be zero. Inbreeding coefficients were calculated and the mean yearly inbreeding is shown in Appendix A. The effect of inbreeding does not form part of this study but was documented by Van Wyk *et al.* (2002).

A period of eight years has elapsed since the study of Van Wyk *et al.* (1993a, b, c, d, e). Although there have been no real quantum leaps in methodology developments, much is being made of Gibbs sampling, employing a Bayesian approach. There are, however, questions as to its practical application in large data sets. The first aim of this study was to compare Gibbs sampling to REML in terms of estimates obtained and practicality of use utilising data from the Elsenburg Dormer stud.

Secondly, an updated genetic analysis (genetic parameter estimates) for the stud was considered important especially in view of inevitably increased inbreeding.

Reproduction is of vital importance in any sheep breeding enterprise. A third objective was therefore to estimate genetic parameters for reproduction traits not considered by Van Wyk *et al.* (1993a, b, c, d, e). Van der Merwe (1976) assessed aspects of reproduction but his methods have become completely outdated.

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GENETIC PARAMETER ESTIMATES USING GIBBS SAMPLING AND RESTRICTED MAXIMUM LIKELIHOOD (REML)

2.1 Introduction

The primary goal of animal breeding is to genetically improve production and reproduction traits in animal populations through selection. Selection is often based on best linear unbiased prediction (BLUP) of breeding values at present. Prediction of breeding values relies on knowledge about variance components, which in practice need to be estimated. Animal breeders have focused mainly on algorithms, yielding point solutions. Restricted Maximum Likelihood (REML) estimation of (co)variance components has become the method of choice for many. The development of alternative computing procedures, such as Markov Chain Monte Carlo (MCMC) linked to increased computing capacity enable the analysis of problems considered computationally too demanding previously (Hofer, 1998).

Bayesian inference in a Gaussian model using Gibbs sampling was considered by Gelfand *et al.* (1990) and applied to animal breeding by Wang *et al.* (1993,1994), Jensen *et al.* (1994), Sorensen *et al.* (1994), Van Tassell *et al.* (1995) and Magnabosco *et al.* (2000). The Gibbs sampler, a numerical integration technique that allows inferences about joint or marginal densities (Geman & Geman, 1984), is the most often used MCMC method in animal breeding. Gibbs sampling is based on elementary properties of Markov chains. The Gibbs sampler generates random variables from a marginal distribution indirectly without having to calculate the posterior density. It generates or simulates a sample with mean and variance that reflects the actual population values. Accuracy can be improved by simply simulating a large enough sample (Casella & George, 1992). The number of equations to be solved is no longer a problem due to inexpensive comprehensive computer hardware. The use of Gibbs sampling allows calculation of the point estimates and confidence intervals for the posterior distributions of the variance components, without approximations or adherence to normality assumptions (Van Tassell *et al.*, 1995).

The aim of this study was to investigate the feasibility of using Gibbs sampling techniques to estimate genetic parameters for birth- and weaning weight in the Elsenburg Dormer sheep stud. Gibbs sampling methods will be compared to traditional methods (REML). Additional information, gained by using the Bayesian method, will also be presented.

2.2 Materials and Methods

2.2.1 Environment

Data were obtained from the Dormer sheep stud of the Elsenburg Agricultural Development Institute near Stellenbosch comprising a flock of approximately 110-180 breeding ewes. The farm Elsenburg is situated in the Boland sub region of the Winter Rainfall Region, about 50 km east of Cape Town and 10 km north of Stellenbosch at an altitude of approximately 177 m above sea level (33° 51' S, 18° 30' E). The farm has an average annual predominantly winter (June - August) rainfall of 642 mm. Average maximum (minimum) summer and winter temperatures are 25.4 °C (12.6 °C) and 17.9 °C (8.1 °C).

2.2.2 Animals

The Dormer sheep breed originated from a small number of animals (two first-cross rams and 77 first-cross ewe lambs). It can be assumed that, being a cross between two unrelated breeds (Dorset Horn x German Merino), the inbreeding coefficients of the base animals were zero. The stud was closed since its inception with all replacements coming from within. However, in 1997 three totally unrelated rams were introduced in an effort to lower the level of inbreeding

During the early stages, selection emphasis was mainly on visually assessed conformation. In later years, rams and ewes were selected on the reproduction performance and fecundity of their dams and high lamb growth. Additionally, replacements had to comply with the breed standards required for purebred Dormer registration. Sires were used for two consecutive years while ewes were not replaced after any specific time but were culled for failure to lamb in subsequent seasons, excessive teeth wear or other abnormalities.

Flock management was designed to ensure uniform treatment as far as practically possible. Each ram was paddock-mated to 25-30 identified ewes. Limited cross-fostering of orphaned lambs apparently did take place and may have some effect on the validity of the data. This however, is a universal problem in sheep breeding research and almost impossible to control effectively.

2.2.3 Data

The data used were collected in the period 1941 to 1999. A total of 10701 birth weight and 9242 weaning weight records, the progeny of 265 sires (Table 2.1), were available after editing.

According to Johnson & Garrick (1990), crossbred performance records should be excluded or analysed as a separate contemporary group to remove the possible average effect of heterosis. Records of the two years 1941 and 1942 represent the progeny of the initial crosses and also, since sires were nested within these first two years, these records were excluded. A more detailed description of the genetic base (history), selection criteria and management of the stud is given by Van Wyk *et al.* (1993a).

The data analysed consisted of records of birth (BW) and weaning weights (WW). All weaning weights were adjusted *a priori* to a 100-day equivalent using the following formula:

$$\frac{(\text{WW - BW})}{(\text{Age at weaning})} \text{ X } 100 + \text{BW}$$

This was necessary since prior to 1970 records were adjusted to a 100-day equivalent before recording. A description of the data used in the analyses is given in Table 2.1

Table 2.1 Description of data used (1943 to 1999)

	Birth weight	Weaning weight
Number of records	10701	9242
Number of sires	265	265
Average weight (kg)	3.91	29.06
Standard deviation (kg)	0.83	6.38
Coefficient of variation (%)	21.30	21.96

2.2.4 Statistical analysis

The SAS procedure for general linear models (PROC GLM) was used to test which fixed effects should be included in the models for the REML and Bayesian methods (SAS, 1988). The effects that were included were all highly significant ($P < 0.001$).

Mixed linear sire models, with relationships, were fitted to obtain variance components and breeding values using MTDFREML software (Boldman *et al.*, 1995). Sex (male or female), age of dam (2 to 7 and older), birth status (single, twins or triplets) and years (1943 through 1999), were considered as fixed effects and the effect of sire as random. The effects are neither random nor fixed but merely effects when considered from a Bayesian point of view.

A sire model was fitted since an animal model would also have to make provision for maternal and permanent environmental effects (Van Wyk *et al.*, 1993b). Fitting an animal model with existing software at our disposal and using Gibbs sampling was not possible.

The model fitted for both methods was as follows:

$$y_i = X_i \beta + Z_i u_i + \varepsilon_i$$

Where

y_i = a nx1 vector of observed records,

β = a px1 vector of "fixed effects" (sex, age of dam, birth status and year effect) with association matrix X,

u_i = the "random effect" of the i^{th} sire with association matrix Z and

ε_i = vector of residual effects.

Bayesian analysis of the univariate models for the two traits were carried out using the Gibbs sampling algorithm (Geman & Geman, 1984; Gelfand *et al.*, 1990) to obtain uncorrelated samples from the joint posterior density and subsequently from the marginal posterior densities of all the unknowns in the model. Samples were generated using MATLAB software. The full conditional posteriors were updated after every iteration. Multiple chains were run, i.e. 11 000 of the Gibbs sampler to obtain draws from the posterior distributions of the model parameters given the data. The first 1 000 draws of each chain were discarded, and then every 10th draw was saved. By saving every 10th draw, the chain yielded a posterior sample of 1 000 uncorrelated draws. All posterior analyses were based on these 1 000 draws, giving a full Bayesian solution to all the mixed linear model parameters without convergence problems (Pretorius & Van der Merwe, 2000; Van der Merwe *et al.*, 2001; Van der Merwe & Pretorius, 2002).

To compare the results with traditional methods, estimates of genetic parameters and variance components were also obtained by restricted maximum likelihood methods, using the MTDFREML software (Boldman *et al.*, 1995) also fitting a sire model. The search for the maximum of the likelihood was considered completed, if the variance of the Simplex function values was less than $10^{-9.}$ Restarts were performed to ensure global convergence. Since the output of MTDFREML is formulated in terms of an animal model, the heritability estimates had to be recomputed, i.e. four times the heritability stated on the output (Boldman *et al.*, 1995). The sire solutions are for transmitting ability or one-half of predicted breeding values.

2.3 Results and Discussion

2.3.1 Estimates of fixed effects

Non-genetic factors referred to by frequentists as fixed effects and by Bayesians as nuisance parameters were estimated and bear mentioning. Sex, birth status, age of dam and year of birth made a significant ($P<0.01$) contribution to a lamb's BW and WW.

Results of the estimates of the "fixed effects" for WW using REML and Gibbs sampling are given in Table 2.2 The effect of year is not shown, as this would make the table too extensive (56 years).

Table 2.2 Estimates of fixed effects for WW from REML (SE) and Gibbs sampling.

				95% Confidence interval for Gibbs sampler	
Effect	REML	(SE)	Gibbs sampler	Lower	Upper
Sex					
Male	2.602	0.099	2.599	2.414	2.781
Female	0.000	0.000	0.000	0.000	0.000
Birth status					
Single	7.651	0.286	7.660	7.101	8.243
Twins	2.159	0.105	2.168	1.633	2.729
Triplets	0.000	0.000	0.000	0.000	0.000
Age of dam (year)					
2	-0.975	0.206	-0.971	-1.388	-0.589
3	0.706	0.108	0.697	0.284	1.067
4	1.402	0.152	1.397	0.993	1.785
5	1.207	0.166	1.208	0.765	1.633
6	0.632	0.194	0.621	0.154	1.075
7+	0.000	0.000	0.000	0.000	0.000

The estimates from the REML and Gibbs methods were calculated for each effect and are given as deviations from zero. The two methods yielded similar point solutions for which confidence intervals can be calculated. In addition, the Gibbs method produces posterior distributions. Confidence intervals for example show that single lambs are expected to have WW's between 7.1 and 8.2 kg heavier than triplets.

2.3.2 Variance components

Estimates of variance components with standard errors or confidence intervals and resulting heritabilities with standard errors or confidence intervals obtained from REML analyses and Gibbs sampling are presented in Table 2.3. The 95% confidence intervals, in the case of the Gibbs sampling results, were calculated from the posterior distributions of the variance parameters.

Table 2.3 Estimates of variance components and (SE) or 95% confidence intervals for BW and WW obtained from REML and Gibbs sampling

	REML		GIBBS			
	BW	WW	BW	95% CI	WW	95% CI
σ^2_s	0.029 (0.007)	0.849 (0.007)	0.029	(0.022 - 0.043)	0.894	(0.558 - 1.293)
σ^2_e	0.457 (0.006)	21.353 (0.319)	0.458	(0.446 - 0.470)	21.364	(20.699 - 22.079)
σ^2_p	0.487 (0.093)	22.203 (0.635)	0.486	(0.474 - 0.506)	22.257	(21.257 - 23.372)
h^2	0.240 (0.056)	0.153 (0.047)	0.234	(0.180 - 0.341)	0.161	(0.101 - 0.231)

σ^2_s = sire variance; σ^2_e = residual variance; σ^2_p = phenotypic variance; h^2 = heritability, 95% CI = 95% confidence intervals; BW = birth weight; WW = weaning weight.

It is evident from Table 2.3 that the Gibbs estimates of variance components for BW and WW are close to those of REML. This is not surprising since, as shown by Harville (1974), when uniform or "flat" priors are assigned to the vector of fixed effects and variance components, the modes of the marginal posterior distributions are close to the REML estimates.

The obtained heritability estimates are lower than most of the values reported in the literature when fitting animal models (Fogarty, 1995; Snyman *et al.*, 1995, 1998a; Neser *et al.,* 2001) but correspond with Van Wyk *et al.* (1993b) on the same Dormer stud also fitting a sire model but without taking relationships into account. The authors reported a large maternal effect when an animal model was fitted, with considerable higher heritability estimates than using a sire model.

A heritability estimate (h^2), when calculated from the variance components σ^2_s and σ^2_p generated by the Gibbs sampler, is a point estimate (Table 2.3), with a probability distribution (Figure 2.3). The traditional REML method yields only point estimates for the sire and residual variance components of the model. The Gibbs sampling method has the advantage of not only giving a point estimate (mode of the sire and mean of residual variance) but also the posterior distributions of the sire and residual effects. Confidence intervals can also be calculated for all parameters with posterior distributions.

Figures 2.1, 2.2 & 2.3 show posterior distributions, obtained from Gibbs sampling, for the residual, sire variance and heritability estimates of WW, respectively. Similar distributions were obtained for BW but are not shown.

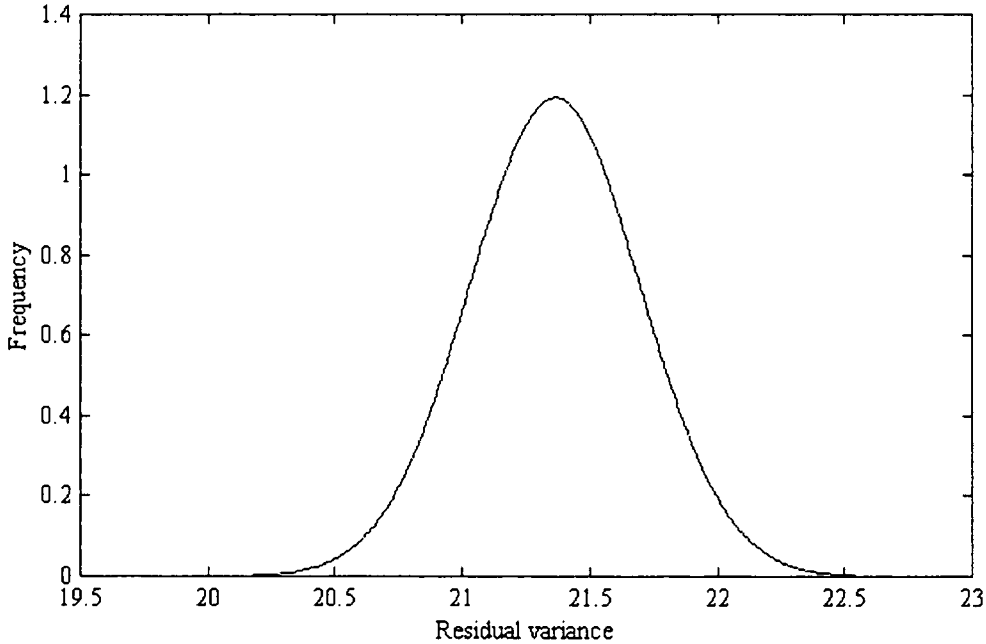

Figure 2.1 Marginal posterior density for the residual variance of WW (kg^2)

The residual variance of WW (21.36) obtained from Gibbs sampling (Table 2.3) is similar to the 21.35 obtained from REML procedures. Bayesian estimation using

Gibbs sampling produces more than a single point estimate. The variance (21.36) obtained using the Gibbs sampling has a probability distribution (Figure 2.1) with 95% confidence intervals of 20.70 and 22.01. The distribution and 95% confidence intervals for the variance give the researcher a more comprehensive insight into the data.

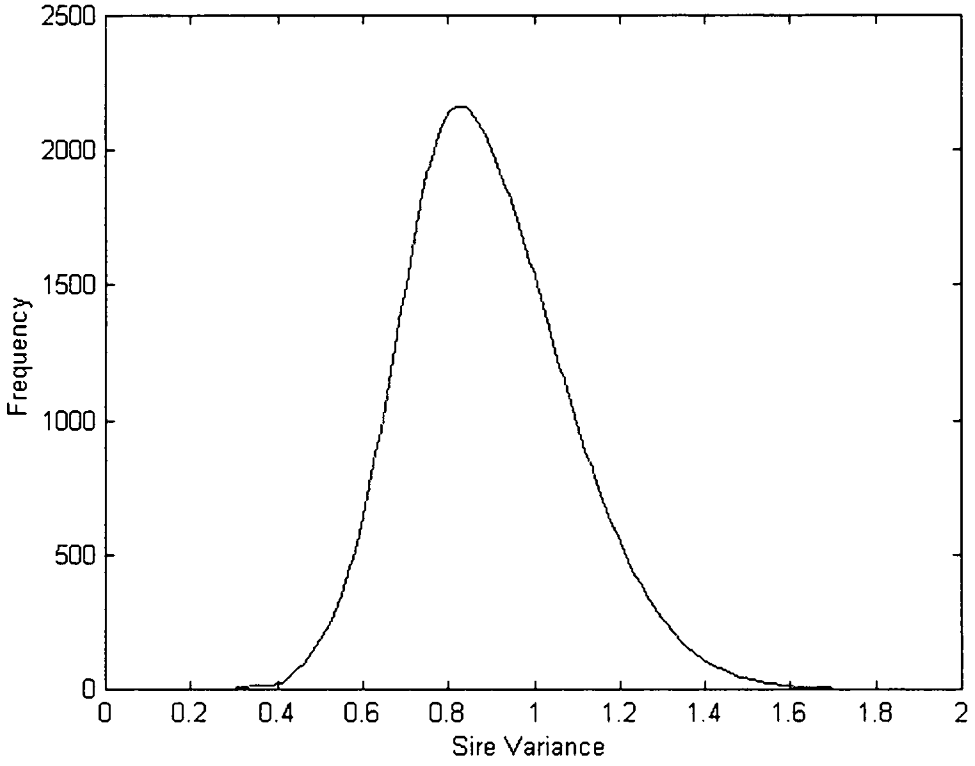

Figure 2.2 Estimated posterior density of the sire variance.

The sire variance estimate of WW using REML (0.85) is comparable with 0.89, the mode of the sire variance obtained from the Gibbs sampling method (Table 2.3). The distribution of the sire variance is skew (Figure 2.2), necessitating the use of the mode rather than the mean.

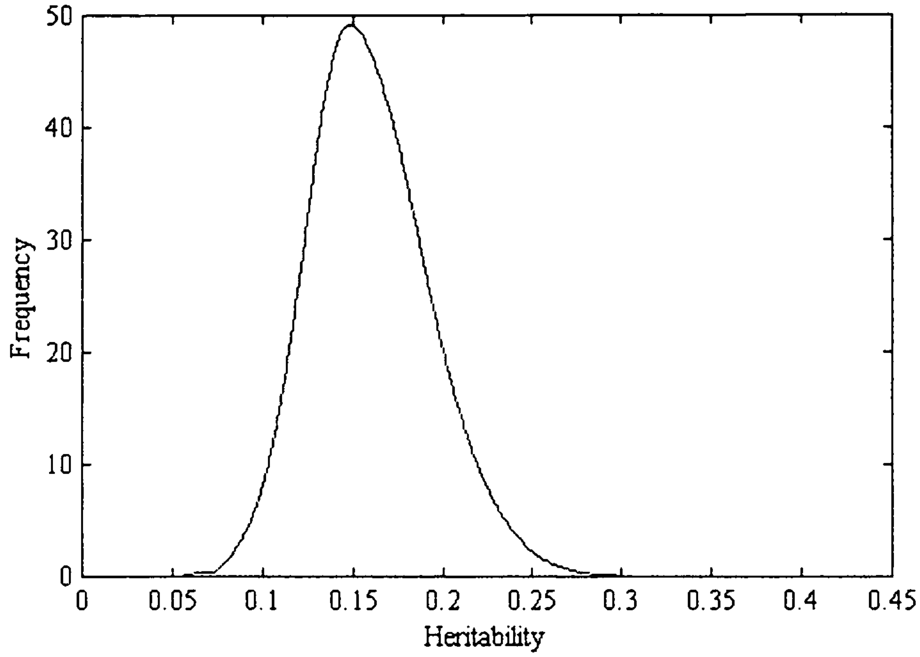

Figure 2.3 Estimated marginal posterior density of h^2 for WW

Heritability for WW was 0.16 and 0.15 from the mean and mode respectively when using the Gibbs sampler with 95% confidence intervals of 0.10 to 0.23. The point estimate for h^2 was 0.15 using REML.

Heritability, when estimated using REML, is a point estimate of "highest probability". This point estimate (parameter) leaves the impression that h^2 is a constant which is a misconception. The term parameter conveys an understanding of something in a given range rather than a fixed value. Expressing h^2 as a mean or mode with a distribution helps keep the perspective that the h^2 of a trait could vary as shown by the posterior distribution (Figure 2.3).

2.3.3 Breeding values

A key difference between REML/BLUP predictions and Bayesian inference is the treatment of the variance components. To obtain the BLUP estimates, the variance components are fixed at a single value, ignoring uncertainty associated with estimating their values. The Bayesian analysis incorporates this uncertainty by averaging over the plausible values of the variance components. This property makes it a more appropriate method of analysis, since these components are very important in evaluating the breeding value of sires.

An advantage of using the Bayesian method of breeding value estimation is that distributions for breeding values are given. An example is presented in Figure 2.4 for two sire's posterior distributions of breeding values with equal means (-0.05) but different variances.

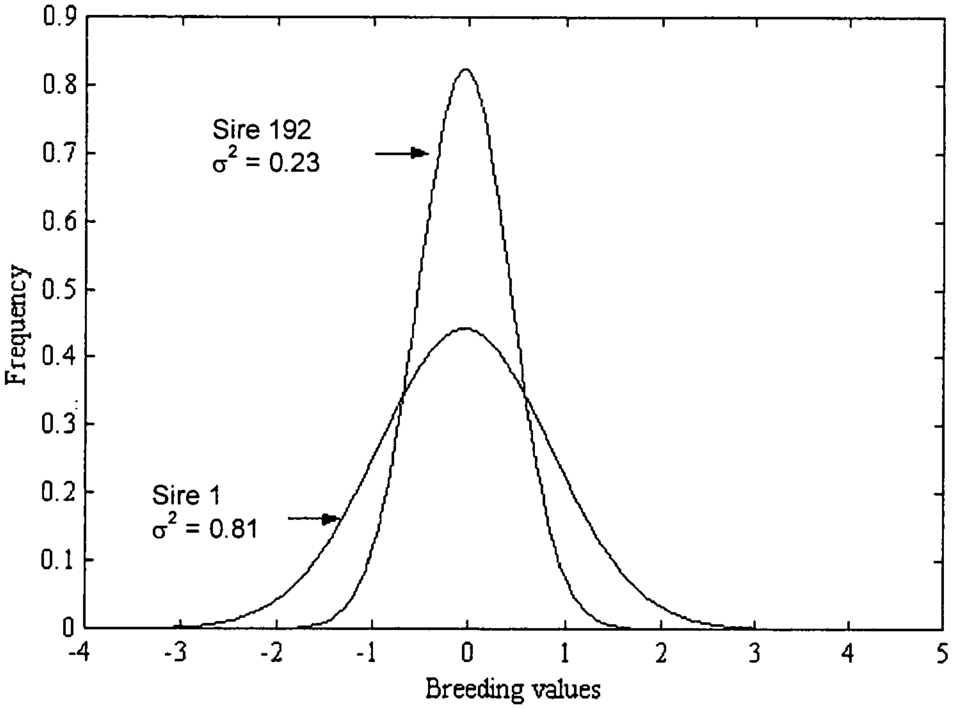

Figure 2.4 Posterior distribution of breeding values for two sires with equal means (-0.05) but different variances.

Both sires have a breeding value of -0.05. When the sire's distributions are taken into account sire 1 has a variance larger than sire 192. Sire 1 can be expected to produce progeny with a wider range of WW's than sire 192. Sire 192 will be more consistent with less difference between highest and lowest as indicated by Figure 2.4. The 95% confidence intervals for sire 1 and 192 were respectively -1.85 to 1.7 and -1.02 to 0.86.

Figure 2.5 shows two sires with equal variance (0.3) but different means. Sire 125 and 222 had means of 1.72 and -0.04 respectively. Sire 125 would be selected if higher WW's were sought. Sire 222's best progeny would have WW on par with sire 125's worst progeny. As can be seen from figures 2.4 & 2.5 the mean and variance of breeding values can be taken into account when selecting future sires. This extra information would not be available when using REML.

The correlations between breeding values obtained from Gibbs sampling and REML for WW and BW were 0.99943 and 0.99948 respectively. Both methods will result in the same sires being selected.

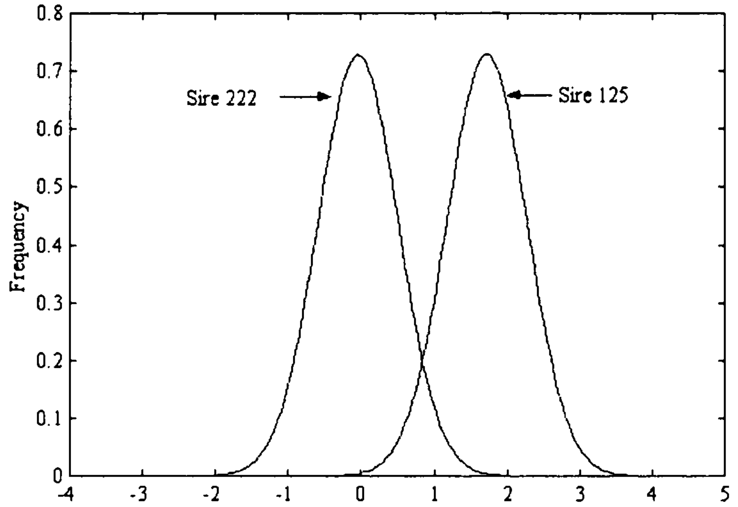

Figure 2.5 Posterior distribution of breeding values for sires (125 and 222) with equal variance (0.3) but different means.

2.4 Conclusions

From the results it is clear that all the available information about the variable being predicted is contained in the posterior distribution when applying the Bayesian method. The point estimates are consistent with those obtained using REML. More information is supplied using the Bayesian method. The Bayesian method was, however, far more time consuming than REML (some 120 hrs vs. approximately 3 min). Future developments in faster algorithms for the MCMC methods will undoubtedly close this considerable time gap.

Distributions for "fixed" and "random" effects when using the Gibbs sampler give the researcher a fuller picture and understanding of the data. REML procedures are much faster but do not yield as much information. Ranking of animals was in this case not affected by the method of analysis. The posterior distributions given by a Bayesian method could, however, prove useful in final selection especially when information on relatives is sparse.The Bayesian and frequentist schools of inference are well established. Choice of method should be related to whether there are solutions in one school that the other does not offer, how easily the problems are solved and to how comfortable the scientist feels with the particular way of expressing the results (Blasco, 2001).

3

GENETIC PARAMETER ESTIMATES FOR PRE-WEANING GROWTH TRAITS

3.1 Introduction

Breeding programs designed to improve production require accurate identification of genetically superior animals for selection purposes. A suitable statistical model is needed for the estimation of (co)variance components. These estimates are used in turn to estimate genetic parameters such as heritabilities of the traits, genetic correlations between traits and breeding values for the animals.

When pre-weaning growth traits are included in the selection goal, a further partitioning of the genetic effects is necessary. A negative correlation may exist between the direct and maternal effect of the dam. The dam contributes to the phenotypic value of her offspring not only by a sample half of her genes (direct effect) but also through her genes responsible for maternal effects (Ligda *et al.*, 2000). This correlation, if negative, can hamper selection progress and must be carefully considered when selecting breeding animals for replacement. Animals with superior breeding values, for both direct and maternal effects concerning a trait, should be identified and selected.

Pre-weaning growth trait studies have previously been done for the Elsenburg Dormer stud (Van Wyk *et al.*, 1993 a, b). The current study has subsequent years of data (1991 to 1999) added and has utilised hard- and software development by using new statistical programs.

The objective of this study was to estimate genetic parameters for pre-weaning growth traits of the Elsenburg Dormer sheep stud for use in the development of appropriate breeding objectives and improvement programs.

3.2 Materials and Methods

3.2.1 Data

Data used in this study consisted of records of the Elsenburg Dormer sheep stud collected from 1941 to 1999. A detailed description of the management and animals used is given in Chapter 2.

Data were edited to exclude the following: incomplete records, records of stillborn lambs and records from years 1941 and 1942 (as discussed in chapter two). These exclusions represented less than 7 % of the original data. Dam ages greater than seven and birth status greater than three were coded to seven and three respectively before analysis. The final data set included 10701 birth weight (BW) and 9242 weaning weight (WW) records, the progeny of 265 sires and 2400 dams. Of the dams 17.08% had one lambing record, 49.42% had two to five lambing records, 30.42% had six to ten lambing records and 3.08% had eleven or more lambing records. A description of the fixed effects, sex of lamb (male or female), birth status (single, twins and triplets or more) and age of dam (2 to 7+ years) used in the analysis is given in Table 3.1. A summary of the year effect is not given in the table due to the excessive length, but rather in Appendix B.

Table 3.1 Description of the fixed effects of the data used from 1943 to 1999.

Fixed Effect	*n*	BW (kg) Mean (SD)	*n*	WW (kg) Mean (SD)
Sex				
Male	5208	4.03 (0.86)	4455	30.38 (6.76)
Female	5493	3.79 (0.79)	4787	27.84 (5.75)
Birth status				
Single	3735	4.30 (0.87)	3386	32.49 (5.80)
Twins	6533	3.72 (0.73)	5542	27.16 (5.80)
Triplets	433	3.37 (0.69)	314	25.56 (6.25)
Age of dam (year)				
2	2569	3.68 (0.80)	2222	28.44 (6.43)
3	2521	3.88 (0.81)	2178	29.46 (6.12)
4	2152	3.94 (0.81)	1888	29.53 (6.51)
5	1593	4.05 (0.83)	1380	29.10 (6.49)
6	1010	4.12 (0.83)	852	28.74 (6.22)
7+	856	4.03 (0.88)	722	28.83 (6.49)
No of sires	265		265	
No of dams	2400		2400	
Total	10701	3.91 (0.83)	9242	29.06 (6.38)

n = No of records; SD = Standard deviation; BW = birth weight; WW = weaning weight.

3.2.2 Statistical analyses

The statistical analysis was divided into three consecutive steps. Firstly, the significance of fixed effects was tested conducting least squares analyses of variance using the GLM procedure of SAS (1988) leaving only significant effects in the model.

The second step was the estimation of (co)variance components for each trait. This was obtained using the ASREML program (Gilmour *et al.*, 1999) fitting univariate animal models. Six general forms of mixed-models were fitted and are presented in Table 3.2. Convergence was considered to have been obtained when the variance of the -2log likelihoods in the simplex was less than $1\text{x}10^{-6}$. Tests of significance of each random effect were performed using log likelihood ratio tests after deleting each random effect (excluding residual) from the model. An effect was considered significant when its inclusion in the model caused a significant increase in the log likelihood. A Chi-square distribution for $\alpha = 0.05$ and one degree of freedom was used as the critical test statistic (3.841). When –2 times the difference between log likelihoods was greater than 3.841 the inclusion of the effect was considered significant. When differences between log likelihoods were not significant the model with the fewest random effects were chosen.

The third and final step was to estimate (co)variance components and breeding values using the ASREML program (Gilmour *et al.*, 1999) by fitting a bivariate model for the traits BW and WW. Starting values for the (co)variance components were obtained from the univariate models fitted in step two. By fitting bivariate models the covariances and correlations between birth- and weaning weight could be examined.

Table 3.2 Six models describing the random effects used.

Model	Random Effects	(Co)variance components
1	Animal	σ^2_a
2	Animal + PE	$\sigma^2_a + \sigma^2_{PE}$
3	Animal + Maternal	$\sigma^2_a + \sigma^2_m$
4	Animal + Maternal + σ_{am}	$\sigma^2_a + \sigma^2_m + \sigma_{am}$
5	Animal + Maternal + PE	$\sigma^2_a + \sigma^2_m + \sigma^2_{PE}$
6	Animal + Maternal + PE + σ_{am}	$\sigma^2_a + \sigma^2_m + \sigma^2_{PE} + \sigma_{am}$

Animal = Direct animal effect; Maternal = Maternal effect; PE = Permanent environmental effect due to the dam; σ_{am} = Covariance between animal and maternal effect; σ^2_a = Additive direct animal variance; σ^2_m = Maternal variance; σ^2_{PE} = Permanent maternal environmental variance.

Additive direct and maternal effects were assumed to be normally distributed with mean zero and variances $A\sigma^2_a$ and $A\sigma^2_m$ respectively, where A is the numerator relationship matrix and σ^2_a and σ^2_m are additive direct and maternal variances respectively. Permanent environmental maternal and residual effects were assumed to be normally distributed with mean 0 and variances $I_d\sigma^2_{PE}$ and $I_n\sigma^2_e$ respectively, where I_d and I_n are identity matrices with orders equal to the number of dams and records, respectively, and σ^2_{PE} and σ^2_e are permanent environmental maternal and residual variances, respectively. Additive direct, additive maternal and permanent environmental maternal variances were also expressed as proportions of the phenotypic variance (h^2_a, m^2 and c^2_{pe}).

3.3 Results and Discussion

3.3.1 Fixed effects

All the fixed effects (sex, birth status, age of dam and year of birth) were significant ($P<0.001$). The solutions for the fixed effects are given in Table 3.3 excluding those for year. The solutions for years can be seen in Appendix C

Table 3.3 Fixed effects solutions and standard errors for birth weight and weaning weight respectively.

		BW	WW
Fixed effect		Solutions (SE)	Solutions (SE)
Age of dam			
	2	0.000 (0.000)	0.000 (0.000)
	3	0.321 (0.017)	1.688 (0.137)
	4	0.447 (0.019)	2.337 (0.140)
	5	0.514 (0.021)	2.145 (0.162)
	6	0.563 (0.025)	1.607 (0.190)
	7	0.581 (0.028)	0.780 (0.211)
Birth status			
	1	0.000 (0.000)	0.000 (0.000)
	2	-0.690 (0.014)	-5.446 (0.106)
	3	-1.218 (0.036)	-7.416 (0.293)
Sex			
	1	0.000 (0.000)	0.000 (0.000)
	2	-0.269 (0.012)	-2.618 (0.093)

Solutions as deviations (+ or -) from first level of effect given as zero; (SE) = standard error
BW = birth weight; WW = weaning weight.

The fixed effects were as expected: birth weights were heaviest for older dams, birth weights for triplets were lighter than those for twins which in turn were lighter than singles while male lambs were heavier than females. Weaning weight increased with age of dam up to 4 year olds and then decreased, single lambs were heavier than twins and twins heavier than triplets, while male lambs were heavier than females. This is in accordance with findings from others (Van Wyk *et al.,* 1993a and Saatci, 1999).

3.3.2 Random effects

The log likelihoods obtained for each trait under the six different models of analyses and the most appropriate model (in bold) from log likelihood ratio tests are given in Table 3.4. The most appropriate model for birth weight and weaning weight included additive direct and maternal effects, the genetic covariance between direct and maternal effects as well as permanent environmental effects (Model 6).

Table 3.4 Log likelihoods obtained for pre-weaning growth traits under six different models with the 'best' model in bold.

Model	(Co)Variance components	BW	WW
1	σ^2_a	-1114.60	-18783.20
2	σ^2_a + PE	-705.15	-18680.50
3	$\sigma^2_a + \sigma^2_m$	-678.83	-18673.70
4	$\sigma^2_a + \sigma^2_m + \sigma_{am}$	-669.05	-18671.70
5	$\sigma^2_a + \sigma^2_m$ + PE	-643.96	-18658.10
6	$\sigma^2_a + \sigma^2_m + \sigma_{am}$ + PE	**-637.25**	**-18656.00**

Chi^2 for $\alpha = 0.05$ and 1 df. = 3.841

σ^2_a = Additive direct animal variance; σ^2_m = Maternal variance; σ^2_{pe} = Permanent environmental variance due to the dam; σ_{am} = Covariance between animal and maternal effect; BW = birth weight; WW = weaning weight.

3.3.2.1 (Co)variance components and heritability estimates

Genetic parameters obtained by fitting the most appropriate models for birth weight (BW) and weaning weight (WW) from univariate and bivariate analyses are given in Table 3.5. Published heritability estimates for birth- and weaning weight fitting the same random effects are summarised in Table 3.6.

Table 3.5 Genetic parameters for BW and WW.

	Univariate analysis		Bivariate analysis	
	BW (SE)	WW (SE)	BW (SE)	WW (SE)
σ^2_a	0.11	2.57	0.11	2.84
σ^2_m	0.13	2.61	0.13	2.62
σ_{am}	-0.04	-0.86	-0.05	-1.06
σ^2_{pe}	0.07	1.86	0.07	1.92
σ^2_e	0.27	16.68	0.26	16.68
σ^2_p	0.53	22.86	0.53	23.00
CV(%)	13.18	14.05	13.16	14.05
h^2_a	0.21 (0.03)	0.11 (0.02)	0.22 (0.03)	0.12 (0.03)
m^2	0.24 (0.03)	0.11 (0.02)	0.24 (0.03)	0.11 (0.02)
c^2_{pe}	0.13 (0.02)	0.08 (0.01)	0.13 (0.02)	0.08 (0.01)
r_{am}	-0.37 (0.08)	-0.33 (0.13)	-0.38 (0.08)	-0.38 (0.12)

SE = standard error; σ^2_a = direct variance; σ^2_m = maternal variance; σ_{am} = covariance between direct and maternal effect; σ^2_{pe} = permanent maternal environmental variance; σ^2_e = residual variance: σ^2_p = phenotypic variance; CV(%) = coefficient of variation; h^2_a = direct heritability; m^2 = maternal heritability; c^2_{pe} = permanent maternal environmental variance as a proportion of phenotypic variance and r_{am} = genetic correlation between animal effects.

The direct heritability (h^2_a) estimates for birth- and weaning weight using bivariate analyses was 0.22 and 0.12 respectively. There was no change in the h^2_a when using the bivariate analysis compared to the univariate model (Table 3.5). Numerous estimates for birth- and weaning weight have been reported in literature fitting different models regarding the random effects. For comparison reasons, only estimates from studies fitting the same models were considered. The h^2_a estimate for birth weight (0.22) was higher than most estimates reported in the literature for other sheep breeds fitting the same model (Table 3.6) except for the 0.39 found in Hampshire sheep (Tosh & Kemp, 1994). The estimate for weaning weight (0.12), although on the lower end of the scale, was within the range of reported values (0.05 – 0.20).

Maternal variance (σ^2_m) for BW and WW as estimated by the bivariate model was 0.13 and 2.62 respectively. This for all purposes was unchanged with respect to the univariate models (there were only changes at the 3rd decimal). Direct maternal variance ratios (m^2) were 0.24 and 0.11 for BW and WW, respectively. These m^2

values fall within the range of 0.06-0.31 found in literature (Table 3.6). The decrease in maternal estimates with age is in accordance with literature values.

Table 3.6 Estimates of direct heritability (h^2_a), maternal heritability (m^2), permanent environment of the dam (c^2_{pe}), and direct-maternal genetic correlation (r_{am}) from the literature for birth and weaning weight of lambs.

h^2_a	m^2	c^2_{pe}	r_{am}	Literature source	Breed
BW					
0.39	0.22	0.37	-0.56	Tosh & Kemp (1994)	Hampshire
0.12	0.31	0.27	-0.35	Tosh & Kemp (1994)	Polled Dorset
0.07	0.13	0.32	-0.13	Tosh & Kemp (1994)	Romanov
0.17	0.10	0.08	0.17	Yazdi *et al.* (1997)	Baluchi
0.09	0.17	0.09	0.09	Mousa *et al.* (1999)	Composite
0.11	0.10	0.12	0.35	Neser *et al.* (2001)	Dorper
0.05	0.05	0.00	-0.55	Boujenane & Kansari (2002)	Timahdite
0.25	0.12	0.08	-	Matika *et al.* (2003)	Sabi
0.22	**0.24**	**0.13**	**-0.38**	**Present study**	**Dormer**
WW					
0.16	0.14	0.27	-0.57	Tosh & Kemp (1994)	Hampshire
0.21	0.19	0.18	-0.42	Tosh & Kemp (1994)	Polled Dorset
0.05	0.06	0.21	-0.39	Tosh & Kemp (1994)	Romanov
0.19	0.09	0.10	-0.55	Neser *et al.* (2000)	SA Mutton Merino
0.20	0.10	0.08	-0.58	Neser *et al.* (2001)	Dorper
0.16	0.11	0.23	0.06	Ap Dewi *et al.* (2002)	Welsh Mountain
0.13	0.06	0.07	-	Matika *et al.* (2003)	Sabi
0.12	**0.11**	**0.08**	**-0.38**	**Present study**	**Dormer**

BW = birth weight; WW = weaning weight

3.3.2.2 Genetic correlation between animal effects

There is conflicting evidence in the literature on the magnitude and direction of the genetic correlation (r_{am}) between direct and maternal animal effects. This correlation is of major concern in animal breeding. According to Maniatis & Pollot (2002) these correlations could be negative for reasons other than the existence of a true antagonistic biological relationship between direct and maternal genetic effects. It could be the result of the structure of the data available (Lewis & Beatson, 1999). However, negative estimates of the direct-maternal correlations are a common feature of most recent analysis of field data. In Romanov sheep it varied between –0.99 and 0.99 (Maria *et al.*, 1993). In the present study the genetic correlation between direct and maternal effects (r_{am}) was -0.38 for both traits. The value of -0.38 for birth weight was intermediate compared to literature values (-0.56 to +0.35) when fitting the same model (Table 3.6). The r_{am} of -0.38 for BW is similar to that of -0.35 found by Van Wyk *et al.* (1993b) also on the Dormer, using part of the same data set. The estimate for weaning weight was higher (-0.38) than the value of -0.16. The difference in r_{am} between the two studies can in part be explained by the fact that permanent maternal environment was not included in the previous study by Van Wyk *et al.* (1993b).

3.3.2.3 Permanent maternal environmental effects (PE).

Permanent maternal environmental effects had an important influence on lamb birth- and weaning weights accounting respectively for 13% and 8% of the phenotypic variance. These values, although on the lower end of the scale, are within the range reported by the literature fitting the same random effects (0.08 to 0.37) (Table 3.6). The permanent environmental effect due to the dam can be ascribed to the uterine environment, the effect of multiple births and on milk production. As lambs became increasingly independent of the dam, these effects decline in importance (Tosh & Kemp, 1994).

3.3.2.4 Correlations between traits

The direct, maternal, permanent environmental and phenotypic correlations between birth- and weaning weight are presented in Table 3.7.

The direct genetic correlation estimate between birth and weaning weight of the present study (0.41) is in close agreement with the weighted average of 0.39 (Fogarty, 1995) and the 0.45 of Mousa *et al.* (1999) but higher than the 0.27 of Neser *et al.* (2001) and the 0.05 obtained by Simm *et al.* (2002). The maternal genetic correlation of 0.54 is in accordance with Neser *et al.* (2001) indicating that selection based on maternal bv's for weaning weight will lead to an increase in birth weight. A large increase in birth weight is undesirable and could get a negative weighting if multiple trait selection procedures are to be followed.

The moderate permanent maternal environmental correlation estimate could be due to the high percentage of multiple births in the stud. The phenotypic correlation represents the combined effect of the genotype and environmental influence.

Table 3.7 Correlations between birth (BW) and weaning weight (WW) obtained from bivariate analysis.

	BW x WW
Residual, r_e	0.30 (0.02)
Direct, r_a	0.41 (0.11)
Maternal, r_m	0.53 (0.10)
Phenotypic, r_p	0.39 (0.02)
Permanent maternal environmental, r_{PE}	0.56 (0.08)

r_e = correlation between BW and WW for residual effect; r_a = correlation between BW and WW for direct animal effect; r_m = correlation between BW and WW for maternal effect; r_p = phenotypic correlation between BW and WW; r_{PE} = correlation between BW and WW for permanent maternal environmental effect;

3.4 Conclusions

Generally, estimates of heritability found in this study indicate that sufficient additive genetic variance exists in pre-weaning growth traits, which should lead to response from selection. The negative direct-maternal correlation should be taken into account when using estimated breeding values for selection. The antagonism between these two effects need further investigation to determine the nature of the negative correlated response.

The correlations of BW with WW for direct, maternal, phenotypic and permanent maternal environmental effects were 0.56 and lower. Selection of replacement animals on birth weight alone is very seldom recommended since higher birth weight could increase the rate of dystocia.

4

GENETIC PARAMETER ESTIMATES FOR REPRODUCTION AND SURVIVAL

4.1 Introduction

Reproduction and survival, collectively referred to as Darwinian fitness, are undoubtedly the most important traits in any sheep production system regardless of environment.

Breeding programs designed to improve reproduction efficiency in sheep require accurate identification of superior animals for selection purposes. Reproduction is a complex trait made up of components such as fertility, litter size, lamb survival and number of lambs born and weaned per ewe exposed to the ram (Snyman *et al.*, 1997). Many studies have been done on various sheep breeds to obtain genetic parameters and heritability estimates for these components (Fogarty, 1995).

Among reproductive traits, litter size (number of lambs born per ewe lambing) has most often been used as a selection criterion. Reported heritability estimates for litter size are generally higher than those of other reproductive traits such as fertility or lamb survival (Rao & Notter, 2000).

Lamb survival is a complex trait influenced by the lamb's own ability to survive and by its dam's rearing ability (Burfening, 1993). Selection for lamb survival would depend on there being genetic variation (direct and /or maternal) for this trait.

Total weight of lamb weaned per ewe joined (TWW) combines all the traits mentioned previously into a single entity. TWW is the best single measure of the productivity of a flock (Snyman *et al.*, 1997). Selection for TWW would favour animals with larger litters, able to rear all lambs born to an acceptable weaning weight.

An appropriate model is needed to estimate genetic (co)variance parameters for the calculation of heritabilities and correlations for TWW. The heritability and correlation estimates would determine whether or not the trait, TWW, could be used effectively in a selection program to increase production efficiency.

The objective of this study was to determine genetic parameters for litter size, number of lambs weaned, TWW at first and subsequent parities over the reproductive lifetime of the ewe as well as lamb survival in an effort to find the best way of increasing reproduction performance genetically.

4.2 Materials and Methods

4.2.1 Data

Data from the Elsenburg Dormer sheep stud collected from 1941-1999 were used in the analyses. The general management is described in Chapter 2.

The ewe reproduction traits considered were: litter size defined intwo ways, viz number of lambs born dead or alive per ewe lambing (NLB) and number of lambs born alive per ewe lambing (NLBA), number of lambs weaned (NLW) per ewe lambing and total weight of lamb weaned (TWW).

Lamb survival (whether a lamb born alive was dead or alive at weaning) was considered a trait of the lamb.. A description of the data used is summarized in Table 4.1.

Total weight of lamb weaned per ewe joined (TWW) was calculated for each ewe. All weaning weights were corrected to a 100-day weight equivalent. This, as explained earlier, was necessary, as early records were pre-corrected to 100 days before recording. The weaning weights were also corrected for the effects of sex, year and sire. The corrections were done by subtraction of the solutions obtained from a univariate model with the effects included. Only ewes joined in three consecutive years were used.

TWW was calculated for each ewe over three lambing opportunities (TWW1, TWW2 and TWW3). TWW2 and TWW3 represented the accumulated total weights up to and including the second and third joinings.

The data were not corrected for birth status of the ewe and birth year. These variables were include as fixed effects in the models.

Table 4.1 Description of data used in analyses for reproduction traits and survival

Trait	No of lambs	No of ewes	No of service sires	Mean	CV%	Range
Ewe traits						
TWW1 (kg)	1531	1402	261	34.9	16	0-99.5
TWW2 (kg)	3342	1402	261	53.8	16	0-151.2
TWW3 (kg)	5420	1402	261	83.6	13	22.2-218.6
NLB (dead or alive)	10814	2343	276	1.5	36	1-3
NLBA (alive)	10412	2325	276	1.5	36	1-3
NLW	8889	2343	276	1.1	69	0-3
Lamb trait						
Survival	10701	1319	257	0.9	40	0-1

NLB = number of lambs born dead or alive; NLBA = number of lambs born alive; NLW = number of lambs weaned; TWW1 TWW2 and TWW3 are accumulated total weight of lamb weaned for first, second and third parity respectively; CV% = Coefficient of variation.

Ewes with no record of weaning weights for the three consecutive years were eliminated from the data. Table 4.1 shows the range of TWW for the 1402 ewes that had three consecutive parities. Some ewes did not wean lambs in their first and second lambing opportunities. This accounts for the ranges of TWW1 and TWW2 starting at 0. The mean TWW increased from 34.9 to 83.6 over the three lambing opportunities. TWW3 as expected had the highest range, from 22.2 to 218.6, while TWW1 had the lowest range of 0 to 99.5.

4.2.2 Statistical analysis

Univariate animal models with birth status of ewe, age of dam and year as fixed effects and random effects additive direct, maternal, permanent maternal environmental, service sire (except TWW) and covariance between animal and maternal effect as random were tested to determine the best model for estimation of (co)variance components.

Tests of significance of each random effect were performed using log likelihood ratio tests after adding subsequent random effects (excluding residual) from the model. An effect was considered significant when its inclusion in the model caused a significant increase in the log likelihood. Changes in log likelihood was not the only criteria used to determine the best model, the biological feasibility of the model was also taken into account.

Estimates of (co)variance components for litter size, defined as number of lambs born dead or alive (NLB), and number of lambs born alive (NLBA) and NLW were obtained fitting these models using the ASREML program (Gilmour *et al.*, 1999).

For TWW, weaning weight records were firstly corrected for the known significant fixed effects of sex, year of birth and random direct additive bv of sire. The correction of the weaning weights were achieved by subtracting the solutions, obtained from univariate models with sex and year as fixed effects and sire as random effect, from the 100-day pre-corrected weaning weights. The models were rerun to test the effects of sex, year and sire. As expected these effects after correction were no longer significant ($P = 0.9$). Log likelihood ratio tests were used as before to determine the best models.

The second step was the estimation of (co)variance components using the ASREML program (Gilmour *et al.*, 1999) fitting univariate animal models indicated as best by the log likelihood ratio tests. Bivariate models for the traits TWW1, TWW2 and TWW3 in all pair combinations were also run to estimate correlations between the traits together with their appropriate standard errors. Starting values for the bivariate models were obtained from the univariate analyses.

Survival was analysed by fitting a univariate model with a logit link function to link the binomially distributed data to the normal distribution. Non-genetic factors included in the model were sex, birth status, age of dam, year of birth and birth weight as a co-variat. Survival was defined as a zero if the lamb was not alive at weaning and one if alive at weaning. Stillborn lambs were excluded.

4.3 Results and Discussion

The log likelihood of model six for NLB and NLBA was the highest and significantly ($P<0.05$) different to the other models but was rejected as the best model since the random maternal effect is from the contribution made by the grandmother of the lambs. The variance of this effect was also very low (0.001) and inclusion of the maternal variance component did not reduce the error variance but increased it when compared with model 4 for NLBA (model six = 0.237223; model four = 0.237180). The use of model six would only be appropriate when a significant log likelihood change is considered. It was felt, however, that for comparative and biological reasons model four should be used. Model four was also used for NLW. Rosati *et al.* (2002) also reported little evidence of maternal genetic effects on NLB and NLBA. Model four included the fixed effects of age of dam and year of birth and the random effects of direct animal, permanent maternal environmental and service sire.

When considering TWW, model one was significantly different ($P < 0.05$) to a model containing only fixed effects. All changes in log likelihoods for the models with random effects included were smaller than one, thus the simplest model was considered to be the "best" model. This was the case for TWW1, TWW2 and TWW3. Model one with the following fixed effects; birth status of the ewe and year of the ewes birth and additive direct random effect were used to estimate genetic parameters for TWW for the three consecutive parities.

Model seven with additive direct animal, maternal and permanent maternal environmental random effects as described in Table 4.2 was used for the analysis of survival. The fixed effects of sex, birth status, age of dam, year of birth and birth weight as a co-variable were all significant ($P<0.05$).

Results of the log likelihoods for the reproduction and survival traits are presented in Table 4.2

While (co) variance components and heritabilities for the reproduction and survival traits are given in Table 4.3.

Heritability estimates for direct genetic effect of NLB and NLBA was 0.10. This was in accordance with the mean heritability estimate for litter size of 0.10 and a mean coefficient of variation of 36% reported in literature (Fogarty, 1995). The coefficient of variation for NLB and NLBA in this study was 36.2 and 36.3% respectively, indicating potential for genetic improvement. Table 4.4 gives a summary of reported heritabilities subsequent to Fogarty's (1995) review and verifies previous findings.

Permanent maternal environmental variance and service sire variance as a proportion of phenotypic variance were 0.013 and 0.005 for NLB and 0.008 and 0.007 for NLBA, respectively. The contribution of permanent maternal environmental and service sire to the phenotypic variance was thus negligible. Rosati *et al.* (2002) reported the variance of ewe-mate (service sire) as 0.01 and taken as a proportion of total phenotypic variance would also be negligible.

The direct heritability for NLW was low at 0.03, which is typical of values, found in literature (0.00-0.10; see Table 4.2).

Table 4.2 Log likelihoods obtained for reproduction traits and survival under nine different models (with the model used in bold.)

Model	(Co)Variance components	TWW2	TWW3	TWW4	NLB	NLBA	NLW	SURV
F	Only fixed effects	-4885.30	-5405.66	-5729.55	972.84	1031.26	-1396.68	-30654.5
1	σ^2_a	**-4880.70**	**-5400.34**	**-5726.72**	1037.30	1084.43	-1379.22	-30191.2
2	$\sigma^2_a + \sigma^2_{PE}$	-4880.70	-5400.34	-5726.74	1038.61	1084.84	-1374.51	-30020.0
3	$\sigma^2_a + \sigma^2_{ssire}$	-	-	-	1038.86	1086.99	-1376.74	-
4	$\sigma^2_a + \sigma^2_{PE} + \sigma^2_{ssire}$	-	-	-	**1040.13**	**1087.41**	**-1372.00**	-
5	$\sigma^2_a + \sigma^2_m$	-4880.36	-5400.28	-5726.72	1037.30	1084.41	-1378.95	-30177.5
6	$\sigma^2_a + \sigma^2_m + \sigma_{am}$	-4880.28	-5400.24	-5726.83	1044.16	1090.68	-1375.38	-30169.2
7	$\sigma^2_a + \sigma^2_m + \sigma^2_{PE}$	-4880.36	-5400.28	-5726.74	1038.61	1084.84	-1374.51	**-30018.3**
8	$\sigma^2_a + \sigma^2_m + \sigma^2_{PE} + \sigma_{am}$	-4880.28	-5400.24	-5727.27	1042.98	1088.96	-1373.76	-30016.9

Chi^2 for $\alpha = 0.05$ and 1 df. = 3.841

σ^2_a = Additive direct animal variance; σ^2_m = Maternal variance; σ^2_{PE} = Permanent maternal environmental variance; σ^2_{ssire} = Random effect of service sire; σ_{am} = Covariance between animal and maternal effect; TWW1,2 & 3 = total weight of lamb weaned for first second and third parity; NLB = number of lambs born dead or alive; NLBA = number of lambs born alive; NLW = number of lambs weaned; SURV = born alive and survived to weaning.

Table 4.3 Genetic parameters for reproduction traits and survival.

	Traits						
	NLB	NLBA	NLW	TWW1	TWW2	TWW3	SURV
σ^2_a	0.028	0.027	0.016	53.43	142.20	161.01	0.105
σ^2_m	-	-	-	-	-	-	0.000
σ^2_{pe}	0.004	0.002	0.012	-	-	-	0.289
σ^2_{ssire}	0.002	0.002	0.003	-	-	-	-
σ^2_e	0.242	0.238	0.468	411.118	870.493	1463.61	1.000
σ^2_p	0.275	0.270	0.498	464.600	1013.00	1625.00	3.673
h^2_a	0.103	0.101	0.031	0.115	0.140	0.099	0.027
(SE)	(0.016)	(0.016)	(0.011)	(0.047)	(0.050)	(0.048)	(0.018)
c^2_{pe}	0.013	0.008	0.023	-	-	-	0.077
(SE)	(0.009)	(0.009)	(0.008)	-	-	-	(0.017)
c^2_{ssire}	0.005	0.007	0.006	-	-	-	-
(SE)	(0.004)	(0.004)	(0.003)	-	-	-	-

TWW1,2 & 3 = total weight of lamb weaned for first, second and third parity; NLB = number of lambs born dead or alive; NLBA = number of lambs born alive; NLW = number of lambs weaned; SURV = born alive and survived to weaning; SE = standard error; σ^2_a = direct variance; σ^2_m = maternal variance σ^2_{pe} = permanent maternal environmental variance; σ^2_{ssire} = service sire variance; σ^2_e = residual variance; σ^2_p = phenotypic variance; h^2_a = direct heritability; c^2_{pe} = permanent maternal environmental variance as a proportion of phenotypic variance and c^2_{ssire} = service sire variance as a proportion of phenotypic variance.

Heritability estimates for direct and maternal genetic effect of survival were 0.03 and 0.00. This was in accordance with literature (0.04), when a mixed model least squares procedure was used (Burfening, 1993). Lopez-Villalobos & Garrick (1999) reported direct and maternal estimates of 0.01 and 0.04 for lamb survival and Cloete *et al.* (2001) reported a direct heritability estimate of 0.09 and "no evidence of maternal genetic variation" for lamb survival. The heritability of lamb survival is frequently estimated at basically zero (Yapi *et al.*, 1992; Konstantinov *et al.*, 1994; Olivier *et al.* 1998; Fogarty & Gilmour, 1998), causing analysts to assert that genetic progress would be unlikely. Cloete & Scholtz (1998) however reported response in survival after selection for maternal multiple rearing ability. The permanent environmental variance as a ratio of phenotypic variance was 0.08 which was slightly higher than the 0.04 reported by Cloete *et. al.* (2001). Table 4.4 summarises heritability estimates from literature for reproductive traits and survival in sheep.

Table 4.4 Summary of published heritability estimates of reproductive traits and survival in sheep

Breed	Method	h^2	Reference
NLB			
Romanov	REML	0.07	Maria (1995)
Segurena	REML	0.08	Analla *et al.* (1997)
Rambouillet Finnsheep	TAM, TSM	0.13 - 0.45	Matos *et al.* (1997)
Rasa Aragonesa	TAM	0.08 - 0.02	Altarriba *et al.* (1998)
Romney,Coopworth. Perendale	REML	0.07 - 0.14	Davis *et al.* (1998)
Boutsico	REML	0.06 - 0.03	Kominakis *et al.* (1998)
SA Merino	TSM	0.17 - 0.31	Olivier *et al.* (1998)
Afrino	TSM	0.42	Snyman *et al.* (1998a)
Hungarian Merino	REML	0.01 - 0.07	Nagy *et al.* (1999)
Rambouillet	REML	0.01 - 0.17	Okut *et al.* (1999)
Rambouillet	REML	0.05 - 0.02	Lee *et al.* (2000)
Various	REML	0.11 - 0.23	Hagger (2000)
Chios	REML	0.16	Ligda *et al.* (2000)
Suffolk, Polypay, Targhec	REML	0.09 - 0.11	Rao & Notter (2000)
Various	REML	0.07 - 0.12	Bromley *et al.* (2001)
Dorset, Finnsheep, Rambouillet, Suffolk, Targhee	REML	0.10	Rosati *et al.* (2002)
Dormer	REML	0.10	**Present study**
NLW			
Various	REML	0.00 - 0.10	Okut *et al.* (1999)
Various	REML	0.02 - 0.05	Bromley *et al.* (2001)
Dorset, Finnsheep, Rambouillet, Suffolk, Targhee	REML	0.01	Rosati *et al.* (2002)
Dormer	REML	0.03	**Present study**
SURVIVAL			
Dormer	TSM	0.12	Konstantinov *et al.* (1994)
Merino	TSM	0.00	Olivier *et al.* (1998)
Afrino	TSM	0.02	Snyman *et al.* (1998a)
Dormer	REML(Logit)	0.03	**Present study**
TWW			
Various		0.08 - 0.19	Fogarty (1995)
Afrino, Merino	REML	0.05 - 0.22	Snyman *et al.* (1997, 1998b)
Various	REML	0.06 - 0.17	Okut *et al.* (1999)
Various	REML	0.00 – 0.10	Bromley *et al.* (2001)
Merino	REML	0.19	Olivier *et al.* (2001)
Merino	REML	0.21	Olivier *et al.* (2001)
Austr Merino	REML	0.15	Cloete *et al.* (2002)
Dormer	REML	0.10 - 0.14	**Present study**

NLB = number of lambs born; TSM = threshold sire model; TAM = threshold animal model; REML = Restricted Maximum Likelihood; NLW = number of lambs weaned; TWW = total weight of lamb weaned.

Direct heritabilities (h^2_a) of 0.12, 0.14 and 0.10 were obtained for TWW1, TWW2 and TWW3 respectively. These estimates are in accordance with the literature average value of 0.13 reported by (Fogarty, 1995). The obtained estimates also fall within the range of subsequent comparable studies by (Snyman *et al.*, 1997) of 0.05 to 0.22 and 0.15 by (Cloete *et al.*, 2002).

The estimates of variance and heritabilities obtained suggest that selection response for TWW is possible. The heritabilities can be considered medium to low for this very important trait.

Genetic and phenotypic correlations obtained from bivariate analysis between all pairs of TWW's are given in Table 4.5.

Table 4.5 Phenotypic and genetic correlations between TWW1, TWW2 and TWW3.

		TWW2	TWW3
TWW1	r_p	0.71 (0.01)	0.62 (0.02)
	r_g	0.90 (0.10)	0.99 (0.14)
	r_e	0.68 (0.02)	0.57 (0.02)
TWW2	r_p		0.83 (0.01)
	r_g		0.9995 (0.06)
	r_e		0.81 (0.01)

r_p = Phenotypic correlation; r_g = genetic correlation; TWW1, 2 & 3 = total weight of lamb weaned for first, second and third parity

The genetic correlations were all positive and high ranging from 0.90 to 0.9995. The correlation between TWW1 and TWW3 is virtually unity indicating that selection of superior animals using solutions obtained from direct estimates based on TWW at fist parity is possible. These correlations are similar to those of 0.61 to unity reported by Snyman *et al.* (1997).

4.4 Conclusions

Heritability of TWW was medium to low, at 10 - 14 %. Direct genetic correlations between first through third parities were positive and very high 0.900 to 0.999 and significant ($P \leq 0.01$)(i.e. more than three times the corresponding standard error). These results suggest that total weight of lamb weaned, which is a combined expression of traits such as fertility, prolificacy, lamb survival and lamb weaning weight, could be used as a selection criteria for reproductive efficiency of the flock.

The TWW from first through third parity were not independent and thus cannot be used as a measure of repeatability.

Selection for TWW would only be feasible for sheep enterprises with extensive record keeping (pedigrees, birth and weaning weights and dates) and access to customised, fast and accurate genetic parameter estimation facilities. These have, however, become essential for the modern stud breeder.

5

GENERAL CONCLUSIONS

Progress in computer technology, hard- and software, as well as improved and new statistical methods necessitate the re- and continued evaluation of data to assist in helping define selection strategies for sheep production. Mixed model and other methodologies have improved and developed over the last 20 years resulting in a vast range of statistical tools being available for the animal breeder.

Evaluation of these statistical procedures is necessary to determine their usefulness from a practical as well as scientific point of view. Model specification remains a "thorn in the animal breeders flesh" particularly as modern statistical procedures accommodate complicated models with many random and interaction effects.

This study showed that results from the Bayesian and frequentist schools did not differ, however the Gibbs sampling method used far more time. The added information about the genetic parameters distributions when using the Bayesian approach could be of use to the animal breeder. The decision whether or not to use Bayesian or frequentists methods should be based on solutions needed, ease of use and the scientists preference (Blasco, 2001).

The Elsenburg Dormer stud was initially evaluated by Van der Merwe (1976) then later by Van Wyk *et al.* (1993a, b, c, d, e) and now in this study. More sophisticated statistical procedures were used with each subsequent study necessitating the specification of new models. This study explored the use of a Bayesian approach and included the added random effects of permanent maternal environmental and service sire..

The negative covariance between direct and maternal effects still remains a vexing enigma, needing further elucidation. Animals with superior breeding values for both direct and maternal effects concerning a trait, should be identified and selected for breeding programs. Such animals are however scarce due to the high negative genetic correlation.

Total weight of lamb weaned, which is a combined expression of traits such as fertility, prolificacy, lamb survival and lamb weaning weight, could be used as a selection criteria for reproductive efficiency of the flock.

The Elsenburg Dormer stud is a valuable South African asset with accurate records from 1941 and should be maintained for further research and development of animal science in general and specifically to aid the Dormer breed in planning breeding strategies for the future.

Abstract

Genetic parameter estimates were compared using Gibbs sampling and REML methods. Variance components and resulting heritabilities of birth weight (BW) and weaning weight (WW) in the Elsenburg Dormer sheep stud were estimated using a conventional (REML) and a Bayesian (GIBBS sampling) approach. A sire model with relationships included were fitted in both cases. Data from 10701 lambs recorded from 1943 to 1999 were used in the analyses. Effects fitted as fixed were sex (male, female); birth status (single, twin, triplet); year (1943-1999) and age of dam (two to seven years, and older). Sire and residual were the only random effects fitted. The posterior means (h^2) of BW and WW were 0.24 and 0.15 for REML and 0.23 and 0.16 for the Bayesian method respectively. The heritability estimates obtained were of the same magnitude and in accordance with estimates found in the literature where sire models were used.

Genetic parameters for the pre-weaning growth traits BW and WW were also calculated from the (co)variance components estimated using the ASREML program by fitting univariate animal models. Log likelihood ratio tests were done to determine the appropriate mixed models. Bivariate models were also fitted for BW and WW using as starting values for the (co)variance components the values obtained from the univariate analysis. Fixed effects fitted were the same as in the previous section. The direct heritability (h^2_a) for BW and WW for the bivariate model was 0.22 and 0.12 respectively. The maternal effects (m^2) were 0.24 and 0.11 for BW and WW respectively. These m^2 values fall within the range 0.09 to 0.31 found in literature. The direct-maternal genetic correlations (r_{am}) of -0.38 and -0.38 for BW and WW were similar to those found in literature.

Genetic parameter estimates for reproduction traits, i.e. number of lambs born (NLB), number of lambs born alive (NLBA), number of lambs weaned (NLW), total weight

weaned (TWW) and survival traits were obtained using the ASREML program fitting univariate animal models. Data for TWW were pre-corrected for fixed and random effects of sex, year and sire respectively. An animal model with only the direct random effect of animal and fixed effects of birth status and birth year of the ewe was fitted. Direct heritability (h^2_a) estimates of 0.12, 0.14 and 0.10 were obtained for TWW1, TWW2 and TWW3 respectively.

Direct heritability (h^2_a) and (SE) estimates of 0.103 (0.016), 0.101 (0.016) and 0.031 (0.011) were obtained for NLB, NLBA and NLW respectively. Permanent maternal environmental variance components as proportions of phenotypic variance for the three traits were 0.013 (0.005), 0.008 (0.009) and 0.023 (0.008) respectively, with service sire variance as a proportion of phenotypic variance of 0.005 (0.004), 0.007(0.004) and 0.006 (0.003) respectively for the traits mentioned.

Heritability estimates for direct and maternal effect of survival were 0.03 (0.018) and 0.00 (0.00). Permanent maternal environmental variance as a proportion of phenotypic variance for survival was 0.077 (0.017).

It was concluded that Gibbs sampling could be of use to the animal breeder while the question of negative covariances between direct and maternal genetic effects still need further investigation. TWW could be used as selection criteria for reproductive efficiency.

Opsomming

Beramings van genetiese parameters is deur van Gibbs-monstering en REML-metodes te gebruik, vergelyk. Variansie-komponente en gevolglike oorerflikhede van geboortegewig (Ggew) en speengewig (Sgew) is in die Elsenburg-Dormerskaapstoet deur 'n konvensionele (REML) en 'n Bayes (GIBBS-monstering)-benadering beraam. 'n Vaarmodel met ingeslote verwantskappe is in beide gevalle gepas. Data van 10701 lammers, wat vanaf 1943 tot 1999 aangeteken is, is in die ontledings gebruik. Effekte wat as vas gepas is, was: geslag (manlik, vroulik); geboortestatus (enkel, tweeling, drieling); jaar (1943-1999) en ouderdom van moeder (twee tot sewe jaar, en ouer). Vaar en fout was die enigste toevallige effekte wat gepas is. Die posterior gemiddeldes (h^2) van Ggew en Sgew was onderskeidelik 0.240 en 0.153 vir REML en 0.234 en 0.161 vir die Bayes-metode. Die oorerflikheidsberamings wat verkry is, was van dieselfde omvang en in ooreenstemming met beramings in die literatuur waar vaarmodelle gebruik is.

Genetiese parameters vir die voorspeense groei-eienskappe Ggew en Sgew is ook bereken vanaf die (ko)variansie-komponente, beraam deur ASREML-deur die passing van 'n enkelveranderlike dieremodel. Log-aannneemlike verhoudingstoetse is gebruik om die geskikte gemengde modelle te bepaal. Dubbelveranderlike modelle is ook vir Ggew en Sgew gepas, deur die waardes wat van af die enkelveranderlike ontledding verkry is, as beginwaardes vir die (ko)variansie-komponente te gebruik. Vaste effekte wat gepas is, was dieselfde as in die vorige afdeling. Die direkte oorerflikheid (h^2_a) vir Ggew en Sgew vir die dubbelveranderlike model was onderskeidelik 0.22 en 0.12. Die maternale oorerflikhede (m^2) was onderskeidelik 0.24 en 0.11 vir Ggew en Sgew. Hierdie m^2-waardes val binne die omvang van 0.09 - 0.31 wat in die literatuur gevind word. Direk-maternale genetiese korrelasie (r_{am}) van –0.38 en –0.38 vir Ggew en Sgew onderskeidelik was dieselfde as dié wat in die literatuur gevind is. Genetiese parameterberamings vir vrugbaarheidseienskappe, i.e. aantal lammers gebore (ALG), aantal lammers lewendig gebore (ALLG), aantal lammers gespeen (ALS) en totale gewig gespeen (TGS); en oorlewings- (OORL) eienskappe is verkry deur die ASREML-program te gebruik waarin enkelveranderlike eienskappe gepas is. Data vir TGS was vooraf gekorrigeer vir die vaste en toevallige effekte van geslag, jaar en vaar onderskeidelik. 'n Dieremodel met slegs die direkte toevallige effek van dier, en vaste effekte van geboortestatus en geboortejaar van die ooi is gepas. Direkte oorerflikheid (h^2_a) en SF-beramings van 0.12 (0.05), 0.14 (0.05) en 0.10 (0.05) is onderskeidelik vir TgewS1, TgewS2 en TgewS3 verkry..

Direkte oorerflikheid (h^2_a) en SF-beramings van 0.103 (0.016), 0.101 (0.016) en 0.031 (0.011) is onderskeidelik vir ALG, ALLG en ALS verkry. Permanente maternale omgewingsvariansie as 'n proporsie van fenotipiese variansie vir die drie eienskappe was 0.013 (0.005), 0.008 (0.009) en 0.023 (0.008) onderskeidelik, met diensvaar-variansie as 'n proporsie van die fenotipiese variansie van onderskeidelik 0.005 (0.004), 0.007 (0.004) en 0.006 (0.003) vir genoemde eienskappe..

Oorerflikheidsberamings vir direkte en maternale effek van OORL was 0.03 (0.018) en 0.00 (0.00). Permanente maternale omgewingsvariansie as 'n proporsie van fenotipiese variansie vir OORL was 0.077 (0.017).

Gibbs-monstering kan van nut wees vir die diereteler. Negatiewe ko-variansies tussen direkte en maternale effekte benodig verdere ondersoek. TGS kan as 'n seleksie kriteria vir reproduksiedoeltreffendheid gebruik word.

REFERENCES

Altarriba, J.L., Varona, L., Garcia–Cortes L.A.& Moreno, C., 1998. Bayesian inference of variance components for litter size in Rasa Aragonesa sheep. *J. Anim. Sci.* 76, 23 - 28.

Analla, M., Munoz-Serrano, A. & Serradilla, J. M., 1997. Analysis of the genetic relationship between litter size and weight traits in Segurena sheep. *Can. J. Anim. Sci.* 77, 17 - 21.

Ap Dewi, I., Saatci, M. & Ulutas, Z., 2002. Genetic parameters of weights, ultrasonic muscle and fat depths, maternal effects and reproductive traits in Welsh Mountain sheep. *Anim. Sci.* 74, 399 - 408.

Blasco, A., 2001. The Bayesian controversy in animal breeding. *J. Anim. Sci.* 79, 2023 - 2046.

Boldman, K.G., Kriese, L.A., Van Vleck, L.D., Van Tassell, C.P. & Kachman, S.D., 1995. A manual for use of MTDFREML. A set of programs to obtain estimates of variances and covariances (DRAFT), U.S. Department of Agriculture, Agricultural Research Service.

Boujenane, I. & Kansari, J., 2002. Estimates of (co)variances due to direct and maternal effects for body weights in Timahdite sheep. *Anim. Sci.* 74, 409 - 414.

Bromley, C.M., Van Vleck, L.D. & Snowder, G.D., 2001. Genetic correlations for litter weight weaned with growth, prolificacy and wool traits in Columbia, Polypay, Rambouillet and Targhee sheep. *J. Anim. Sci.* 79, 339 - 346.

Burfening, P.J., 1993. Direct and maternal genetic effects on lamb survival. *Small Rum. Res.* 11, 267 - 274.

Casella, G. & George, E.I., 1992. Explaining the Gibbs Sampler. *Amer. Stat.* 46, 167 - 174.

Cloete, S.W.P., Greeff, J.C. & Lewer, R.P., 2001. Environmental and genetic aspects of survival and early body weight in Western Australian Merino sheep. *S. Afr. J. Anim. Sci.* 31, 123 - 130.

Cloete, S.W.P., Greeff, J.C. & Lewer, R.P., 2002. Heritability estimates and genetic and phenotypic correlations of lamb production parameters with hogget liveweight and fleece traits in Western Australian Merino sheep. *Aust. J. Agric. Res.* 53, 281 - 286.

Cloete, S.W.P. & Scholtz, A.J., 1998. Lamb survival in relation to lambing and neonatal behaviour in medium wool Merino lines divergently selected for multiple rearing ability. *Aust. J. Exp. Agric.* 38, 801 - 811.

Davis, G.H., Morris, C.A. & Dodds, K.G., 1998. Genetic studies of prolificacy in New Zealand sheep. *Anim. Sci.* 67, 289 - 297.

Fogarty, N.M., 1995. Genetic parameters for live weight, fat and muscle measurements, wool production and reproduction in sheep: a review. *Anim. Breed. Abstr.* 63, 101 - 143.

Fogarty, N.M. & Gilmour, A.R., 1998. Effect of season on lambing performance of selection and control flock ewes tested in an 8 - monthly lambing system, In: *Proc. 6th World Congr. Gen. Appl. Livest. Prod.*, 11 – 16 January 1998, Armidale, NSW, Australia. 27, 55 - 58.

Gelfand, A.E., Hills, S.E., Racine-Poon, A. & Smith, A.F.M., 1990. Illustration of Bayesian inference in normal data models using Gibbs sampling. *J. Amer. Stat. Assoc.* 85, 972 - 985.

Geman, S. & Geman, D., 1984. Stochastic relaxation, Gibbs distributions and the Bayesian restoration of images. *IEEE Trans. Pattern Anal. Machine Intelligence* 6, 721 - 741.

Gilmour, A.R., Cullis, B.R., Welham, S.J. & Thompson, R., 1999. ASREML- Reference manual. NSW Agriculture Biometric Bulletin 3, NSW, Agriculture, Orange Agricultural Institute, Forest Road, Orange 2800, NSW, Australia.

Hagger, C., 2000. Genetic and environmental influences on size of first litter in sheep, estimated by the REML method. *J. Anim. Breed. Genet.* 117, 57 - 64.

Harville, D.A., 1974. Bayesian inference for variance components using only error contrasts. *Biometrika* 61, 383 - 385.

Hofer, A., 1998. Variance component estimation in animal breeding: a review. *J. Anim. Breed. Genet.* 115, 247 - 265.

Jensen, J., Wang, W.S., Sorenson, D.A. & Gianola, D., 1994. Bayesian inference on variance and covariance components for traits influenced by maternal and direct genetic effects, using Gibbs sampler. *Acta Agric. Scand.* 44, 193 - 201.

Johnson, D.L. & Garrick, D.J., 1990. Data collection, processing and prediction of breeding values. *Proc. 4th World Congr. Gen. Appl. Livest. Prod.* XV, 337 - 346.

Kominakis, A., Rogdakis, E. & Koutsotolis, K., 1998. Genetic parameters for milk yield and litter size in Boutsico dairy sheep. *Can. J. Anim. Sci.* 78, 525 - 532.

Konstantinov, K.V., Erasmus, G.J. & Van Wyk, J.B., 1994. Evaluation of Dormer sires for litter size and lamb mortality using a threshold model. *S. Afr. J. Anim. Sci.* 24, 119 - 121.

Lee, J.W., Waldron, D.F. & Van Vleck, L.D., 2000. Parameter estimates for number of lambs born at different ages and for 18-month body weight of Rambouillet sheep. *J. Anim. Sci.* 78, 2086 - 2090.

Lewis, R.M. & Beatson, P.R., 1999. Choosing maternal-effect models to estimate (co)variances for live and fleece weight in New Zealand Coopworth sheep. *Livest. Prod. Sci.* 58, 137 - 150.

Ligda, C.H., Gavriilidis, G., Papadopoulos, T.H. & Georgoudis, A., 2000. Estimation of genetic parameters for production traits of Chios sheep using a multitrait animal model. *Livest. Prod. Sci.* 66, 217 - 221.

Lopez-Villalobos, N. & Garrick D.J., 1999. Genetic parameter estimates for lamb survival in Romney sheep. *Proc. NZ Soc. Anim. Prod.* 59, 121 - 124.

Magnabosco, C. De U., Lobo, R.B. & Famula, T.R., 2000. Bayesian inference for genetic parameter estimation on growth traits for Nelore cattle in Brazil, using the Gibbs sampler. *J. Anim. Breed. Genet.* 117, 169 - 188.

Maniatis, N. & Pollot, G.E., 2002. Genotype by environment interactions in lamb weight and carcass composition traits. *Anim. Sci.* 75, 3 - 14.

Maria, G.A., 1995. Estimates of variances due to direct and maternal effects for reproductive traits of Romanov sheep. *Small. Rum. Res.* 18, 69 - 73.

Maria, G. A., Boldman, K. G. & Van Vleck, L. D., 1993. Estimates of variances due to direct and maternal effects for growth traits of Romanov sheep. *J. Anim. Sci.* 71, 845-849.

Matika, O., Van Wyk, J.B., Erasmus, G.J. & Baker, R.L., 2003. Genetic parameter estimates in Sabi sheep. *Livest. Prod. Sci.* 79, 17 - 28.

Matos, C.A.P, Thomas, D.L., Gianola, D., Tempelman, R.J. & Young, L.D., 1997. Genetic analysis of discrete reproductive traits in sheep using linear and non-linear models: I. Estimation of genetic parameters. *J. Anim. Sci.* 75, 76 - 87.

Mousa, E., Van Vleck, L.D. & Leymaster, K.A., 1999. Genetic parameters for growth traits for a composite terminal sire breed of sheep. *J. Anim. Sci.* 77, 1659 - 1665.

Nagy, I., Solkner, J., Komlosi, I. & Safar, L., 1999. Genetic parameters of production and fertility traits in Hungarian Merino sheep. *J. Anim. Breed. Genet.* 116, 399 - 413.

Neser, F.W.C., Erasmus, G.J. & Van Wyk, J.B., 2000. Genetic studies of the South African Mutton Merino: growth traits. *S. Afr. J. Anim. Sci.* 30, 172 - 177.

Neser, F.W.C., Erasmus, G.J. & Van Wyk, J.B., 2001. Genetic parameter estimates for pre-weaning weight traits in Dorper sheep. *Small Rum. Res.* 40, 197 - 202.

Olivier, W.J., Snyman, M.A., Van Wyk, J.B. & Erasmus, G.J., 1998. Genetic parameter estimates for fitness traits in South African Merino sheep. *Livest. Prod. Sci.* 56, 71 - 77.

Olivier, W.J., Snyman, M.A., Olivier, J.J., Van Wyk, J.B. & Erasmus, G.J., 2001. Direct and correlated responses to selection for total weight of lamb weaned in Merino sheep. *S. Afr. J. Anim. Sci.* 31, 115-121.

Okut, H., Bromley, C.M., van Vleck, L.D. & Snowder G.D., 1999. Genotypic expression at different ages: 1. Prolificacy traits of sheep. *J. Anim. Sci.* 77, 2357 - 2365.

Pretorius, A.L. & Van Der Merwe, A.J., 2000. A non-parametric Bayesian approach for genetic evaluation in animal breeding. *S. Afr. J. Anim. Sci.* 30, 138 - 148.

Rao, S. & Notter, D.R., 2000. Genetic analysis of litter size in Targhee, Suffolk and Polypay sheep. *J. Anim. Sci.* 78, 2113 - 2120.

Rosati, A., Mousa E., Van Vleck, L.D. & Young, L.D., 2002 Genetic parameters of reproductive traits in sheep. *Small Rum. Res.* 43, 65 - 74.

Saatci, M., Ap Dewi, I. & Ulutas, Z., 1999. Variance components due to direct and maternal effects and estimation of breeding values for 12-week weight of Welsh Mountain lambs. *Anim. Sci.* 69, 345 - 352.

SAS, 1988. SAS Institute Inc. SAS® Procedures Guide, Release 6.03 Edition. Cary, NC.

Simm, G., Lewis, R.M., Grundy, B. & Dingwall, W.S., 2002. Responses to selection for lean growth in sheep. *Anim. Sci.* 74, 39 - 50.

Snyman, M.A., Erasmus, G.J., Van Wyk J.B. & Olivier, J.J., 1995. Direct and maternal (co)variance components and heritability estimates for body weight at different ages and fleece traits in Afrino sheep. *Livest. Prod. Sci.* 44, 229 - 235.

Snyman, M.A., Cloete, S.W.P. & Olivier, J.J., 1998b. Genetic and phenotypic correlations of total weight of lamb weaned with body weight, clean fleece weight and mean fibre diameter in three South African Merino flocks. *Livest. Prod. Sci.* 55, 157-162.

Snyman, M.A., Erasmus, G.J., Van Wyk J.B. & Olivier, J.J., 1998a. Genetic and phenotypic correlations among production and reproduction traits in Afrino sheep. *S. Afr. J. Anim. Sci.* 28(2), 74 - 81.

Snyman, M.A., Olivier, J.J., Erasmus, G.J. & Van Wyk, J.B., 1997. Genetic parameter estimates for total weight of lamb weaned in Afrino and Merino sheep. *Livest. Prod. Sci.* 48, 111 - 116.

Sorenson, D.A., Wang, C.S., Jensen, J. & Gianola, D., 1994. Bayesian analysis of genetic change due to selection using Gibbs sampling. *Genet. Sel. Evol.* 26, 333 - 360.

Tosh, J.M. & Kemp, R.A., 1994. Estimation of variance components for lamb weights in three sheep populations. *J. Anim. Sci.* 72, 1184 - 1190.

Van der Merwe, C.A., 1976. Genetiese en nie-genetiese faktore wat die produksie- en reproduksie eienskappe van die Elsenburgse Dormerskaapkudde beïnvloed. PhD thesis, University of Stellenbosch, Stellenbosch.

Van der Merwe, A.J. & Pretorius, A.L., 2002. A Bayesian non-parametric approach to the mixed linear model with an application to animal breeding. *S. Afr. Stat. J.*, 36, 1 - 39.

Van der Merwe, A.J., Pretorius, A.L., Hugo, J. & Zellner, A., 2001. Traditional Bayes and the Bayesian method of moment analysis for the mixed linear model with an application to animal breeding. *S. Afr. Stat. J.* 35, 27 - 76.

Van Tassell, C.P., Casella, G. & Pollak, E.J., 1995. Effects of selection on estimates of variance components using Gibbs sampling and restricted maximum likelihood. *J. Dairy Sci.* 78, 678 - 692.

Van Wyk, J.B., Erasmus, G.J. & Konstantinov, K.V., 1993a. Non-genetic factors influencing early growth traits in the Elsenburg Dormer sheep stud. *S. Afr. J. Anim. Sci.* 23, 67 - 71.

Van Wyk, J.B., Erasmus, G.J. & Konstantinov, K.V., 1993b. Variance component and heritability estimates of early growth traits in the Elsenburg Dormer sheep stud. *S. Afr. J. Anim. Sci.* 23, 72 - 76.

Van Wyk, J.B., Erasmus, G.J. & Konstantinov, K.V., 1993c. Inbreeding in the Elsenburg Dormer sheep stud. *S. Afr. J. Anim. Sci.* 23, 77 - 80.

Van Wyk, J.B., Erasmus, G.J., Konstantinov, K.V. & Van Der Westhuizen, J., 1993d. Relationships between early growth traits in the Elsenburg Dormer sheep stud. *S. Afr. J. Anim. Sci.* 23, 81 - 84.

Van Wyk, J.B., Erasmus, G.J. & Konstantinov, K.V., 1993e. Genetic and environmental trends in the Elsenburg Dormer stud. *S. Afr. J. Anim. Sci.* 23, 85 - 87.

Van Wyk, J.B., Fair, M.D. & Erasmus, G.J., 2002. An Update of inbreeding in the Elsenburg Dormer stud. *Proc. GSSA/SASAS Jnt. Congr.*, 13 - 16 May, Christiana, pp 29.

Wang, C.S., Rutledge, J.J. & Gianola, D., 1993. Marginal inferences about variance components in a mixed linear model using Gibbs sampling. *Genet. Sel. Evol.* 25, 41 - 62.

Wang, C.S., Rutledge, J.J. & Gianola, D., 1994. Bayesian analysis of mixed linear models via Gibbs sampling with an application to litter size in Iberian pigs. *Genet. Sel. Evol.* 26, 91 - 115.

Yapi, V.V., Boylan, W.J. & Robinson, R.A., 1992. Heritability and repeatability estimates and correlations of lamb mortality with birth weight and litter size. *World Rev. Anim. Prod.* 27, 55-60.

Yazdi, M. H., Engstrom, G., Nasholm, A., Johansson, K., Jorjani, H. & Liljedahl, L.E., 1997. Genetic parameters for lamb weight at different ages and wool production in Baluchi sheep. *Anim. Sci.* 65, 247 - 255.

Appendix A

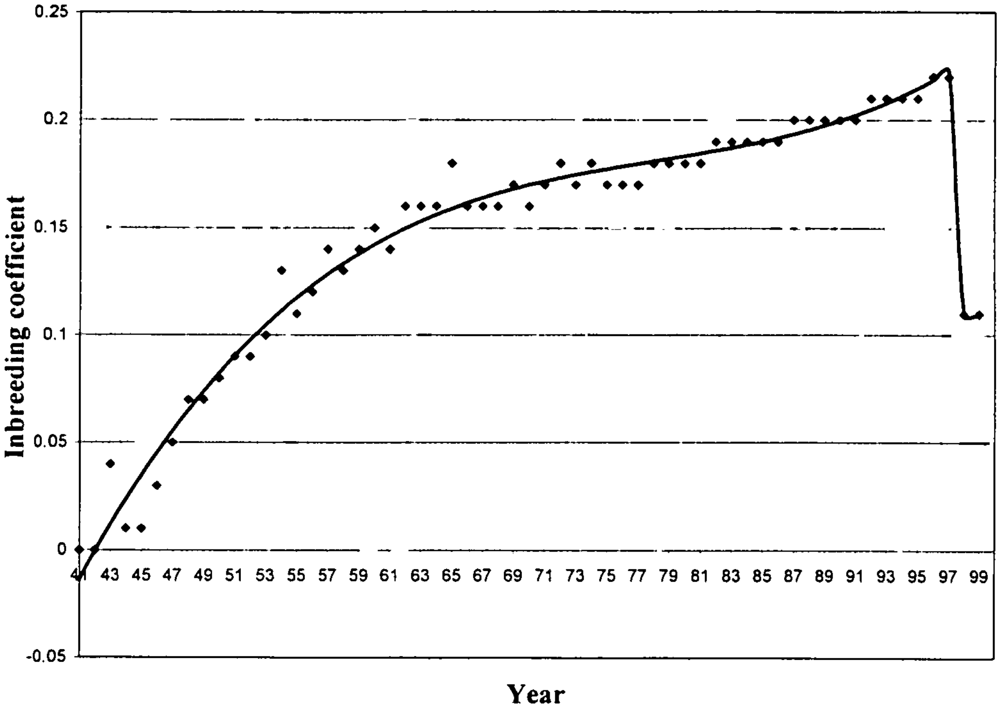

Figure 1 Mean annual inbreeding coefficients from 1941 to 1999

The mean annual inbreeding steadily increased from zero in 1941 to 0.22 in 1997. Three unrelated rams from commercial flocks were introduced in 1997. The introduction of the three rams reduced the mean annual inbreeding coefficient by half (0.11) as shown in Figure 1.

No significant effect of lamb or dam inbreeding on average litter size (lamb born/ewe lambing) and survival rate (lambs weaned/lambs born) was observed (Van Wyk *et al.*, 2002).

Appendix B

	BW			WW		
Year	*n*	Mean	SD	*n*	Mean	SD
43	71	4.1	0.96	70	33.3	5.12
44	90	3.6	0.82	84	33.3	4.84
45	92	3.8	1.09	89	35.0	7.28
46	92	4.5	0.77	85	31.5	6.04
47	127	4.3	0.87	104	26.9	5.49
48	155	3.9	0.84	142	31.3	6.51
49	169	3.9	0.79	160	34.9	6.53
50	165	4.0	0.94	146	29.8	5.96
51	189	3.6	0.90	171	29.9	6.62
52	168	3.7	0.98	151	32.8	6.17
53	130	3.7	0.73	115	29.5	5.18
54	177	4.0	0.81	168	30.9	5.90
55	154	3.9	0.82	134	24.8	5.03
56	181	3.8	0.78	166	31.8	5.01
57	177	3.7	0.85	160	30.2	5.37
58	196	4.0	0.70	171	31.4	4.93
59	219	3.7	0.86	193	27.6	6.75
60	226	4.2	0.88	203	30.6	5.82
61	217	4.1	0.71	202	28.1	5.49
62	204	4.1	0.63	180	28.8	4.60
63	213	3.5	0.76	171	27.9	6.72
64	182	3.6	0.73	165	31.2	6.04
65	150	3.5	0.67	126	31.0	5.13
66	212	4.0	0.73	176	31.1	5.48
67	222	3.6	0.76	171	31.6	5.53
68	185	3.6	0.74	161	29.2	5.41
69	207	3.6	0.79	175	29.5	5.52
70	268	3.5	0.72	235	30.9	4.80
71	193	3.4	0.62	174	30.5	5.57
72	188	3.5	0.80	162	30.5	5.68
73	279	4.0	0.91	199	31.4	6.39
74	165	4.1	0.96	140	30.5	5.74
75	189	4.0	0.93	170	29.6	6.95
76	164	3.7	0.84	136	32.9	5.52
77	161	3.8	0.88	141	31.2	5.36
78	180	4.3	0.80	156	33.2	6.15
79	193	4.4	0.86	166	29.8	5.20
80	227	4.0	0.81	199	31.3	4.42
81	245	4.2	0.82	220	31.3	4.89
82	218	4.1	0.68	185	31.3	4.92
83	211	4.1	0.72	180	24.7	4.78
84	219	3.9	0.68	195	23.9	5.84
85	209	3.9	0.71	160	26.4	5.40
86	228	4.0	0.82	194	30.1	6.36
87	201	4.1	0.76	165	24.9	4.62
88	203	3.8	0.75	170	27.5	5.07
89	209	4.0	0.70	170	30.6	5.68
90	146	4.2	0.77	146	28.4	4.95
91	184	4.5	0.82	184	26.0	5.72
92	190	4.1	0.80	150	31.3	5.55
93	184	3.9	0.74	129	21.1	4.13
94	209	4.0	0.76	158	21.6	4.88
95	202	4.1	0.83	175	21.8	4.58
96	223	3.9	0.71	201	22.8	5.17
97	203	4.1	0.78	161	24.9	4.32
98	213	3.7	0.86	186	26.6	5.74
99	227	3.6	0.69	196	24.8	5.10
Total	10701	3.9	0.83	9242	29.06	6.43

n = No of records, SD = Standard deviation; BW = birth weight WW = weaning weight

Appendix C

Fixed effect	BW		WW	
Year	Solution	SE	Solution	SE
43	0.0000	0.0000	0.0000	0.0000
44	-0.6251	0.0961	-0.3011	0.7207
45	-0.3590	0.1097	1.9060	0.7763
46	0.1613	0.1106	-2.5930	0.7901
47	0.1606	0.1108	-5.4510	0.7886
48	-0.3487	0.1102	-0.6458	0.7700
49	-0.3882	0.1176	2.7210	0.7973
50	-0.2365	0.1204	-2.4660	0.8150
51	-0.5690	0.1215	-2.1530	0.8109
52	-0.6292	0.1241	-0.3591	0.8278
53	-0.6058	0.1285	-3.6300	0.8591
54	-0.2173	0.1277	-1.6040	0.8358
55	-0.3367	0.1308	-7.7370	0.8649
56	-0.2701	0.1294	0.1759	0.8476
57	-0.4672	0.1309	-2.3140	0.8551
58	-0.2488	0.1309	-1.0950	0.8547
59	-0.5500	0.1303	-4.9950	0.8468
60	-0.1367	0.1311	-2.4220	0.8476
61	-0.3450	0.1323	-5.0580	0.8538
62	-0.2015	0.1334	-3.4510	0.8618
63	-0.8537	0.1348	-4.8020	0.8726
64	-0.8597	0.1377	-2.1490	0.8846
65	-1.1080	0.1398	-3.8240	0.9069
66	-0.6333	0.1375	-3.3670	0.8825
67	-1.0510	0.1382	-2.5880	0.8875
68	-1.0420	0.1393	-5.0010	0.8916
69	-1.0630	0.1393	-4.2620	0.8889
70	-1.0690	0.1382	-3.0730	0.8729
71	-1.2380	0.1407	-3.3970	0.8931
72	-1.1070	0.1430	-3.8780	0.9076
73	-0.6461	0.1421	-2.9750	0.8988
74	-0.4348	0.1450	-3.0720	0.9160
75	-0.5945	0.1449	-4.5850	0.9086
76	-0.9803	0.1478	-1.0580	0.9336
77	-0.9064	0.1491	-3.8590	0.9350
78	-0.2634	0.1485	-0.6654	0.9278
79	-0.1933	0.1497	-3.9770	0.9310
80	-0.4171	0.1498	-2.1570	0.9245
81	-0.3209	0.1500	-2.5550	0.9197
82	-0.5297	0.1528	-2.7470	0.9389
83	-0.5868	0.1538	-9.5860	0.9448
84	-0.6365	0.1549	-10.0400	0.9451
85	-0.7659	0.1567	-8.3610	0.9621
86	-0.5659	0.1583	-3.3590	0.9626
87	-0.4063	0.1596	-9.1820	0.9728
88	-0.6789	0.1612	-6.7880	0.9772
89	-0.6020	0.1629	-3.2890	0.9857
90	-0.4518	0.1656	-6.6330	0.9971
91	-0.1507	0.1659	-8.6600	0.9894
92	-0.4648	0.1673	-3.0830	1.0070
93	-0.7531	0.1702	-14.3500	1.0290
94	-0.8311	0.1696	-14.5000	1.0140
95	-0.5659	0.1720	-14.0500	1.0170
96	-0.7491	0.1728	-12.7300	1.0160
97	-0.5908	0.1755	-10.9100	1.0360
98	-0.8879	0.1757	-8.6740	1.0220
99	-0.9624	0.1770	-10.1600	1.0290

Solutions as deviations (+ or -) from first level of fixed effect given as zero, SE = standard error.