

**GENETIC ANALYSIS OF SHEEP DISCRETE  
REPRODUCTIVE TRAITS USING  
SIMULATION AND FIELD DATA**

by

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Key words: Reproduction, Growth, Fleece Characteristics, Simulation,  
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# GENETIC ANALYSIS OF SHEEP DISCRETE REPRODUCTIVE TRAITS USING SIMULATION AND FIELD DATA

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## (ABSTRACT)

The applicability of restricted maximum likelihood (REML) in genetic analyses of categorical data was evaluated using simulation and field data. Four genetic models were used to simulate underlying phenotypic variates, which were derived as the sum of additive genetic and environmental effects (Model 1A and 1B) or additive genetic and permanent and temporary environmental effects (Model 2A and 2B). Fifty-eight replicates were simulated, each of which contained 5000 ewes by 500 sires and 5000 dams and with up to five records per ewe. The usual transformation of heritability estimated on the categorical scale to the normal scale for fertility and litter size performed better for a simple animal model than for a repeatability model. Genetic correlation estimates between the two categorical traits for Model 1B and 2B were  $.49 \pm .01$  and  $.48 \pm .04$ , respectively, and were close to the expected value of .50. However, permanent and temporary environmental correlations whose input values were each .50 were underestimated with estimates of  $.41 \pm .05$  and  $.26 \pm .03$ , respectively for Model 2B, and  $.33 \pm .02$  for the temporary environmental correlation for Model 1B.

Bivariate genetic analyses of litter size with growth and fleece traits were carried out by REML for the data of Suffolk, Targhee and Polypay. Direct heritabilities for most growth traits in all the breeds were low ( $<.20$ ). Maternal genetic and maternal permanent environmental effects were important for all body weights except for the weaning weight at 120 d for Polypay sheep. Estimates of heritability and permanent environmental effects for litter size for these breeds ranged from .09 to .12 and .00 to .05, respectively. Heritabilities

for grease fleece weight and fiber diameter were high for Targhee and Polypay sheep. Direct genetic correlations between growth and litter size were favorable for Suffolk and Targhee but weak for Polypay sheep. Genetic correlations between maternal effects for growth and direct effects for litter size for the breeds were generally small. Within-trait maternal-direct genetic correlations for growth in the breeds were variable and generally negative. Direct genetic correlations of litter size with grease fleece weight and fiber diameter were variable across the breeds.

Key words: Reproduction, Growth, Fleece Characteristics, Simulation, REML, Sheep

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# **CHAPTER 1. Introduction**

## **1.1. General Background**

## **1.2. Objectives of the Study**

## **Reference**



# CHAPTER 1

## Introduction

In this chapter, the general motivation of the thesis is presented, along with the specific objectives of the study. In Chapter 2, genetic parameter estimates for growth, fleece (fleece weight and fiber diameter) and reproductive traits (litter size and fertility) are reviewed. Because Fogarty (1995) has already published a review of this material, this chapter emphasizes papers not included in his review, especially on maternal effects on growth traits, genetic improvement for these traits by selection and genetic relationships of litter size with growth and fleece traits in sheep. Also the theory of categorical traits and methodologies for analyses of discrete data in animal breeding are reviewed. Several studies comparing the performance of linear and non-linear methods in statistical genetic analyses of discontinuous traits in different livestock species by field data and simulation are discussed. Finally in Chapter 2, different methodologies for (co)variance component estimation are discussed. Mathematical representations for within-trait covariance estimation for growth traits and across-trait covariance estimation between litter size and growth traits are given. Efforts are made to address the models used in our study.

In Chapter 3, methodologies used in a Monte Carlo simulation study on reproductive traits (litter size and fertility) are described. The randomness of the SAS pseudo-random number generator is tested by simulating 20 independent variates. The simulated phenotypic values in underlying normal and categorical scales are summarized and discussed. The derived genetic parameters obtained from multiple-trait restricted maximum likelihood analyses are presented in Chapter 4. Estimation of additive genetic, permanent environmental and residual covariance between fertility and litter size are emphasized. Also the effect of setting residual covariance to zero and failure of open ewes

to produce a litter size record on (co)variance estimation are studied. In Chapter 5, field data of three breeds, Suffolk, Targhee and Polypay, are used for bivariate analyses of litter size with growth and fleece traits. The importance of (co)variance components in the various bivariate animal models was evaluated by likelihood ratio tests. In addition, to obtain the genetic parameters required for multiple-trait genetic evaluation for National Sheep Improvement Program, some related issues to (co)variance estimation by the derivative-free approach, such as flat-ridge, dependence between two across-trait genetic covariances and the effect of setting residual covariance to zero on estimation of (co)variance components are examined.

## **1.1 General Background**

Dickerson (1970) stated that the cost of animal products depends primarily upon the efficiency of three basic functions: (1) female production, (2) reproduction, and (3) growth of the young. The female production conceptually contributes to all the outputs directly and indirectly from those breeding females that are kept for reproducing next generation. Outputs such as wool, milk etc. represent important sources of income for sheep production, especially in western ranch conditions. Most of female productive traits are normally and continuously distributed. Genetic analyses of these traits are well understood. During the history of sheep breeding, these productive traits have been the focus and tremendous genetic improvement has been made in these traits.

Growth of lamb, indicated by body weights and rate of gain at different phases of growth are among the most economically important and easily-measured traits. Knowledge of the particular trait and phase of the animal's growth upon which to base selection is therefore of utmost importance. In the eastern lamb production regions, fast lamb growth is definitely a desirable property. In recent years, more studies have addressed how to efficiently utilize maternal genetic effects in genetic improvement of these traits.

Also in sheep production, reproductive traits such as fertility, prolificacy, fecundity and lamb survival have been recognized as major factors influencing profitability, but were less studied than the other two groups of traits. Genetic relationships involving reproductive traits were seldom studied. These reproductive traits generally have not been selected for in sheep improvement programs because they have low heritabilities, a discrete phenotypic expression, and are expressed only in sexually mature ewes leading to low selection intensities and long generation intervals (Bradford, 1985). Among these reproductive traits, litter size is the most important, and thus most studied as an increase in the numbers of lambs weaned per ewe per year offers the greatest single opportunity for increasing the efficiency of any kinds of sheep production systems. Several successful selection experiments have changed the perception that genetic improvement for litter size by selection cannot be justified due to its low heritability. Litter size has been included in genetic improvement programs in many countries. Litter size is the trait receiving the highest relative economic value in the Norwegian scheme (Perez-Enciso, 1995); the British Meat and Livestock Commission includes ewe reproductive performance in the selection indices in all except terminal sire breeds; selection schemes to improve litter size are implemented in most breeds in France; and LAMBPLAN, Australia's performance recording and genetic evaluation programme for meat sheep also takes ewes' reproductive traits explicitly into consideration (Fogarty, 1995).

In the U.S., the National Sheep Improvement Program (NSIP) was established in 1986 to provide within-flock genetic evaluations for U. S. sheep producers. The program utilized single-trait prediction methods with variances derived from literature values. In 1995, the program was extended to provide across-flock evaluations for Targhee sheep, with (co)variance estimates derived from NSIP Targhee flocks (Notter and Hough, 1995).

The studies for genetic improvement of sheep reproductive traits in the past were focused on two major areas: (1) methodologies for (co)variance estimation and genetic evaluation for these categorical traits, and (2) selection criteria and methods to maximize

genetic gains for these traits. Land et al. (1983) suggested two possible courses of action for the development of selection criteria for sheep reproductive traits: 1) to assume that the phenotypic expression of the trait depends on the value of an underlying continuous variable (Falconer, 1989) and of fixed thresholds or 2) to assume that reproduction in both sexes is under a similar genetic and hormonal control, and use the so-called physiological traits as indirect measures of reproductive merit.

Generally there are two groups of methodologies for (co)variance component estimation and genetic evaluation for categorical sheep reproductive traits: linear and non-linear methods. Analyses of discrete traits assuming the threshold model in sheep breeding are scarce. Pattersson and Danell (1985) analyzed litter size and lamb survival in four Swedish sheep breeds, and Bodin and Elsen (1989) studied variability of litter size in different French sheep breeds using a threshold model. Other studies in sheep where the discrete nature of the data was taken into account are those of Gilmour (1983), who analyzed data on foot-shape in lambs, and of Thompson et al. (1985) who estimated heritability of fleece rot incidence and score in Australian Merino. More recently, comparisons of linear vs non-linear models in analyses of sheep reproductive traits were made in several studies (Olesen et al., 1994; Perez-Enciso et al., 1995; Motos, 1993). Theoretically, non-linear methods appear to be more appropriate for threshold traits than linear models. However, they are computationally more difficult than linear model techniques. This aspect has prompted the question ‘how advantageous are non-linear over linear procedures when compared under the same circumstances?’ Most studies by simulation and field data did not support non-linear models (Meijing and Gianola, 1985; King, 1991; Matos, 1993; Perez-Enciso, 1995). Except for very rare cases, the two approaches performed similarly on many measures.

In linear methods, for the purpose of genetic evaluation, Henderson’s BLUP is considered the best procedure, while for the purpose of (co)variance component estimation, recently developed restricted maximum likelihood (REML) has been the method of choice

in animal breeding. Henderson's mixed model equations under general conditions yield best linear unbiased estimators (BLUE) of fixed effects and best linear unbiased predictors (BLUP) of random effects (Henderson, 1984). A strong argument favoring the use of Henderson's BLUP resides in the fact that when joint multivariate normality of genotypes and data is assumed and dispersion parameters are known, BLUP can be viewed as the 'maximum likelihood estimator' of the best predictor or optimal decision rule to rank candidates for selection. Moreover, BLUP that maximizes the probability of correct pairwise ranking among all linear, translation invariance predictors is unbiased under certain selection schemes (Henderson, 1980). The merit of REML in (co)variance estimation is that REML estimators maximize only the portion of the likelihood that does not depend on the fixed effect and can eliminate the bias of Maximum Likelihood estimators. REML estimators have most of these optimal properties; they are marginally sufficient, consistent, minimum variance, efficient and asymptotically normal (Harville, 1977). Thus all information available is utilized in an optimal way.

Development of breeding objectives and effective improvement program requires simultaneously considering the three kinds of economically important traits defined by Dickerson (1970). Knowledge of the genetic variation for these traits and covariation among these traits is prerequisite. Here, our special interest is the relationship of litter size with growth and fleece traits. Litter size is not only an economically important trait and categorical in nature but is also a fitness trait. Reduction in fitness associated with genetic improvement programs has been detected in several livestock species. Kerr and Cameron (1994) observed that selection for aspects of efficient lean growth adversely affected reproductive performance in Large White pigs. Uribe (1995) estimated genetic correlations of seven health traits with milk yield in dairy cattle and found that most were antagonistic. Genetic correlations between production and reproduction were moderate to large and antagonistic in dairy cattle (Distl et al., 1989; Hansen et al., 1983; Hermas et al., 1987; Jansen, 1985; Johan et al., 1989). Also several long selection experiments in dairy cattle

and poultry confirmed the negative relationship between fitness and production traits (Shank et al., 1978; Short et al., 1990; Dunklee et al., 1994a, b; Kress et al., 1994; Gowe et al., 1993). However, there is a dearth of information on reduced fitness associated with our past sheep breeding programs.

## **1.2. Objectives of the Study**

The objective of the first part of this study was to examine the theory of threshold traits and the robustness of derivative-free restricted maximum likelihood in genetic analyses of two reproductive traits, fertility and litter size, both in underlying and categorical scales. The objective was accomplished by:

(i). simulating two underlying normal variates in a traditional nested design using Monte Carlo simulation techniques in a four parameter setting, named Model 1A, 1B, 2A and 2B. In Model 1A and 1B, a simple animal model was used while in Model 2A and 2B, a repeatability model was used for both traits. In Model 1B and 2B, two traits were correlated with all correlations (genetic, permanent environmental and residual correlations) of .5. Realized categorical values were derived from underlying variates by a set of threshold values.

(ii). studying the statistical properties of underlying normal and categorical distributions of two independent traits or two correlated traits.

(iii). estimating genetic parameters, especially three correlations, using derivative-free REML methods and statistically testing the location parameters for the estimates of various second moment statistics obtained from genetic analyses of the replicates assorted by models.

(iv). simulating 4 replicates for each of Model 1B-X and Model 1B-Y, which were modified from Model 1B. In Model 1B-X, input values of genetic and environmental correlations were .50 and .00 and the reverse was true for Model 1B-Y.

(v). studying the effect of fixing environmental covariance to zero by comparing the (co)variance estimates with or without this restriction.

(vi). studying the effect of selection on fertility on (co)variance component estimation.

The objective of the second part was two-fold. The first was to construct appropriate bivariate models between litter size and growth or fleece traits for Suffolk, Targhee and Polypay sheep using National Sheep Improvement Program data and to provide genetic parameters required for multiple-trait genetic evaluation. The second was to examine the issues related to covariance estimation by derivative-free REML, such as flat-ridge phenomena, dependence among different estimates and the effect of setting residual covariance to zero on genetic parameter estimation.

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# CHAPTER 2

## Literature Review

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## **CHAPTER 2**

### **Literature Review**

#### **Abstract**

In this chapter, genetic parameters, including maternal effects for sheep reproductive, growth and fleece traits as well as genetic relationships of litter size with fertility, growth traits and two fleece traits (grease fleece weight and fiber diameter) were reviewed. Also some selection experiments for genetic improvement of litter size and fertility in sheep were discussed. Heritabilities for sheep reproductive traits were generally low while heritabilities for growth and fleece traits were medium to high. Maternal effects were more important for growth traits than for reproductive and fleece traits. The selection experiments reviewed here generally support that genetic improvement for litter size and fertility can be made through selection. A positive correlation between litter size and fertility appears to be a general pattern. The genetic correlations among growth traits were medium to high. It is generally believed that more progress in weaning weight or gain can be made by selection on postweaning weights and gains than on preweaning weights and gains. The reported genetic correlations between liveweights at various age and litter size were very variable. The weighted average correlations of litter size with all liveweights were .41. It seems a very weak or no genetic correlation between litter size and fleece traits.

In the second part, some basic concepts for the theory of categorical traits were introduced. Also genetic analyses of categorical traits in animal breeding were reviewed. The result from several studies using simulated or field data did not prove that non-linear models performed better than linear models for genetic analysis of categorical data except for some special cases. Joint considering the fact that non-linear methods are computationally more demanding, their merit relative to linear models was not justified

Finally, different methodologies for (co)variance estimation were discussed. Restricted maximum likelihood (REML) was the method of choice for estimating variance components in animal breeding. Thus derivative-free REML was described in detail. The reliability, robust and convergence of Simplex method were also discussed. Mathematical representation for within-trait covariance estimation for growth traits and across-trait covariance estimation between litter size and growth traits were given in last two sections. Throughout the methods, efforts was made to accommodate the models used in our research.

## **2.1. Genetic Improvement of Sheep Reproductive, Growth and Fleece Traits**

Genetic improvements for the three kind of traits, reproductive, growth and fleece are major goals for sheep breeding because the efficiency of sheep production depends primarily upon three functions: female production, reproduction and growth of lambs (Dickerson, 1970). For wool and dual purpose breeds, wool production and fiber quality would likely be major components that contribute to female production. Fleece traits rank third in importance following reproductive rate and growth (Botkin et al., 1988) although not all sheep producers agree with it. Range producers are likely to consider fleece traits of greater importance than growth because of the importance of wool as an insulator essential for adaptation to undesirable climate conditions, as well as the relative proportion of income from wool in sheep industries of Southwestern and Western states. Regardless of

viewpoints, wool is a valuable product in most regions and countries, although tremendous variation exists. Several measurements are used to indicate wool value. Fleece weight is the most indicative of value, but staple length, fiber diameter, and clean wool yield are major variables influencing values. Most fleece traits are relatively high in heritability. Genetic improvement through selection in wool or dual purpose breeds is common and successful.

Ewe productivity, defined as number ( or total weight ) of lambs weaned per ewe exposed, is dependent upon the component traits of fertility, litter size, lamb survival and growth (Fogarty et al., 1985 ), and is also a major concern of the sheep industry. Improving female reproductive performance is an important objective for increasing the profitability of sheep ( Abdulkhaliq et al., 1989 ), especially in lamb production. There is much greater potential for increasing both biological and economic efficiency of lamb production through genetic improvement in reproductive rate than through improvement in growth rate or body composition ( Dickerson , 1978 ). Total production costs accounted for by replacement and maintenance of breeding females are proportionally much higher for sheep and beef cattle than for the other meat-producing species, mainly because of their relatively low reproductive rate. Improving reproductive performance is likely to increase both the biological and economic efficiency of animal production enterprises (Dickerson, 1970). Among these reproductive traits, litter size was of major interests as an increase in the number of lambs marketed per ewe per year offers the greatest single opportunity (Shelton, 1971). Turner (1969) concluded that litter size seemed to be the most useful selection criterion for genetic improvement of this trait. Although selection for litter size has been successful (Clark, 1972; Turner, 1978), the rate of improvement has not been large, partly because the trait is lowly heritable, categorical in nature and expressed only in females of reproductive age that conceive and maintain pregnancy.

The growth of lambs is more important for meat breeds than for wool breeds. Its economic importance is only next to female reproduction. However the economic value of growth of lamb is difficult to evaluate in Western range condition while in lamb production

regions of Eastern states fast lamb growth is definitely a desirable property. The traits indicating growth mostly include birth weight, weaning weight at generally 2-5 months of age, postweaning weight and gain up to 9 months of age and yearling weight. Selection for growth has been common practice in sheep (Al-Shorepy, 1995). Selection criteria usually are those weights which can be measured early in the animal's life.

Development of breeding objectives and effective genetic improvement programs requires simultaneously considering the measures of all three kind economically important traits mentioned above. Knowledge of the genetic variation for economically important traits and genetic covariance among these traits is prerequisite. The common practice in wool and dual-purpose sheep breeding often did not take reproductive traits such as litter size explicitly into account. Recently, possible reduction in fitness including reproduction performance associated with today's and past breeding programs have been a concern to many animal breeders. Therefore, Fogarty (1995) suggested that for genetic improvement in lamb breeding enterprises, the important traits associated with reproduction and wool production of ewe and survival, growth and carcass characteristics of the lamb should be included.

### **2.1.1. Reproductive Traits**

#### **2.1.1.1. Litter Size**

The importance of litter size is that an increase in the number of lambs weaned per ewe per year offers the greatest single opportunity for increasing the efficiency of any kind of sheep production. More studies have addressed to genetic improvement of this trait than any other sheep reproductive trait. A lot of genetic variation for litter size exists between and within breeds.

Litter size has low heritability and repeatability (Abdulkhaliq et al., 1989 ). However, there is a considerable range in heritability estimates for litter size in sheep. Gonzalez (1982; cited by Bradford, 1985) reviewed thirty estimates of heritability of litter size for

different breeds or methods of estimation. The range in the estimates was from -.15 to .35 with a mean of .10. A more recent review by Fogarty (1995) gave a range of <0 to .34 with a weighted mean of .10 (53 estimates) for litter size and <0 to 0.54, with a weighted mean of  $0.08 \pm 0.08$  for lambs born per ewe joined. There are high standard errors associated with many of the estimates, and many reports did not include standard errors. Three estimates of realized heritability averaged approximately .07 (Fogarty, 1995). Published estimates in the past 15 years were generally in the same range ( Abdulkhalig, 1989; Atkins, 1986; Bunge, 1990; Clarke and Hohenboken, 1983; Gabina, 1989; Gama et al., 1991; Fahmy, 1990; Fogarty et al., 1985; Fossceco and Notter, 1995; Iniquez et al., 1986; Long and Thomas, 1989; Mohd-Yusuff et al., 1992; Owen et al., 1986; Shelton and Menzies, 1970; Shrestha and Heaney, 1987; Waldron and Thomas, 1992 ). The largest value reported was .41 (Gabina, 1989 ). Basuthakur et al. (1973) reported a heritability of  $.12 \pm .09$  for number of lambs born per ewe joined for Targhee sheep. Two estimates of heritability for litter size for Suffolk sheep were .02 and .09 ( Abdulkhalig et al., 1989; Barwick, 1989), smaller than the average value across all the breeds. Few estimates of heritability for litter size in fall lambing are available. Al-Shorepy and Notter ( 1996 ) reported a heritability estimate of .10, which was higher than the estimate of .05 using data from all seasons for the same flock.

Repeatability theoretically should represent the upper limit of heritability, assuming that the traits being considered at different times are genetically identical ( Falconer, 1989 ). Although not as useful as heritability, repeatability provides information on the joint magnitude of genetic and permanent environmental effects. Repeatabilities of litter size are generally low, ranging from .08 to .24 ( Abdulkhalig, 1989; Atkins, 1986; Bunge et al., 1990; Clarke and Hohenboken, 1983; Gabina, 1989; Fahmy, 1989, 1990; Fogarty et al., 1985; Long and Thomas, 1989; Shelton and Menzies, 1970 ). These results imply that the maternal genetic and permanent environmental effects for litter size would be small.

There are few studies that explicitly considered the maternal effects for litter size of sheep. Generally it is believed that litter size is seldom affected by maternal effects. However, Vangen (1980, 1986) thought that maternal effects were important when analyzing genetic parameters of reproductive traits, particularly litter size in pigs. Maternal effects are defined as the effects contributing to the phenotypic value of an individual contributed by its dam, excluding the dam's direct contribution through the sampled half of her genes. A negative correlation between direct genetic effects and maternal effects exists for litter size in swine (Robinson, 1972; Vangen, 1986; Southwood and Kennedy, 1990). This negative correlation could help explain the low heritability estimates for litter size from daughter-dam regression and the small response to selection for litter size. Southwood and Kennedy (1990) estimated direct and maternal additive genetic variances, their covariance and error variance for total numbers born, born alive, and weaned for Yorkshire and Landrace gilts using a derivative-free restricted maximum likelihood procedure under an animal model. Except for Landrace litters, estimates of maternal variance were relatively low for number born alive, and increased for number weaned. Estimates of the covariance were negative, except for number born and number born alive with crossbred litter, and became increasingly negative for number weaned. Van der Steen (1985a, b) found that gilts raised in large litters produced smaller litters than those raised in small litters which demonstrates a maternal permanent effect on litter size. These maternal influences decreased the daughter-dam regression coefficient by 5 to 10%. Standardizing the litters from which gilts were to be selected eliminated this maternal influence. Rutledge (1980) also found that gilts raised in small litters produced more pigs than gilts in large litters. Nelson and Robison (1976) raised gilts in litters of 6 or 14 pigs to compare reproductive performance of female swine reared in small and large litters. Gilts raised in small litters had an advantage of 1.0 corpora lutea and 1.2 embryos over gilts raised in large litters.

Several scientists demonstrated that maternal effects existed in mice. Falconer (1955, 1960, 1965, 1971) selected one line of mice for increased litter size, another for decreased



litter size and maintained a control line. The daughter-dam regression in the unselected control line was zero. However, fairly rapid response was obtained from within-litter selection. He thought that maternal effects reconciled this apparent inconsistency. The litters were not standardized at birth, so the litter size in which a female was raised became part of the environmental variation which influenced the size of the litter size that she later bore. Females raised in larger litter were retarded in growth and tended to have smaller litters. Durrant et al. (1980) also found this maternal effect on litter size in mice. At generation 17, second parity dams from lines selected for large litter size, large 6-wk body weight, index for increased litter size and decreased 6-wk body weight, and a control line were randomly assigned to have litters standardized to 8, 12 or 16 pups. Females raised in litters of 16 pups had significantly smaller litter size, fewer number born alive and fewer number born alive per female exposed than those raised in the litters of 8 or 12. The importance of maternal effects on initial response of litter size to selection in mice was also demonstrated by Vangen (1986). In this study, four lines were selected for increased litter size at birth for 10 generations. One line was standardized to 4 pups, a second to 8 pups and a third to 12 pups, while the fourth was not standardized. Selection response was highest in the line with fewest pups and zero in the unstandardized line. Realized heritabilities were high for the low level of standardization, moderate in the other 2 standardized lines and zero in the unstandardized line. However, standardization of the litters had no clear effect on the total number born in response to selection for increased litter size after 20 generations (Vangen, 1986). This may indicate that maternal effects are not important for long term selection of increased litter size in mice.

For the first few decades of the modern era of genetics, animal breeders generally believed, based on heritability estimates, that genetic variation in twinning rate or litter size was too low to justify trying to change it by genetic means for sheep, except perhaps to utilize the one-time increase from crossing breeds (Bradford, 1985). The expected change in litter size per year due to selection for sheep would be low ( Hanrahan, 1980). However,

several successful experiments for selection for litter size of sheep changed the perception. Today it is generally accepted that genetic potential for mean litter size in sheep can be set at any desired level from one to three. There are at least three methods potentially available for genetic improvement in litter size in sheep: use of breed resources, selection within breeds and use of major genes such as the Booroola (Elsen et al. 1994). Selection within breed for litter size was successful although the rate of response was not large. Bradford (1985) reviewed seven experiments dated to 1985, which included four breeds in four countries. These experiments generally supported that a potential genetic improvement of 1-2% or better per year in lambs born per ewe lambing could be made through selection.

Radomska et al. (1984, cited by Bradford, 1985) created a nucleus flock of Polish Merino sheep by selecting the 500 ewes with highest litter size from a population of 4000 ewes. The remaining ewes were put into cooperative flocks each containing 1500 ewes. An index based on litter size was used as the criterion of selection. Each breeding ram was selected from the nucleus flock based on his dam's index. Replacement ewes from the cooperative flocks that entered the nucleus flock were selected on the basis of their own index. Each replacement ewe born in the nucleus flock was selected based on her dam's index. One half of the nucleus replacement ewes were from the nucleus flock and the other half were from the cooperative flocks. All replacement ewes in the cooperative flocks were from those flocks. Litter size at first parity in the nucleus flock was 1.28 compared to 1.23 in the cooperative flocks for ewes born in the first year of selection.

More recently, Saboulard et al. (1995) reported their selection experiment for litter size and clean fleece weight. Two flocks of approximately 200 Western white-faced ewes per flock were maintained at two locations. Each flock was divided into four selection groups of similar initial birth type and age. The basis of selection in each flock was as follows: Line I, single trait selection for litter size; Line II, single trait selection for clean fleece weight; Line III, multiple trait selection for litter size and clean fleece weight; and Line IV, visual selection based on conformation and general fleece quality. Repeatability and

heritability estimated were .18 and  $.16 \pm .04$  for litter size, respectively. Linear regression coefficients (number born/year) of annual response for litter size in Line I to IV were  $.018 \pm .008$ ,  $.009 \pm .006$ ,  $.011 \pm .005$ , and  $.009 \pm .005$ , respectively.

Change in ovulation rate has been found to reasonably explain the selection responses in litter size ( Hanrahan, 1980). Trounson and Moore (1972, Cited by Bradford, 1985) collected fertilized ova from ewes in a line selected for multiple births and in a line selected against multiple births. Recipient ewes from each line received either one or three eggs donated by ewes from ewes either in their line or in the other line. Ovulation rates were determined on all ewes in the study. Ovulation rates were higher for the line selected for multiple births than for the line selected against multiple births. When three eggs were transferred, neither the line of the recipient nor of the donor had any effect upon the number of multiple births, indicating that uterine capacity had not changed with selection for multiple births. Therefore, change in ovulation rate accounted for the response in selection.

Ovulation rate was measured by laparoscopy in three lines of Romney ewes selected for high fecundity, low fecundity and at random for 5 years followed by 10 years of relaxed selection (Meyer and Clarke, 1982). Subsequent lambing records were kept for each ewe. Uterine efficiency was estimated for the line as the marginal litter size response in ewes conceiving to twin versus single ovulation. Litter size was significantly higher for the high than the other two lines. Difference between lines were not significant for uterine efficiency. Ovulation rate differed by about .7 ovum between the high and low selection lines. Therefore, change in ovulation rate accounted for the difference between the high and low lines in litter size.

Rambouillet sheep were selected for high and low reproductive performance for 19 years using the index :  $I = \text{total number of lambs born in dam's lifetime} / (\text{age of dam} - 1)$  (Schoenian and Burfening, 1990). A control line was also maintained. Ovulation rate was highest in the high line, intermediate in the control line and lowest in the low line. Embryo survival was similar in all three lines. Litter size was largest in the high line, intermediate in

the control line and smallest in the low line. Again, change in ovulation rate accounted for the difference between the lines in litter size.

A faster rate response in litter size is expected to occur if selection is based on ovulation rate due to its higher heritability (Hanrahan, 1980; Bradford, 1985; Quirke et al., 1985). Heritability of ovulation rate was found to be  $.45 \pm .07$  for Finn sheep and  $.57 \pm .28$  for Galway sheep (Hanrahan, 1980). Quirke et al. (1985) reported heritabilities for ovulation rate ranging from .05 to .50.

Fahmy (1989) found that ova loss and /or embryonic mortality played an important role in determining the number of lambs born. Perez-Enciso et al. (1995) examined the usefulness of measuring ovulation rate in genetic progress of litter size in sheep and to study different selection criteria combining ovulation rate and prenatal survival performance. Response to selection for 5 generations within a population of 20 male and 600 female parents were compared using Monte-Carlo simulation techniques with 50 replicates per selection method. Two breeds with low (Merino) and medium (Lacaune) prolificacy were considered. Records were generated according to a bivariate threshold model for ovulation (OR) and prenatal survival (ES). Four methods of genetic evaluation was compared: univariate best linear unbiased prediction (BLUP) using litter size (LS) records only (b-LS); univariate BLUP on ovulation records (b-OR); bivariate BLUP using OR and LS records (b-ORLS); and a maximum a posteriori predictor of a generalized linear model where OR was analyzed as a continuous trait and ES as a binary threshold trait (t-ORES). Response in LS was very similar to b-LS, b-ORLS and t-ORLS, whereas it was significantly lower with b-OR, indicating that indirect selection for litter size by selecting ovulation rate was not a advantage in this model. Response in OR was maximum with b-OR and minimum with b-LS. In contrast, response in ES was maximum with b-LS.

In another experiment (Fogarty, 1994), Ewes of Hyfer sheep, which was derived from two generations of crossing with Dorset (1/2), Boorola Merino (1/4) and Tangie Fertility Merino, were selected into the Selection Flock on the basis of their average weight of lamb

weaned from three joinings in two years. Rams were selected primarily on the basis of the performance of their dams. Unselected ewe progeny from the Selection Flock had 15% higher weight of lamb weaned than Control Flock ewe progeny for three of four cohort groups when they were exposed to three joinings at 8-month intervals. The response was similar to that predicted from the selection differentials achieved and heritability for Hyfer sheep.

Bradford et al. (1994) reported litter size, fertility, lamb survival and 120-d weight of lamb per ewe lambing for four lines of Targhee sheep maintained for over 30 years in a range environment. Two lines were selected for 120-d individual weight (HW, DH), and one for multiple births (HT); HC was an unselected control. Litter size was increased by about .2 from initial screening of ewes into line HT, but did not increase subsequently in spite of continued selection. Litter size increased significantly in line HW, selected continuously in the range environment, while fertility and lamb livability declined. Rams in line DH were imported from a more favorable environment for 17 years, and during that period ewe fertility and lamb livability declined significantly. With selection in this line in the range environment during the second phase, there was significant improvement in these traits. Total 120-d lamb weight per ewe increased modestly in all three selected lines.

Some scientists believed that indirect selection on male testis size may provided an alternative for genetic improvement of litter size of ewe, because heritability of testis size at early life of males ( 90 to 180 day of age) is usually high ( Matos et al, 1992; Fossceco and Notter , 1995) and testis size has a positive genetic correlation with litter size (Matos and Thomas, 1992)

#### **2.1.1.2. Fertility**

Fertility is generally high and may not have a large effect on profitability in fall breeding systems. However, for out of season breeding in late spring and early summer

when conception rates are often low, improving fertility could be quite important to a successful accelerated breeding system.

Fertility for sheep is also lowly heritable. Most reported estimates are less than .1 ( Atkins, 1986; Bunge et al., 1990; Clarke and Hohenboken, 1983; Fogarty et al., 1985; Gibina, 1989; Long and Thomas, 1989; Mohd-Yusuff et al., 1992; Shelton and Menzies, 1970; Shrestha and Heaney, 1987 ). The only estimate for out-of-season fertility is from Al-Shorepy and Notter (1996 ) with a mean heritability of .09 and a range of .07 to .11. In addition, a heritability of .09 was obtained by Fossceco and Notter ( 1995 ) for fertility of fall-bred 7-month old ewe lambs used to form the base population for the same study.

Analyses of reproductive traits present problems in devising adequate models, especially to account for the discrete or binomial nature of the data, a combination of full-sib and half-sib progeny and extended relationships amongst parents (Fogarty, 1995). The recent development of restricted maximum likelihood (REML) procedures and associated software has provided more widely available means of estimating genetic parameters for these traits. Therefore, Fogarty (1995) thought that more recent studies using animal model REML procedures might be regarded as more reliable than earlier estimates for these traits.

Fogarty (1995) gave a through review on genetic parameters for fertility. The weighted mean heritability estimates from 24 studies was .06 and the range was from < 0 to .22, being generally smaller than that for litter size. Animal model REML estimates were about half this. However, Iniquez et al. (1986) reported a estimate of .30 for Molam sheep, which is mainly used in acceleration systems. There was only a slight increase when average ewe lifetime performance was considered. High variation exists for fertility with a average coefficient of variation of 45% (Fogarty, 1995), indicating that potential genetic improvement through selection is possible. The average repeatability were .09 for fertility, slightly larger than its heritability, suggesting other genetic and non-genetic sources than additive genetic effects are small.

Fertility may be dependent on a maternal and a paternal genetic component because mating behaviors of both parents and the quality of their gametes are responsible for the success of a mating. Nitter (1985) discussed genetic and maternal effects on sheep reproduction and their influence on selection. However, there is a dearth of information about maternal effect on fertility.

A number of non-genetic factors such as type of birth of dam, age of dam, season of breeding, nutrition and management have profound effects on fertility. However, this paper did not intend to review these factors. Shrestha and Heaney (1987) gave an estimate of heritability of essentially zero for fertility in a ewe lamb flock treated with Fluorogestone Acetate and PMSG. They thought that genetic progress achieved by selection for fertility was limited and of no practical value in ewe lambs. However, there is overwhelming evidence of genetic variation in the reproductive traits of mature ewes bred at a natural estrus.

There were few selection experiments on fertility, especially for fertility of out-season breeding. Al-Shorepy and Notter (1996) summarized the results of a selection experiment for fertility. They applied mixed-model methodology to estimate genetic and environmental trends for spring fertility and fall litter size in a composite sheep flock containing 50% Dorset, 25% Rambouillet and 25% Finnsheep inheritance. Genetic trends were  $1.32 \pm .11\%$  in the selected line compared with  $.57 \pm .19\%$  in the environmental control for spring fertility and correlated response for litter size was  $.0065 \pm .0015$  lambs/yr in the selected line compared with  $.0024 \pm .0022$  lambs/yr in the environmental control line. Estimates of permanent environmental trends for spring fertility were similar in the selected and environmental control flocks ( $.21 \pm .7\%$  Vs  $.22 \pm .13\%$ ). However, Gabina (1989) thought that fertility should not be selected in Rasa Aragonesa flocks under the system of 3 lambing every 2 years in any of the mating seasons, because its repeatability and heritability were close to zero.

### **2.1.1.3. Relationship Between Fertility and Litter Size**

Few estimates of the genetic correlation between fertility and litter size have been reported. Fogarty et al.(1985 ) reported a genetic correlation of  $-.34 \pm .28$  between fertility and litter size and a phenotypic correlation of  $.03 \pm .02$  for ewes mated in the normal breeding season. However, Al-Shorepy and Notter (1996) obtained a much stronger genetic correlation of .56 between spring fertility and fall litter size, suggesting that selection for multiple births in an out-of-season breeding system should result in genetic improvement in spring fertility. Bradford ( 1985 ) noted an increase in fertility ( decrease in barrenness ) in several selection experiments for litter size. A positive correlated response thus appears to be a general pattern, and is consistent with the decline in fertility of the line selected against twinning (Bradford, 1985).

Combining 6 estimates of genetic correlation between litter size and fertility in the review by Forgaty (1995) , the mean and range are .31 and  $-.34$  to .82. Of 6 estimates, only one is negative (  $-.34$ , Fogarty et al., 1985). It seems that litter size and fertility are favorably related.

### **2.1.2. Growth Traits**

Body weight and rate of gain are among the most economically important and easily-measured traits of sheep. Knowledge of the particular trait and phase of the animal's growth upon which base selection is therefore of utmost importance. The potential for genetic improvement is largely dependent on the heritability of the trait and its relationship with other traits of economic importance.



### **2.1.2.1. Heritabilities for Growth Traits**

#### **2.1.2.1. Birth Weight**

Heritability for birth weight was generally low to medium. According to the review by Fogarty (1995), the mean and range of heritability estimates were .13 and .02 to .21, summarized over 6 estimates for wool breeds, .23 and .07 to .45 over 19 estimates for dual purpose breeds, and .17 and .06 to .31 over 7 estimates for meat breeds. The estimates obtained from REML methodologies were generally lower than these from traditional methodologies ( paternal half sib, regression, etc.) and were lower than .10, indicating that direct additive genetic effect for birth weight was small; other effects such as maternal effect may be important. Mavrogenis et al. (1980) gave an estimate of .13 for birth weight for Chios sheep, which was generally lower than the range above.

#### **2.1.2.1.2. Weaning Weight**

In the meat breeds, lamb were usually weaned at 60 day or less, while lambs from most dual purpose or wool breeds were weaned at 4 month of age depending on production systems. Estimates of heritabilities for weaning weight in the literature range from .08 to .41 ( 9 estimates) for wool breeds, .03 to .45 ( 43 estimates) for dual-purpose breeds and .05 to .57 ( 14 estimates ) for meat breeds, respectively (Fogarty, 1995 ). The weighted means of literature estimates for the three types of breeds are  $.33 \pm .10$ ,  $.21 \pm .11$ , and  $.21 \pm .18$ , respectively. A heritability estimate not included in Fogarty's review was  $.36 \pm .12$  for Chios sheep ( Mavrogenis et al, 1980 ),

The estimates of heritability for birth weight and early growth are generally low to medium, which is usually attributed to the importance of variation in dam effects, especially

in milk production, and to competition between litter mates. The estimates tend to increase with age ( Wolf et al., 1981). Also the low estimates of heritability of early growth rate ( e.g. up to 70 days) may be due to absence of controlled environment and uniform condition and large differences in solid food intake following initial restricted milk feeding before weaning (Shrestha and Heaney, 1985).

#### **2.1.2.1.3. Postweaning Weights and Gains**

Few reported estimates of heritabilities for postweaning gain are available, especially for the cumulative postweaning gain. Thrift (1973) obtained a heritability of  $.23 \pm .12$  for rate of gain from 70 days to market in a Dorset  $\times$  Western ewe flock, which was lower than a previous estimate of  $.38 \pm .13$  for postweaning gain by Harrington et al (1962). Waldron et al (1990) reported heritabilities of .07, .22 and .33 for gain from birth to 60 days, birth to 120 days and from 60 to 120 days, respectively for Suffolk sheep. Fogarty (1995) summarized 42 estimates of heritabilities for postweaning weight up to 9 months of age for dual-purpose breeds and 15 estimates for meat breeds. The range and means are .03 to .49 and  $.26 \pm .09$  for the dual-purpose breeds, and .06 to .41 and  $.28 \pm .09$  for meat breeds. The heritabilities for growth traits tended to increase with increasing age, from birth to weaning to postweaning measurements. The interests in different weights is simply in choosing the most adequate weight to use as a selection criterion to improve growth to weaning (Al-Shorepy and Notter, 1995). A common finding is that more progress in weaning weight can be made by selection on postweaning weight than on weaning weight itself, due to the higher direct heritability of the postweaning weight and its high genetic correlation with direct components of weaning weight. Therefore, Bradford (1985) suggested that a weight collected in early life should be adequate for use in selecting for the direct component of weaning weight in sheep.

Marvrogenis et al. (1980) observed that body weight at 15 weeks of age had the highest heritability estimate of  $.73 \pm .17$  among 10 growth traits of Chios sheep. Chios sheep were usually weaned at 39 days. Heritabilities for body weight at 10, 15, and 20 weeks and average daily gain from weaning to 20 weeks were  $.63 \pm .16$ ,  $.73 \pm .17$ ,  $.66 \pm .16$  and  $.56 \pm .15$ . Postweaning growth was more heritable than pre-weaning growth, probably because nutrition was not a limiting factor after weaning. Given these large heritabilities, it appears that mass selection for rapid growth would be effective.

#### **2.1.2.2. Maternal Effects for Growth Traits**

The importance of maternal effects on the growth of lambs is well known. Such effects arise from the ability of the mother to produce the milk needed for growth and other maternal behaviors. In the NSIP (National Sheep Improvement Program), both additive and maternal EPD for growth traits have been included in the breeding program. For sheep, lambs were usually weaned at four months of age and maternal influences are often expected to be more pronounced than in cattle or swine (Bradford, 1972). Accounting for maternal effects would increase accuracy of selection (Robinson, 1996). Results from recent studies have shown that maternal effects have explained much of the variation in lamb weight (Nasholm and Danell, 1996; Burfening and Kress, 1993; Marie et al, 1993; Notter and Hough, 1996). Willham (1972) discussed the utilization of maternal effects in animal breeding.

Because Fogarty (1995) did not explicitly consider maternal effects in his review, I intent to give a more detail review here. Wolf et al. (1981) obtained litter variance as proportion of phenotypic variance of .37 to .39 for birth weight, 4-week weight, 8-week weight and 12-week weight, which were much larger than direct heritability ( -.02 to .06), indicating that at birth and early growth maternal effect was more important than direct additive effect. Notter and Hough (1996) reported additive maternal genetic and maternal

permanent environmental effects as proportion of phenotypic variance were .10 and .09 respectively, for 60 d weaning weight and .05 and .08 for 120 d weaning weight for Targhee sheep. Burfening and Kress (1993) utilized information of maternal and paternal half-sibs, full-sibs and offspring on dam and sire for three breeds, Rambouillet, Targhee and Columbia, and obtained maternal heritability of .30 to .65 and .07 to .48 for birth weight and 120-d weight, respectively, which are generally larger than direct heritability estimates. Gjedrem (1967) reported that direct and maternal heritabilities were .12 and .17 for birth weight, .12 and .21 for 14-d weight, .12 and .22 for 28-d weight, .13 and .20 for 42-d weight and .18 and .12 for weaning weight, respectively. Maria et al. (1993) obtained the direct, and maternal heritabilities and maternal environmental effect ( $c^2$ ) of .04, .22 and .10 for birth weight, .34, .25 and .00 for weaning weight, .09, .01 and .07 for 90-d weight, .26, .17 and .02 for daily gain from birth to weaning and .15, .01 and .03 for daily gain from weaning to 90 day respectively. Nasholm and Danell (1996) observed that direct heritabilities increased with lamb age from .07 for birth weight to .21 for weight before slaughter and maternal heritabilities declined with age from .30 to .07. Also a non-significant maternal heritability of .22 was noted for mature ewe weight. Tosh and Kemp (1994) analyzed the data for three breeds and found that significant maternal genetic and environmental effect existed up to 100 days of age for all three breeds. Therefore, they suggested that models that describe weight of lambs of diverse biological types should include maternal effects even at 100 d.

Relative few estimates of the within-trait direct-maternal genetic correlation for growth traits are available. Generally unreasonably large negative correlation estimates were obtained in sheep (Al-Shorepy and Notter, 1996; Burfening and Kress, 1993; Marie et al, 1993; Notter and Hough, 1996; Tosh and Kemp, 1994) and in cattle (Koots et al., 1994a, 1994b; Robinson., 1996a, 1996b; Swalwe, 1993). Marie et al. (1993) reported an additive direct-maternal correlation of -.98 for weaning weight, -.99 for birth weight, -.97 for 90-d weight, -.99 for average daily gain from birth to weaning and .99 for average daily gain from

weaning to 90 days. In the presence of such strong negative correlations, estimate of additive direct and (or) maternal variance may be large and can be accepted only if the user also accept and incorporates the additive maternal covariance into any resulting analyses (Notter and Hough, 1996). However, Nasholm and Danell (1996) did not observe a negative relationship between maternal genetic and direct genetic effects. Except for daily gain from 2 wk after being turned out to pasture until weaning ( $r_{am} = -.11$ ), the correlations for 17 growth traits were positive and ranged from .07 to .64. Thus they thought that selection for larger lamb weights alone would not only increase ewe weights but also improve the maternal ability of ewe. Nasholm and Danell (1996) observed that when maternal effects for mature ewe weight were included in the model, the direct genetic variance decreased and was partly replaced by maternal variance and direct-maternal covariance. Therefore, interpretation of genetic parameters for maternally influenced traits from animal models is critically dependent upon the model(s) fitted the data.

### **2.1.2.3. The Relationships among Growth Traits**

Fogarty (1995) listed estimates of genetic and phenotypic correlations from 32 papers dated to 1994 in his review. Birth weight was more closely correlated with weaning weight than other body weights and 16 estimates gave mean of genetic correlation of .41. The genetic correlations between birth weight and other weights were smaller with mean of .11 ( 9 estimates ) with postweaning weight, .30 ( 3 estimates) with yearling weight and .30 ( 6 estimates ) with hogget weight, respectively.

The mean of genetic correlations between weaning weight and other traits were .86 ( 10 estimates ) for postweaning weight, .71 ( 9 estimates ) for yearling weight and .68 for hogget weight, respectively. The mean of genetic correlations between postweaning weight and other traits was .75 ( 4 estimates ) for yearling weight and .88 ( 4 estimates ) for hogget

weight. The mean of genetic correlations between yearling weight and hogget weight was .96 ( 4 estimates ).

Mavrogenis et al. (1980) analyzed genetic relationship between 10 growth traits for Chios sheep, including birth weight, age at weaning, body weight at 5, 10, 15, and 20 weeks and average daily gain from birth to weaning and weaning to 20 weeks. Birth weight had low genetic correlations (.16 to .21) with all weights and gains. These associations were, nevertheless, positive, indicating some expected correlated response. Genetic correlations among the remain weights and gains ranged from .19 to .25. It is evident that, although these genetic correlations are favorable, substantial correlated response from selection on any individual growth trait would not expected. The low genetic correlations, particularly between birth weight and other traits, are of considerable importance since birth weight as a correlated trait should not pose any serious problem of increasing lambing difficulties.

However, Stobart et al. (1986) obtained medium to high genetic correlation between birth weight and various growth traits with  $.68 \pm .20$  with weaning weight,  $.22 \pm .25$  with weight at 12 month of age,  $.44 \pm .20$  with weight at 18 month of age,  $.64 \pm .22$  with weight at 30 months of age and  $.55 \pm .16$  with mature weight for Western range ewes, respectively. The genetic correlations among weaning weight, weight at 12 month of age, weight at 18 month of age, weight at 30 month of age and mature weight are medium to high with range of .21 to .99. Similarly, Martin et al. (1980) also observed that estimates of the genetic correlations among the various lamb weights were high (.62 to 1.04), indicating that selection for weight at one age should result in increased weights in all ages.

The recent published estimates of genetic correlations among growth traits generally followed the pattern of previous literature. Nasholm and Danell (1996) obtained direct genetic correlations of .44, .48 and .36 between birth weight and 120-d weight, weight at 1 day before slaughter and ewe mature weight, respectively. It is obvious that correlated response in birth weight would be expected from selection for growth. They also found that across-trait direct and maternal genetic correlations all were positive and medium to high.

No unfavorable relationship was tested in Swedish Finewool sheep. Also genetic correlations among growth traits of Romanov lambs were, in general, positive, indicating that selection for any of the traits should result in genetic improvement in other traits (Maria et al., 1993).

#### **2.1.2.4. Selection for Growth Traits**

Selection for growth has been common in sheep, though it is not always advantageous (Bradford and Meyer, 1986). Most scientists agreed that selection for growth should be based on traits which can be measured early in the animal life. It is generally agreed that more progress in weaning weight can be made by selection on postweaning weight or gain than preweaning weight or gain, due to the higher direct heritability of the postweaning weight and its high genetic correlation with the weaning trait in sheep (Akins, 1986). Mavrogenis et al. (1980) thought selection for either weight at 15 weeks or post-weaning daily gain would be expected to yield a greater response than selection for preweaning daily gain or weaning weight. The absence of genetic antagonisms among body weights and gains indicate that none of the traits studied should be seriously impaired through correlated responses. A possible exception might be birth weight, although genetic correlations between birth weight and live weight at 10 or 15 weeks of age were low.

Olson et al (1976a,b) studied the relationship among various growth traits and between growth traits and carcass traits. He concluded that with regard to genetic and phenotypic estimates for growth traits, average gain from 14 to 22 weeks of age ( $h^2 = .46$ ) and body weight at 22 weeks ( $h^2 = .44$ ) should be the most effective selection criteria for improving postweaning and preweaning growth with limited effect on birth weight. Expected improvement (in genetic 's) of boneless cuts from 25 week-old lambs per of mass selection differential was nearly as large for selection on 22-week live weight (.63) or 14 - to 22-week gain (.52) as for hypothetical direct selection for boneless cut weight (.66).

Selection for 22-week weight also should increase leg and carcass conformation (.5) and quality grades (.4) as much as direct selection without increasing backfat, but is likely to increase kidney fat (.3).

I do not intend to review all the selection experiments for growth. However, some experiments reported in recent years are described. Jurado et al. (1994) analyzed the weight and growth data on 5136 lambs from 104 sires and 1552 dams collected during 5 yr (13 lambing seasons) of selection for high weaning weight in a single flock under range conditions. Ewes were culled based on fertility and replaced by ewe lambs selected for high weaning weight. Heritabilities of birth weight, weaning weight (30 d), preweaning weaning daily gain, postweaning weaning daily gain, and weight at 90 d, respectively, were .13, .09, .03, .15, and .11. Genetic correlations were generally high. Genetic and phenotypic improvement of weaning weight were  $22 \pm 3.0$  and  $198 \pm 11.3$  g per lambing season, respectively, with three lambing seasons per year. At the end of the experiment, phenotypic mean weight was 2.4 kg higher than initial values. Estimated and theoretical response were similar in the sire population. At the 13th lambing season, average breeding value of 30-d weight of ram population was 600 g higher than the mean initial breeding value in the base population. Projected average breeding value of lamb population under random mating at the 23rd lambing was equal to 404 g.

Lax et al. (1979) compared single trait and index selection for high 90-day weight and low 90-day fat probe at the seventh rib. The index was the standardized deviation in weight minus the standardized deviation in probe. Traits were mass selected in rams only within two replicates of each single trait and three replicates of each index selection group. Selection for about one half of group was done with single born rams and other half with multiple born rams. Ram lambs were used for mating. Ewes were first mated at approximately 19 month of age. Each replicate had approximately 40 ewes and four rams. A repeat mated control was used. Selection was effective in all lines over a 5-year period. Weight selection increased 90-day weight by  $.62 \pm .52$  kg per year,



with correlated increases of  $.035 \pm .051$  cm in fat probe and  $.049 \pm .069$  units in index. Index selection increased 90-day weight by  $.33 \pm .53$  kg per year, decreased fat probe by  $.017 \pm .051$  cm per year and increased index by  $.095 \pm .069$  units per year.

However, selection for growth was not always successful. Sakaul et al (1994) observed that the rate of improvement in growth were slow in the range condition in the selection experiment. In this experiment, two lines (DH and HW) were selected for individual 120-d weight and one was for multiple births (HT) for 30 years; HC was an unselected control. Phenotypic response to selection for 120-d weight occurred, but at a slow rate. An examination of breeding values indicated that both DH and HW lines responded to selection continuously until mid-1980s, but the response seemed to decrease in the line HW thereafter; the trend in DH is less clear. Low selection pressure and inbreeding were ruled out as primary reasons for the observed response, and they thought that inadequate nutrition might have hindered the selection response. Inbreeding increased almost linearly during the experiment, reaching approximately 11% in HC and HW, and 6% in HT by 1992. Realized heritabilities, calculated from response / selection differential measured in each line, were .05, .06 and .07 for DH, HT and HW, respectively. Estimates of direct and maternal heritabilities were .16 and .22, respectively, in the base population. The difference between estimated and realized heritabilities implies that the environment did not permit the full expression of genetic potential for growth.

### **2.1.3. Fleece Traits**

Fleece traits rank third in economic importance following reproductive rate and growth (Botkin et al., 1988). Also fleece traits perhaps are most studied in the past sheep breeding. We do not purpose to summarize all the fleece traits here. Only grease fleece weight and fiber diameter involved in our research were discussed here.

### 2.1.3.1. Grease Fleece Weight

The heritabilities for fleece characters are generally medium to high. The mean and range of heritabilities of 81 estimates for grease fleece weight are .35 and .06 to .84 (Fogarty, 1995). If classified by different kind of breeds, the mean and range of heritabilities are .38 (25 estimates) and .10 to .65 for wool breeds, .35 (29 estimates) and .06 to .84 for dual purpose breeds, .24 (3 estimates) and .16 to .38 for meat breeds, respectively. The mean and range of repeatability estimates are .58 and .34 to .84 for all breeds, which is bigger than its corresponding heritability estimates, suggesting that permanent environment variation exists in the trait.

Very few studies on maternal effect on fleece traits were reported. A recent study detected the presence of significant maternal effects for grease and clean fleece weights and body weights for Merino sheep (Mortimer and Atkins, 1994). Maternal heritability estimates were about one-fifth the size of direct heritability estimates, which are .065 to .093 for grease fleece weight, .054 to .093 for clean fleece weight and .050 to .074 for body weights. Since fleece weight is expressed throughout an animal's life, but selection is often based on measured fleece weight at ages younger than 16 months, there is a need to extended estimates of maternal effects to wider range of ages.

Direct-maternal genetic covariances for fleece weights, although of moderate magnitude, were not significant differently from zero (Mortimer and Atkins, 1994). The estimates of maternal-direct genetic correlations were -.23 for grease fleece weight, -.31 for clean fleece weight and .27 for body weight. Mortimer and Atkins (1994) thought that the detection of significant covariances for these traits apparently requires large data sets. Also the evidence from long-term selection lines for fleece weight would suggest that a negative covariance between direct and maternal genetic effects may exist for fleece weight at hogget age (Mortimer and Atkins, 1994).

In the another study, maternal genetic and permanent effects were estimated in a flock of Merino sheep (Swan and Hickson, 1994). Significant maternal effects were observed for grease fleece weight and body weight measure at weaning. Maternal genetic effects were more important than permanent environment effects at this time. There were carry-over maternal effects on body weight, but not on grease fleece weight measured at same time. Therefore, they thought that there is no immediate need to consider maternal effect on fleece traits in breeding programs. However, the effects on body weight may need consideration.

#### **2.1.3.2. Fiber Diameter**

Average fiber diameter and its variation are both important in wool processing. Mean fiber diameter is the single most important quality character of wool and is directly related to the monetary value of wool (Iman et al., 1992). Heritability of fiber diameter has been estimated by various researchers. The review by Fogarty (1995) gave a mean of .51 (27 estimates ) and range of .17 to .84 for wool breeds and .52 and .18 to .62 for dual purpose breeds. The mean of 12 estimates for repeatability are .70, suggesting that other genetic or non-genetic effects exist.

It is generally believed that fiber diameter is largely not influenced by maternal genetic effects ( Mortimer and Atkins, 1994; Swan and Hickson, 1994). Swan and Hickson (1994) observed that there were no maternal effects on mean fiber diameter. Mortimer and Atkins (1994) thought maternal effects were likely to be significant for wool production in growing animals, through their influence on surface area, but less important in adults.

#### **2.1.4. Relationships Between Litter Size and Growth, and Fleece Traits**

Accurate estimates of genetic parameters of growth and reproduction are essential for planning efficient meat sheep production systems and for predicting response to selection.

Genetic covariances are essential in predicting indirect response to selection, and they are needed to determine the optimum weighting and expected response of selection to improve more than one trait

#### **2.1.4.1. Litter Size and Growth**

There is little information in the literature regarding the relationship between litter size and growth traits. Al-Shorepy (1995) obtained the genetic correlations of litter size with birth weight and 90-day weight of .17 and .33, respectively in a 1/2-Dorset crossbred population. The reported genetic correlations between liveweights at various ages and litter size were very variable, ranged from -.61 to .92, whereas the phenotypic correlations were less variable (.00-.23) (Fogarty, 1995). The weighted average correlations with all liveweights were .19 (genetic) and .10 (phenotypic) for lambs born per ewe joined, and .41 and .15 for litter size, respectively.

Additive direct genetic correlation between live weight at various ages and the components of ewe reproduction were also highly variable. The weighted average genetic and phenotypic correlation between live weights and litter size were .41 ( range from -.46 to .78) and .15, respectively (Fogarty, 1995). Growth traits are generally favorably related with various reproduction traits. The genetic correlations between birth weight and reproductive traits were .30 (1 estimate) for lambs born/ewe joined, .34 (1 estimate) for lambs weaned/ewe joined, .20 ( 1 estimate) for lambs weaned/ewe lambing, .30 (1 estimate) for lambs born/ewe lambing (litter size), .16 (1 estimate) for maternal lamb survival and .01 (1 estimate) for fertility, respectively; The genetic correlations between weaning weight and reproductive traits were .20 (3 estimate, .44, standard deviation) for lambs born/ewe joined, .34 (1 estimate) for lambs weaned/ewe joined, -.27 (4 estimate, .42, standard deviation) for lambs weaned/ewe lambing, -.13 (1 estimate) for ovulation rate, -.10 ( 6 estimates, .39, standard deviation) for lambs born/ewe lambing, .11 ( 1 estimate ) for lamb survival,

maternal and  $-.16$  ( 2 estimates,  $.01$ , standard deviation) for fertility. The genetic correlations between post-weaning weight and reproductive traits were  $.59$  (1 estimate) for lambs born/ewe joined,  $.21$  (1 estimate) for ovulation rate, and  $.30$  (2 estimates) for lambs born/ewe lambing, respectively. The genetic correlations between yearling weight and reproductive traits were  $-.17$  ( 2 estimate, standard deviation of  $.30$ ) for lambs born/ewe joined,  $.13$  (1 estimate ) for lambs born/ewe lambing and  $-.34$  ( 1 estimate) for fertility, respectively.

Stobart et al. (1987) studied the relationship between growth and productivity of range ewes. The genetic correlations between litter size and various growth traits were  $.26 \pm .22$  for birth weight,  $-.09 \pm .27$  for weaning weight,  $-.17 \pm .27$  for weight at 12 month of age,  $.13 \pm .24$  for weight at 18 month of age and  $-.06 \pm .21$  for mature weight. The corresponding phenotypic correlations were  $.04$ ,  $.13$ ,  $.11$ ,  $.20$  and  $.14$ , respectively. The genetic and phenotypic correlations between average lambs weaned and various growth traits were  $.80 \pm .68$  and  $.05$  for birth weight,  $-.01 \pm .58$  and  $.08$  for weaning weight,  $-.05 \pm .59$  and  $.08$  for body weight at 12 month of age,  $.13 \pm .51$  and  $.11$  for body weight at 18 month of age and  $-.05 \pm .44$  and  $.07$  for mature weight, respectively. Akins (1986) obtained a strong genetic correlation between adult body weight and litter size ( $.66$ , s.e.  $.18$ ). Therefore he suggested that greater response for litter size would come from a combination of indirect selection ( on body weight ) and direct selection ( on dam's litter size).

There is a dearth of estimates on across-trait direct-maternal correlations between growth and litter size, which could be important for multitrait genetic evaluation of livestock

#### **2.1.4.2. Litter Size and Fleece Traits**

The correlations, especially genetic, between wool and reproduction traits were also highly variable, but the average of estimates in the literature was close to zero for most of fleece trait and litter size ( Fogarty, 1995). For lambs born per ewe joined, the weighted

average genetic and phenotypic correlations were -.06 and -.10 for grease fleece weight (.12 and .07 for average lambs born), .31 and -.09 for fiber diameter (-.07 and .12 for average lambs born), respectively (Fogarty, 1995). The corresponding correlations for lambs weaned per ewe joined were -.16 and -.10 (.11 and .06 for average performance over a number of records), and -.13 and -.04 (-.12 and .11 for average performance over a number of records), respectively. For litter size, the corresponding correlations were .01 and .03 (.06 and -.02 for average performance over a number of records), respectively for grease fleece weight, .08 and -.04, respectively for fiber diameter. A genetic correlation of  $.09 \pm .48$  and phenotypic correlation of .07 between grease fleece weight and number of lambs born per ewe joined were reported for Targhee sheep (Basuthkar et al., 1973). Considering reproduction as ewe traits and grease fleece weight as a lamb trait, Stein (1985) obtained a genetic correlation of -.04 and -.20 for number of lambs per ewe at birth and weaning, respectively.

## **2.2 Theory of Categorical Traits**

Categorical traits, also called discrete or threshold or quasi-continuous traits, denote a group of traits that have the properties and numerical characteristics of discrete data and can be conformable to one or a mixture of a group of discrete distributions. Although these traits are presumably under polygenic control, their phenotypic values are discontinuous. Therefore, for categorical traits, such as litter size, fertility and survival-related traits in sheep, both discrete phenotypic distributions and some underlying continuous distributions are assumed.

Categorical traits have generated extraordinary levels of interest in the field of animal breeding. The possible reasons are that many important economic traits such as reproductive traits or survival-related traits are categorical in nature, and some selection experiments for categorical traits have proven potential for genetic improvement. Several

authors (Hoeschele, 1986; Foulley, 1987; Soto-Murrillo, 1991) have presented extensive reviews on methods for analysis of discrete data in animal breeding. Generally there are two main groups of procedures for analysis of discontinuous genetic data (Matos, 1993). The distinction between the two groups depends on whether an underlying continuous distribution is assumed or not. The first group includes methods that ignore the discrete nature of categorical data, and the analysis proceeds using linear methodology as if the data were continuous, whereas the second invokes the threshold concept (Falconer, 1989) which assumes an underlying, non-observable, normal distribution for the discrete variate. The link between the observable discrete variable and the underlying continuous scale is generated by a set of fixed thresholds. The underlying variable is described by linear models, but the relationship between the underlying and the outward or observed scale is nonlinear (Gianola and Foulley, 1983 ).

### **2.2.1. Two common discrete distributions**

Several discrete distributions, such as the binomial, multinomial, Poisson or negative binomial distributions, are of importance in animal breeding. Fertility for sheep is generally believed to be conformable to a binomial distribution (0-1 distribution) while litter size for sheep is often conformable to a multinomial distribution. However, several scientists suggested that litter size in sheep may be distributed as a Poisson distribution. Perez-Enciso et al. (1993) suggested that ovulation rate could be viewed as a Poisson process. Together with the high correlation found between ovulation rate and litter size in sheep ( Waldron and Thomas, 1992), this makes the Poisson model appealing for genetic analysis of litter size in polytocous species. A positive relationship between the mean and the residual variance for litter size was observed in an unselected flock by Urioste and Danell (1987), who also suggested that this may indicate that litter size be distributed as Poisson in sheep.

### 2.2.1.1. Binomial Distribution

Definition: Let  $X$  be the number of event  $A$  in the  $n$  Bernoulli experiments, so  $X$  is a random variable and can be values of  $0, 1, \dots, n$ , and,

$$P \{X=k\} = \binom{n}{k} p^k q^{n-k}, k=0, 1, \dots, n \text{ and } 0 < p < 1.$$

We say that  $X$  has a binomial distribution with parameters,  $n$  and  $p$ , denoted  $X \sim B(n, p)$ .

In special case, when  $n=1$ , the binomial distribution become a (0-1) distribution with

$$P \{X=k\} = p^k q^{1-k}, k=0,1$$

For binomial distribution, Mean,  $E(X) = np$  and Variance,  $D(X) = np(1-p)$ .

For (0-1) distribution,  $E(X) = p$  and variance,  $D(X) = p(1-p)$ .

### 2.2.1.2 Poisson Distribution

Definition: A random variable  $X_n$  ( $n=1, 2, \dots$ ) has a Poisson distribution if its probability function has the form:

$$P(X=k) = \text{Po}(k) = \frac{e^{-\lambda} \lambda^k}{k!}, \text{ for } k = 0, 1, 2, \dots$$

For Poisson distribution,  $E(X) = D(X) = \lambda$ .

## 2.2.2. Threshold Concept and Link Functions

### 2.2.2.1. Threshold concept

The threshold concept for categorical traits was first introduced by Wright (1934), when he studied the inheritance of number of digits in an inbred strain of guinea pigs. In threshold model, each phenotype, such as fertility and litter size in categorical scale, is associated with an underlying continuous variable which is not observed. The underlying variable, usually called liability or prevalence in human genetics ( Falconer, 1989), is



affected by polygenes and environmental factors, and the genes are additive and have small effects (Dempster and Lerner, 1950). Like continuous traits, the liability is additive sum of normal distributed genetic effects and independent normally distributed environmental effects. In linear model, the liability of an individual can be expressed as:

$$l_i = \mu + e_i$$

where  $\mu$  is the mean liability and  $e_i \sim N(0,1)$ . Usually the variance of underlying variable is taken as unit for convenience. The association between the realized categorical and underlying continuous scales is given by a set of fixed thresholds in the liability scale. Let us consider  $m$  mutually independent and exhaustive categories of response. If the liability of an individual is between thresholds  $t-1$  and  $t$ , then the individual is scored as responding in the  $t^{\text{th}}$  scale. The link between the underlying and realized scales can be established via the standard normal distribution function. The standardized liability values can be obtained by subtracting the mean from the threshold value and dividing by the phenotypic standard deviation of liability ( $\sigma$ ):

$$\mu = (t - \sigma) / \sigma$$

In the case of two categories, such as sheep fertility,  $\mu$  gives the point in the underlying scale at which there are probability masses equal to  $1 - p$  and  $p$  to the left and to the right of the threshold, respectively, where  $p$  is the proportion of individuals showing the trait. Therefore, given  $p$ ,

$$1 - p = \text{Prob}(l_i < t | \mu) = \int_{-\infty}^{\mu} \phi(u) du = \Phi(\mu)$$

where the  $\phi$  and  $\Phi$  are the standard normal density and cumulative distribution function, respectively. Also, given  $p$ , the distance between the threshold and mean of the standard normal scale is obtained from the following inverse relationship:

$$\mu = \Phi^{-1}(1 - p)$$

### 2.2.2.2. Link Functions

The link function relates the linear predictor  $\eta$  to the expected value  $\mu$  of a datum,  $y$ . Each distribution has a special link function between  $\eta$  and  $\mu$  (the notation here have different meaning from last section). The simplest link function is identity link,  $\eta = \mu$  for normal distribution. If the data is in the form of counts arising from a Poisson process, the restriction  $\mu > 0$  needs to be imposed. In such cases, log link,  $\eta = \log \mu$  with inverse  $\mu = e^\eta$ , is particularly useful and has given origin to the class of log-linear models in which the effects are multiplicative, rather than additive. If the distribution is binomial, the  $\eta$  that  $0 < \mu < 1$  must be satisfied. In this case, three link functions are often employed:

(a). the logit function:

$$\eta = \log \frac{\mu}{1-\mu}$$

(b). the probit function:

$$\eta = \Phi^{-1}(\mu)$$

with inverse

$$\mu = \Phi(\eta) = \int_{-\infty}^{\eta} \frac{1}{\sqrt{2\pi}} e^{-\frac{x^2}{2}} dx$$

where  $\Phi$  is the Normal cumulative distribution function, and

(c). the complementary log-log function:

$$\eta = \log [-\log(1-\mu)]$$

The logit function, being the logarithm of an odds ratio, is easy to interpret. It is symmetric and nearly identical to the probit function in the range  $.1 < \mu < .9$  when both function are appropriately standardized (McCullagh and Nelder, 1983). Finally, the power family of links,  $\eta = \mu^\alpha$  if  $\alpha > 0$  and  $\eta = \log(\mu)$  if  $\alpha = 0$ , can also be considered.

Maximum likelihood estimates of  $\mathbf{b}$  can be obtained through an iterative weighted least-square procedure as demonstrated by Nelder and Wedderburn (1972):

$$\mathbf{X} \mathbf{D} \mathbf{V}^{-1} \mathbf{D} \mathbf{X} \hat{\mathbf{b}} = \mathbf{X} \mathbf{D} \mathbf{V}^{-1} \mathbf{y}$$

where  $\mathbf{X}$  is the incidence matrix,  $\mathbf{D}$  and  $\mathbf{V}$  are diagonal matrices with elements equal to  $(d_i/d\mu_i)$  and a quantity proportional to the variance of  $y_i$ , respectively, and

$$\mathbf{y}^* = \mathbf{Xb} + \mathbf{D}^{-1}(\mathbf{y}-\mathbf{u})$$

is a vector of working variates to be reestimated at each iterate. Therefore,  $\mathbf{D}$  depends on the link function,  $\mathbf{V}$  depends on the distribution assumed, and  $\mathbf{y}^*$  is a linear combination of the linear predictor and the discrepancy between observed and fitted value (Thompson, 1989). Illustrations of generalized linear models can be found in Glimour (1983) and Ducrocq (1990).

### **2.1.3. Estimation of Genetic Parameters for Categorical Traits**

The estimation of genetic parameters for categorical traits may prove complicated, because the real distribution cannot be observed (Olausson and Ronnigen, 1975). The most extreme case arises when a character is classified into only two values. Such characters are fertility of sheep, disease resistance, fleece defect and so on. These traits will mostly be recorded as pregnant or not, healthy or sick, and normal or defective.

Robertson and Lerner (1949) suggested that heritability of a trait be measured in terms of its probability of expression (p scale), with values of 1 and 0 assigned to each individual that expresses or fails to express the trait, respectively. However, using p scale introduces some problem for evaluation of all-or-none traits (Dempster and Lerner, 1950). Considerable measurement errors may result because genetic variation which may be completely additive for the underlying scale may lose this property in the p scale. Since the phenotypic values are 0 and 1, it is unlikely that gene substitution would have the same effect near these two limits on the p scale range. Unlike the underlying variate, the environmental variance is dependent on the range of the p scale. At an incidence around .5, the environmental variance would be minimal and with lower or higher incidence the variance would increase. The categorical nature of measures on the p scale may obscure finer degrees of measurable variation and thus detection of genetic differences between

individuals and families associated with those finer degrees of variation. Robertson and Lerner (1949) recommended arc-sine transformation for binomial traits with only two classes. They and other scientists (Dempster et al., 1950), however, used another way of estimating heritability of threshold characters with special reference to mortality in poultry. Their development has assumed an underlying normal distribution of genetic and environmental values with a linear relationship between the genetic value on the normal scale and the genetic value on the binomial scale. The theory suggests that heritability on the binomial scale is

$$h_b^2 = \frac{h_n^2 z^2}{p(1-p)}$$

where  $h_n^2$  is the heritability on the normal scale,  $z$  is the height of the ordinate of normal distribution at the threshold that determines whether the binomial variable is one or zero, and  $p$  is the frequency of ones. The accuracy of this relationship between the two scales was studied by several scientists (Van Vleck, 1972; Olausson and Ronnigen, 1975). The two simulation studies agreed well each other that transformation of heritability estimates made on the binomial scale for an all-or-none character to the underlying normal scale by multiplying the estimate by  $(p(1-p))/z^2$  was generally applicable for half-sib design data but may be over-estimated substantially if the estimate was from parent-offspring correlation design and particularly when  $p$  is not between .25 and .75. The over-estimate will be greater when normal heritability is larger than when it is small.

Falconer (1965) proposed an efficient method of estimating heritability on the underlying scale for disease liability in human. The heritability is estimated from the regression

$$t = m_R - m_P / i = x_P - x_R / i$$

$$h^2 = t/r$$

where the subscripts P and R refer to the population and relatives respectively,  $m$  is the mean as a deviation from the threshold,  $x$  is the normal deviate of the threshold from the

mean,  $i$  is the mean deviation of affected individuals from population mean and  $r$  is the coefficient of relationship. The error introduced by assuming the variance to be the same in the relatives of affected individuals as it is in the population as a whole leads to the correlation estimates from above equation being too low by a factor of 5 or 10 per cent (Edward, 1969). A modified formula that takes account of the unequal variances is the following:

$$t = \frac{x - x_R \sqrt{[1 - (x^2 - x_R^2)(1 - x/i)]}}{i + x_R^2(i - x)}$$

where  $x$  and  $i$  without subscript refer to the population, and  $x_R$  refer to relatives; the sign of square root is taken to make  $t$  between 0 and 1.

Gianola (1979) derived general expressions relating heritability in underlying normal scale to heritability in observed scale, where the expression of the character is a response in one of the several mutually exclusive and exhaustive categories.

$$h_c^2 = h_n^2 \frac{\sum_{i=1}^{m-1} [z_i(w_{i+1} - w_i)]^2}{\sum_{i=1}^m w_i^2 p_i - \left(\sum_{i=1}^m w_i p_i\right)^2}$$

Where  $m$  is number of response categories,  $p_i$  is the expected incidence in the  $i^{\text{th}}$  category,  $\{z_i\}$  are ordinates of the standard normal density function evaluated at the abscissas to  $\{p_i\}$ , and  $\{w_i\}$  are the scores assigned to the categories, 0-1 for sheep fertility and 1-4 for litter size. With two categories, the formula become identical to the expression derived by Robertson (1950).

Methods for estimation of genetic and phenotypic correlation for threshold characters have not been studied to the same extent as heritability. Olausson and Ronnigen (1975) simulated two correlated traits, one normally distributed and the other binomial distributed (all-or-none). They concluded that the genetic correlation between two traits can be estimated by half-sib correlation method in the ordinary way without transformation of the estimate except for low level (5% and 10%) of the all-or-none trait. The estimates will be

almost the same as if the underlying normal distribution had been used, except for low heritability level (.1) and for low incidence levels (5% and 10%) of all-or-none trait, where correction on the estimate made on the all-or-none data is recommended. However, phenotypic correlation between the two traits was highly biased downward.

Van Vleck and Gregory (1992) utilized multiple trait restricted maximum likelihood to analyze the ovulation rate for simulated measures of ovulation rate with underlying multivariate normal distributions. A data set with eight measures of ovulation rate treated as separate traits was used as a template to simulate data sets of eight multivariate normal traits that were then truncated to binomial traits. Ten replicates for each combination of heritability (.15, .25, and .35) and genetic correlation (.50, .66 and .90) were simulated on normal scale. They concluded that the usual transformation of heritability estimated on the binomial scale overestimated heritability on the normal scale. Genetic correlations on the binomial scale seriously underestimated the correlation on normal scale.

#### **2.2.4 Genetic Analyses of Categorical Traits, A Review**

A brief review of methodologies used for categorical data in animal breeding is presented in this section. Then in later sections, mathematical presentations for some common methods for categorical traits will be given.

##### **2.2.4.1. Linear Models**

Many methodologies for categorical traits have been investigated in animal breeding, which can generally be classified into two groups, linear and non-linear models. In the linear models, Least Squares (Harvey, 1982), generalized least squares (GLS) (Harvey, 1982) and the log-linear model (Gianola, 1982; Rutledge and Gunsett, 1982) are procedures that have been used in the estimation of fixed effects for categorical data.

Harvey (1982) suggested that Ordinary Least Squares (OLS) procedures be used for binomial data and Weighted Least Square procedure for percentage data. He justified his

recommendation by (1) flexibility in model selection and estimation of variance-covariance components and (2) existence of readily available computer software. However, a careful interpretation of results needs to be done since tests of significance, standard errors and confidence intervals are only approximations because no distribution assumptions are required for a least square analysis.

The GSK procedure is used to analyze categorical data arranged in an two-way contingency table, where the  $r$  rows represent combinations of levels of fixed effects and  $c$  columns represent mutually exclusive response categories. This procedure produce minimum  $\chi^2$  estimates. The function of the true cell probabilities of response,  $F(\cdot)$  are modeled as linear or nonlinear combinations of fixed effects:

$$F(\cdot) = \mathbf{Xb},$$

where  $\mathbf{b}$  is the vector of fixed effects and  $\mathbf{X}$  is a known incidence matrix. GSK is then used to estimate  $\tilde{\mathbf{b}}$ .  $\tilde{\mathbf{b}}$  is a best asymptotic normal (BAP) estimate of  $\mathbf{b}$  and has same properties as the maximum likelihood estimator but is easier to obtain.

Log-linear approach utilizes maximum likelihood estimates. However, large sample theory gives asymptotic equivalency to GSK. In log-linear approach, the logarithm of the expected cell number is expressed as a linear function of parameters. A limitation of log-linear models is their general restriction to nested models. If an interaction effect is included in the model, then all lower order interactions and main effects must be included.

Among linear models, perhaps Henderson's mixed models are most often used in genetic analyses of categorical data. This algorithm yields best linear unbiased estimates (BLUE) of fixed effects and best linear unbiased predictors (BLUP) of the random effects when assumptions hold. These methodologies have been extensively used with discrete traits in the areas of dairy cattle (Weller and Ron, 1992; Van Vleck and Gregory, 1992), beef cattle, swine (Keel et al., 1995; Roehe and Kennedy, 1995) and sheep (Waldron and Thomas, 1992).

Linear model procedures do not adequately account for the discrete nature of the data. Thompson (1979), Gianola (1980) and Hoeschele (1986) identified and extensively discussed some problems in the analysis of categorical traits by linear models. Some of most critical problems are: 1) variances of categorical traits are heterogeneous, 2) BLUP solutions do not take into consideration the restriction that the sum of response probabilities must be total 1 across all categories of responses, 3) the additive genetic variance in the outward scale depends on the incidence of the trait in the population, 4) it is possible that non-additive genetic effect are present in the outward scale even in the case where all the genetic variation is additive in the underlying scale, and 5) when the conditional expectation of the predictand given the data is not linear, the ranking properties of the best linear predictor appear not to be optimal.

#### **2.2.4.2. Non-linear models**

The non-linear model methodologies developed for animal breeding situations resulted from combining the theory of generalized linear models (Matos, 1993) and the threshold model (Falconer, 1989). The term “generalized linear model (GLM)” was introduced by Nelder and Wedderburn (1972), and GLMs are an extension of classical linear models that include as special cases linear models and analysis of variance models. Two important features of GLM are that linearity is a property of the fitted values given by the model and not of the data, and variance can be dependent on means. The assumptions of homogeneity of variances and normality for residual term, therefore, are not critical. In GLM, observations are assumed to be independent (or at least uncorrelated), and only one term is allowed in the model (McCullagh and Nelder, 1983).

There are numerous non-linear model methods (Smith, 1989). Gilmour’s method was originally for dichotomous data (Gilmour et al, 1985 ) and later extended to multiple ordered categories (Gilmour et al, 1987), which applied GLM theory directly on the



underlying scale. Iterative procedures are needed to solve the resulting system of equations, which is structurally similar to that obtained by Harville and Mee (1984).

The method of Harville and Mee (1984) is based on a mixed model version of threshold model and can be considered an extension of maximum likelihood. The resulting equations can be resolved by EM algorithm. This approach yields the same results as that of Gianola and Foulley (1983). But, the interpretation is different because the latter approach was derived using a Bayesian approach. Foulley et al (1987) extended the method of Gianola and Foulley (1983) to traits distributed as Poisson-Binomial in a polytocous species.

With regarding to variance component estimation, the methods of Harville and Mee (1984) and Gilmour et al (1985) can be viewed as an extension of REML. With respect to Bayesian methods for variance components, procedures for continuous data assuming normality (Gianola and Fernando, 1986) has been extended for discrete traits (Hoeschele et al, 1987; Foulley et al., 1987). The general principle for obtaining estimators of dispersion parameters is based on integration of joint posterior distribution of the dispersion and location parameters with respect to the location parameters.

Tempelman and Gianola (1993) proposed an algorithm to compute estimates of variance components in Poisson models. This algorithm, termed DFMML ( derivative free marginal maximum likelihood ), invokes the same normal approximation on the conditional posterior of the location parameters as the EM algorithm of Foulley et al. (1987). However, instead of using gradients, DFMML work directly with the logarithm of marginal likelihood of the variance components. Foulley and Im (1993) extended to Poisson variables the approach of Gilmour (1985) for estimating fixed effects by maximum quasi-likelihood in the analysis of threshold discrete data with a generalized linear mixed model.

Recently, Bayesian analysis of binary or polychotomous threshold traits via Gibbs sampling have been investigated (Hoeschele and Tier, 1995). Also several scientists have extended non-linear model methodologies to joint analysis of categorical and continuous

traits (Foulley et al., 1987; Hoeschele et al, 1995; Jenss and Foulley, 1993; Simianer and Schaeffer, 1989; Zhang, 1994).

#### **2.2.4.3. Comparison Between Linear and Non-linear Methodologies**

Meijering and Gianola (1985) compared the ability of BLUP and of the non-linear procedure (GFCAT) of Gianola and Foulley (1983) to rank cattle sires using Monte Carlo simulations of categorical data under three different models. In most cases, both methods performed similarly. Only when response was binary, the layout was highly unbalanced and a mixed model was appropriate to describe the underlying variate, did CFCAT elicit significantly larger responses to truncation selection than BLUP at  $h^2 = .2$  or  $.5$  and when the incidence in the population was below 25%. The largest observed difference in selection efficiency between the 2 methods was 12%.

King ( 1991 ) compared the merit of different methods including those which treated the traits as if they were continuous (REML and Henderson's method 3) and the other methods which recognized the categorical nature of the traits using Bayesian analysis with an informative prior or a generalized linear model analysis. He concluded that the Bayesian method had smaller MSE's for heritability and correlation estimates, produced similar rank correlation and required substantially less total computer time than the pseudo-expectation method. However, nonlinear models are theoretically more complex and computationally more demanding than linear models. In another simulation study, Matos (1993) observed advantages for nonlinear models only in specific instances. For example, heritability estimates on the binomial scale become progressively smaller in relation to the constant value for heritability on the underlying continuous distribution as the frequencies of the binomial classes approach 0 and 1.

Weller and Ron (1992) compared threshold and linear models in the analysis of fertility traits and in the estimation of genetic parameters using field data from Israeli Holsteins. Evaluations of random and fixed effects affecting heifer and cow fertility

computed by threshold model and linear model were highly correlated. In another study (Meuwissen et al, 1995), the ordinary animal or linear mixed model (LMM), which ignored the categorical nature of the trait, was compared to a generalized linear mixed model (GLMMp) that assumes a linear mixed model for underlying continuous variable for selection efficiency on categorical traits. In a closed nucleus breeding scheme, rate of genetic gain increased by 1 to 2 %, when GLMMp was used instead of LMM. However, when considering a binary traits, rate of gain can be increased by up to 84% by gathering more information on high-incidence categories, indicating that in some cases accounting for the categorical nature of traits is recommended, because it involves only a straightforward extension of the linear animal model and increase rates of gain substantially.

Olesen et al (1994) compared different methodologies, which included linear mixed model (LM), threshold model (TM) and Poisson mixed model(PM) for genetic analysis of number of lambs born from 1-yr-old ewes with 37,718 and 18,633 records of two Norwegian breeds, Dala and Spalsau, respectively. Models fitted included flock-year as a fixed effect and the random effect of sire. The models were compared with respect to goodness of fit, predictability, and ranking of sires. All models performed similarly with respect to goodness of fit, predictability, and ranking of sires.

In summary, the result from the above studies using simulated or field data did not show that non-linear models perform better than linear model for genetic analysis of categorical data except for some special cases. Also non-linear methods are computationally more demanding. Their merit relative to linear models was not justified.

### **2.3 (Co)variance Component Estimation**

Statistically, the second moment statistics are called variance parameters, which mainly include variances and covariances for random variable as well as various variance ratios, standard deviations and correlation coefficients derived from variances and covariances such as heritability, genetic correlation and repeatability. Various methodologies exist to

estimate (co)variances. As the estimation of (co)variance components is one of major tasks faced by animal breeders, searching for more reliable, accurate methodologies has been one of the foci in animal breeding. Common methods for variance component estimation encompass analysis of variance (ANOVA), which includes traditional ANOVA, various correlation and regression methodologies, as well as the methodologies with modifications to the ANOVA sum of square for unbalanced data such as Henderson's Method 1, 2, 3, 4 (Henderson, 1984), Minimum-norm-quadratic unbiased estimation (MINQUE) (Searle, 1989), maximum likelihood estimation (ML) (Harville, 1977), restricted maximum likelihood estimation (REML) (Meyer, 1989, 1991) and recently developed non-linear methodologies based on Bayesian approaches.

In the numerous forms of analysis of variance mentioned above, variance components are estimated by equating observed mean squares to expression of their expected values. ANOVA has the nice feature that the estimators are unbiased regardless of whether the data are normally distributed and it is especially useful in the analysis of controlled experiments where the structure of the data has a regular form. However, ANOVA also has two significant practical limitations. First, ANOVA estimates of variance components require that sample sizes be reasonably well balanced among fixed effect classes, with the number of observation for each set of conditions being nearly equal. In field situations, individuals are often lost, and even the most carefully crafted balanced design can quickly collapse into an extremely unbalanced one. Henderson's methodologies was proposed to account for this, but their sampling properties are poorly known. Although a balanced data set can sometimes be constructed prior to analysis by ignoring information from some individuals, this is clearly not an efficient way to utilize data. Second, field observations often yield records on a variety of relatives, such as offspring, parents, sibs etc., that cannot be analyzed jointly with ANOVA.

Unlike ANOVA estimators, maximum likelihood (ML), and most notably, restricted maximum likelihood (REML) estimators do not place any special demands on the design or

balance of data and hence are ideal for the unbalanced designs that arise in quantitative genetics. Further, ML/REML estimates can readily be obtained for any arbitrary pedigree of individuals. A logical approach to estimating variance components from observations in complex pedigree might seem to be the use of maximum likelihood procedures. ML was first introduced for variance component estimation by Hartley and Rao (1967). Conceptually, ML attempts to identify the values of the parameters of the distribution that maximize the likelihood of the observed data. As is the case for almost all ML methods, this distribution is assumed to be multivariate normal. ML estimators are efficient in the sense that they simultaneously utilize all of the available data and also have smallest asymptotic error.

Compared with REML, one drawback with variance estimation via the usual maximum-likelihood approach is that all fixed effects are assumed to be known without error. This is rarely true in practice, and as a consequence, ML estimators of variance components are biased. Most notably, estimates of residual variance tend to be biased downward. The reason for this is that the observed deviations of individual phenotypic values from an estimated population mean tend to be smaller than their deviations from the true (parameter) mean. Such errors can become quite large when a model contains numerous fixed effects, and particularly when sample sizes are small. Unlike ML estimators, REML estimators maximize only the portion of the likelihood that does not depend on the fixed effect. In this sense, REML is a restricted version of ML. The elimination of bias by REML is analogous to the removal of bias that arises in the estimate of a variance component when the mean squared deviation is divided by the degrees of freedom instead of by the sample size. However, REML does not always eliminate all of the bias in parameter estimation, since many methods for obtaining REML estimates cannot return negative estimates of a variance component. While this seems a desirable property, it has the side effect of upwardly biasing estimates.

In the following sections, we will introduce several mathematical methodologies. For general framework of (co)variance component estimation, Derivative-free REML is described. Then, specifically, mathematical formula for estimation of within-trait direct-maternal covariance for growth traits and across-trait genetic covariances between litter size and growth traits was derived. Throughout the methods, effort is made to accommodate the models used in our research. Derivative-free REML will be emphasized with regarding to methodology and application.

### **2.3.1. Derivative-free REML**

REML was first suggested by Thompson (1962) and then developed further by Patterson and Thompson (1971). REML is marginally sufficient, consistent, efficient and asymptotically normal (Harville, 1977). Thus, all information available is utilized in an optimal way. Over the last decade, restricted maximum likelihood (REML) has become the method of choice for estimating variance components in animal breeding and related disciplines trying to partition the phenotypic variation into genetic and other components, thanks to an increase in the general level of computational resources available and the development of numerous specialized algorithms exploiting specific features of the data structure or model of analysis as well as utilizing a variety of numerical techniques (Meyer, 1989). REML requires that the likelihood function be partitioned into two parts including one which is free of fixed effects and operates on the likelihood of linear functions of the data vector with expectations zero, the so-called error contrasts or, equivalently, on the part of the likelihood (of data vector) which is not dependent of fixed effects. This results in the loss in degrees of freedom due to fitting of fixing effects being taken into account (Patterson and Thompson, 1971). The main difference between ML and REML is that REML utilize the likelihood of linear function  $\mathbf{K} \mathbf{y}$  instead of observation vector  $\mathbf{y}$ .

Let us consider a general linear model,

$$\mathbf{y} = \mathbf{X}\mathbf{b} + \mathbf{Z}\mathbf{u} + \mathbf{e}$$

with  $\mathbf{y}$ ,  $\mathbf{b}$ ,  $\mathbf{u}$  and  $\mathbf{e}$  representing the vectors of observations, fixed effects, random effects and residual errors, respectively, and  $\mathbf{X}$  and  $\mathbf{Z}$  the corresponding design matrices. Assume that  $E(\mathbf{y}) = \mathbf{X}\mathbf{b}$ ;  $E(\mathbf{u}) = E(\mathbf{e}) = \mathbf{0}$ ;  $V(\mathbf{u}) = \mathbf{G} = \mathbf{A} \sigma_a^2$ , where  $\mathbf{A}$  is additive relationship matrix;  $V(\mathbf{e}) = \mathbf{R} = \mathbf{I} \sigma_e^2$ , and  $\text{cov}(\mathbf{u}, \mathbf{e}) = \mathbf{0}$ ; then:

$$V(\mathbf{y}) = \mathbf{Z}\mathbf{G}\mathbf{Z}' + \mathbf{R} = \mathbf{Z}\mathbf{A}\mathbf{Z}' \sigma_a^2 + \mathbf{I} \sigma_e^2,$$

Variance components estimates from REML are function of only  $\mathbf{u}$ , which suggests estimating  $\sigma_a^2$  and  $\sigma_e^2$  from a function of data ( $\mathbf{y}$ ), say  $\mathbf{K}\mathbf{y}$  with  $\mathbf{K}\mathbf{X}\mathbf{b} = \mathbf{0}$ , where  $\mathbf{K}$  is a matrix whose rows correspond to different error contrasts and there are at most  $n-p$  linearly independent error contrasts.

$E(\mathbf{K}\mathbf{y}) = \mathbf{K}\mathbf{X}\mathbf{b} = \mathbf{0}$ , so  $\mathbf{K}\mathbf{X} = \mathbf{0}$  (translation invariance) and  $r(\mathbf{K}) = N - r(\mathbf{X})$

$$\mathbf{K}\mathbf{y} = \mathbf{K}\mathbf{Z}\mathbf{u} + \mathbf{K}\mathbf{e}, \text{ with } \mathbf{K}\mathbf{y} \sim N(\mathbf{0}, \mathbf{K}\mathbf{V}\mathbf{K}')$$

The logarithm of the restricted multivariate normal likelihood can be written as :

$$= -.5 [ (n-p)\log(2\pi) + \log |\mathbf{K}\mathbf{V}\mathbf{K}'| + \mathbf{y}\mathbf{K}(\mathbf{K}\mathbf{V}\mathbf{K}')^{-1}\mathbf{K}\mathbf{y} ].$$

Although  $\mathbf{K}\mathbf{X} = \mathbf{0}$  guarantees invariance, the maximization of does not require knowing  $\mathbf{K}$ . A somewhat more familiar identity with constraints already imposed on  $\mathbf{X}$  is

$$= -.5 [ \text{const} + \log |\mathbf{V}| + \log |\mathbf{X}\mathbf{V}^{-1}\mathbf{X}'| + (\mathbf{y} - \mathbf{X}\mathbf{b})' \mathbf{V}^{-1}(\mathbf{y} - \mathbf{X}\mathbf{b}) ].$$

Where  $\text{const} = (n-p)\log(2\pi)$  is affected by choice of  $\mathbf{V}$  to maximize.  $n$  is the number of records and  $p$  is the rank of the part of the coefficient matrix due to fixed effects.

Harville (1977) and Searle (1979) developed an equivalent form of that is important for derivative-free REML (DFREML):

$$= -.5 [ \text{const} + \log |\mathbf{R}| + \log |\mathbf{G}| + \log |\mathbf{C}| + \mathbf{y}\mathbf{P}\mathbf{y} ]. \text{ where,}$$

$\mathbf{C}$  is the full-rank coefficient matrix for the MME and  $\mathbf{y}\mathbf{P}\mathbf{y}$  with  $\mathbf{P} = \mathbf{V}^{-1} - \mathbf{V}^{-1}\mathbf{X}(\mathbf{X}\mathbf{V}^{-1}\mathbf{X})^{-1}\mathbf{X}\mathbf{V}^{-1}$ , is the generalized residual sum of squares.

Often, evaluating the log likelihood is less confusing if instead of maximizing  $\ln L$ ,  $-2 \ln L$  is minimized; i.e.

$$-2 \ln L = \text{const} + \ln |\mathbf{R}| + \ln |\mathbf{G}| + \ln |\mathbf{C}| + \mathbf{y}' \mathbf{P} \mathbf{y}.$$

The derivative-free method, very simply, is to try different  $\mathbf{R}$  and  $\mathbf{G}$  until the combination that minimizes the log likelihood,  $-2 \ln L$ , is found for the data,  $\mathbf{y}$ . Depending on different models, the log-likelihood function,  $-2 \ln L$ , was minimized with respect to direct heritability ( $h_a^2 = \sigma_a^2 / \sigma^2$ ), additive maternal effects ( $m^2 = \sigma_m^2 / \sigma^2$ ), the genetic covariance between direct and maternal effect as a proportion of the product of two variances, the permanent environmental variance due to the animal or dam as a proportion of phenotypic variance ( $PE_a^2$  and  $PE_m^2$ ) as well as all the other across-trait covariances included in the models. The error variance was estimated directly from the residual sum of the squares.

In the expression to be minimized, the constant is ignored. At each round the other four term must be calculated. The easy terms are  $\ln |\mathbf{R}|$  and  $\ln |\mathbf{G}|$ . For example, for the model for growth traits in this dissertation, with  $\mathbf{R} = \mathbf{I}_n \sigma_e^2$ ,  $\ln |\mathbf{R}| = n \ln(\sigma_e^2)$  and with

$$\mathbf{G} = \begin{bmatrix} \mathbf{A}_a^2 & \mathbf{A}_{am} & 0 \\ \mathbf{A}_{am} & \mathbf{A}_m^2 & 0 \\ 0 & 0 & \mathbf{I}_p^2 \end{bmatrix}. \text{ Then,}$$

$$\ln |\mathbf{G}| = 2 \ln |\mathbf{A}| + q \ln \begin{vmatrix} \mathbf{A}_a^2 & \mathbf{A}_{am} \\ \mathbf{A}_{am} & \mathbf{A}_m^2 \end{vmatrix} + p \ln(\sigma_e^2).$$

The  $\ln |\mathbf{A}|$  is also a constant but if wanted can be computed easily as a by-product of a one-time calculation of  $\mathbf{A}^{-1}$ . By Choleski decomposition,  $\mathbf{A} = \mathbf{L}\mathbf{L}'$ ,

$$\ln |\mathbf{A}| = \ln |\mathbf{L}| + \ln |\mathbf{L}'|, \text{ so that } \ln |\mathbf{A}| = 2 \sum \ln(l_{ii}).$$

Similarly, multiple trait versions of  $\ln |\mathbf{R}|$  and  $\ln |\mathbf{G}|$  are not difficult to compute. The difficult terms of  $-2 \ln L$  to evaluate are  $\ln |\mathbf{C}|$  and  $\mathbf{y}' \mathbf{P} \mathbf{y}$ . The strategy proposed by Smith and Graser (1986) to calculate those terms is based on Gaussian elimination. Meyer (1989, 1991) incorporated the idea of Smith and Graser (1986) into a remarkable series of



DFREML programs that took advantage of sparseness of  $\mathbf{C}$  using linked list technique. The search strategy for updating  $\mathbf{R}$  and  $\mathbf{G}$  for MME was the simplex method which is a generally efficient method for non-linear optimization and easily accommodates constraining  $\mathbf{R}$  and  $\mathbf{G}$  to their parameter space.

Several scientists studied the reliability, robustness, convergence properties of the Simplex method (polytope method) (Boldman and Van Vleck, 1993; Meyer, 1989, 1991, 1992). Based on some studies, minimization techniques such as the polytope method which are based on function comparison are not susceptible to rounding error but few guarantees can be made concerning convergence. A potential problem is false convergence to a point other than the minimum. Meyer (1989) reported that while the number of likelihood's required for convergence varied with the starting values, final estimates were invariant to the starting values selected and suggested that local maxima are not a problem with REML estimation via the DF algorithm. Kavac and Groeneveld (1989) used the polytope procedure in a multiple trait animal model to estimate additive genetic and residual covariance matrices of two traits (backfat thickness and daily gain) from 649 field test scores of boars. They found that different starting values converged to two distinct parameter sets and concluded that local maxima can exist in multivariate data sets. Boldman and Van Vleck (1990), working with the simulated data of Meyer (1989), found that different direct-maternal correlation ( $r_{am}$ ) priors converged to different final estimates. They found that the variation in estimates for the DF algorithm may result from the failure of the polytope algorithm to locate the global maximum rather than the existence of local maxima. Further study indicated that when the analyses utilizing the polytope method were restarted at the claimed minimum with an initial step size of .2, the same final parameter vector was obtained in all analyses. The increased reliability of the final estimates would seem to be well worth the additional likelihood evaluations required for a restart. For this restart, a reduced step size, i.e.,  $< .2$ , is likely to be sufficient.

### 2.3.2. Covariance between Direct Genetic and Maternal Genetic Effects for Growth Traits

Consider the following model for growth traits in sheep:

$$\mathbf{Y} = \mathbf{X}\mathbf{b} + \mathbf{Z}_a\mathbf{u} + \mathbf{Z}_m\mathbf{m} + \mathbf{Z}_p\mathbf{p} + \mathbf{e}$$

with  $E(\mathbf{Y}) = \mathbf{X}\mathbf{b}$ ,  $E(\mathbf{u}) = E(\mathbf{m}) = E(\mathbf{p}) = E(\mathbf{e}) = \mathbf{0}$ ,

$$\text{Var} \begin{matrix} \mathbf{u} \\ \mathbf{m} \\ \mathbf{c} \\ \mathbf{e} \end{matrix} = \begin{matrix} \mathbf{A}_a^2 & \mathbf{A}_{am} & 0 & 0 \\ \mathbf{A}_{am} & \mathbf{A}_m^2 & 0 & 0 \\ 0 & 0 & \mathbf{I}_p^2 & 0 \\ 0 & 0 & 0 & \mathbf{I}_e^2 \end{matrix}, \text{ and}$$

$$\text{Var}(\mathbf{Y}) = \mathbf{Z}_a\mathbf{Z}_a^2 + \mathbf{Z}_m\mathbf{Z}_m^2 + (\mathbf{Z}_a\mathbf{Z}_m + \mathbf{Z}_m\mathbf{Z}_a)_{am} + \mathbf{I}_p^2 + \mathbf{I}_e^2$$

where  $\mathbf{Y}$ ,  $\mathbf{b}$ ,  $\mathbf{u}$ ,  $\mathbf{m}$ ,  $\mathbf{p}$ ,  $\mathbf{e}$  denote the vectors of observation and of fixed, direct additive genetic, maternal genetic, permanent environmental and residual effects, respectively and  $\mathbf{X}$ ,  $\mathbf{Z}_a$ ,  $\mathbf{Z}_m$ , and  $\mathbf{Z}_p$  represent the corresponding incidence matrices.

Let  $\tilde{a}^2$ ,  $\tilde{m}^2$ ,  $\tilde{am}$ ,  $\tilde{p}^2$  and  $\tilde{e}^2$  be prior values. Then, **MME** are,

$$\begin{matrix} \mathbf{X}\mathbf{X} & \mathbf{X}\mathbf{Z}_a & \mathbf{X}\mathbf{Z}_m & \mathbf{X}\mathbf{Z}_p & \mathbf{b} & \mathbf{X}\mathbf{Y} \\ \mathbf{Z}_a\mathbf{X} & \mathbf{Z}_a\mathbf{Z}_a + \mathbf{A}_{11} & \mathbf{Z}_a\mathbf{Z}_m + \mathbf{A}_{12} & \mathbf{Z}_a\mathbf{Z}_p & \mathbf{u} & \mathbf{Z}_a\mathbf{Y} \\ \mathbf{Z}_m\mathbf{X} & \mathbf{Z}_m\mathbf{Z}_a + \mathbf{A}_{12} & \mathbf{Z}_m\mathbf{Z}_m + \mathbf{A}_{22} & \mathbf{Z}_m\mathbf{Z}_p & \mathbf{m} & \mathbf{Z}_m\mathbf{Y} \\ \mathbf{Z}_p\mathbf{X} & \mathbf{Z}_p\mathbf{Z}_a & \mathbf{Z}_p\mathbf{Z}_m & \mathbf{Z}_p\mathbf{Z}_p + \mathbf{I}_p & \mathbf{p} & \mathbf{Z}_p\mathbf{Y} \end{matrix} =$$

where,

$$\begin{aligned} 11 &= \tilde{e}^2 \tilde{m}^2 / (\tilde{a}^2 \tilde{m}^2 - \tilde{am} \tilde{am}) \\ 22 &= \tilde{e}^2 \tilde{a}^2 / (\tilde{a}^2 \tilde{m}^2 - \tilde{am} \tilde{am}) \\ 12 &= -\tilde{e}^2 \tilde{am} / (\tilde{a}^2 \tilde{m}^2 - \tilde{am} \tilde{am}) \\ 33 &= \tilde{e}^2 / \tilde{p}^2 \end{aligned}$$

The solution of **MME** can be expressed as:

$$\begin{matrix} \mathbf{b} & \mathbf{C}_{00} & \mathbf{C}_{01} & \mathbf{C}_{02} & \mathbf{C}_{03} & \mathbf{X} \mathbf{Y} & \mathbf{C}_0 \\ \mathbf{u} & \mathbf{C}_{10} & \mathbf{C}_{11} & \mathbf{C}_{12} & \mathbf{C}_{13} & \mathbf{Z}_a \mathbf{Y} & \mathbf{C}_1 \\ \mathbf{m} & \mathbf{C}_{20} & \mathbf{C}_{21} & \mathbf{C}_{22} & \mathbf{C}_{23} & \mathbf{Z}_m \mathbf{Y} & \mathbf{C}_2 \\ \mathbf{c} & \mathbf{C}_{30} & \mathbf{C}_{31} & \mathbf{C}_{32} & \mathbf{C}_{33} & \mathbf{Z}_p \mathbf{Y} & \mathbf{C}_3 \end{matrix} \mathbf{W} \mathbf{Y}$$

For **MINQUE**, choose the following quadratic forms:

$$\hat{\mathbf{u}} \hat{\mathbf{u}}, \hat{\mathbf{m}} \hat{\mathbf{m}}, \hat{\mathbf{u}} \hat{\mathbf{m}} + \hat{\mathbf{m}} \hat{\mathbf{u}}, \hat{\mathbf{p}} \hat{\mathbf{p}}$$

$$\mathbf{Y} \mathbf{Y} - \hat{\mathbf{b}} \mathbf{X} \mathbf{Y} - \hat{\mathbf{u}} \mathbf{Z}_a \mathbf{Y} - \hat{\mathbf{m}} \mathbf{Z}_m \mathbf{Y} - \hat{\mathbf{p}} \mathbf{Z}_p \mathbf{Y}$$

Their mathematical expectations are:

$$\begin{aligned} \mathbf{E}(\hat{\mathbf{u}} \hat{\mathbf{u}}) &= \mathbf{E}(\mathbf{Y} \mathbf{W} \mathbf{C}_1 \mathbf{C}_1 \mathbf{W} \mathbf{Y}) \\ &= \text{tr}(\mathbf{W} \mathbf{C}_1 \mathbf{C}_1 \mathbf{W}) \text{Var}(\mathbf{Y}) \\ &= \text{tr}(\mathbf{W} \mathbf{C}_1 \mathbf{C}_1 \mathbf{W} \mathbf{Z}_a \mathbf{Z}_a) \frac{2}{a} + \text{tr}(\mathbf{W} \mathbf{C}_1 \mathbf{C}_1 \mathbf{W} \mathbf{Z}_m \mathbf{Z}_m) \frac{2}{m} + \\ &\quad \text{tr}(\mathbf{W} \mathbf{C}_1 \mathbf{C}_1 \mathbf{W} (\mathbf{Z}_a \mathbf{Z}_m + \mathbf{Z}_m \mathbf{Z}_a)) \frac{2}{am} + \text{tr}(\mathbf{W} \mathbf{C}_1 \mathbf{C}_1 \mathbf{W}) \frac{2}{p} + \\ &\quad \text{tr}(\mathbf{W} \mathbf{C}_1 \mathbf{C}_1 \mathbf{W}) \frac{2}{e} \end{aligned}$$

$\mathbf{E}(\hat{\mathbf{m}} \hat{\mathbf{m}})$ ,  $\mathbf{E}(\hat{\mathbf{u}} \hat{\mathbf{m}} + \hat{\mathbf{m}} \hat{\mathbf{u}})$ ,  $\mathbf{E}(\hat{\mathbf{p}} \hat{\mathbf{p}})$  can be derived similarly.

$$\begin{aligned} &\mathbf{E}(\mathbf{Y} \mathbf{Y} - \hat{\mathbf{b}} \mathbf{X} \mathbf{Y} - \hat{\mathbf{u}} \mathbf{Z}_a \mathbf{Y} - \hat{\mathbf{m}} \mathbf{Z}_m \mathbf{Y} - \hat{\mathbf{p}} \mathbf{Z}_p \mathbf{Y}) \\ &= \mathbf{E}(\mathbf{Y} \mathbf{Y} - \mathbf{Y} \mathbf{W} \mathbf{C} \mathbf{W} \mathbf{Y}) \\ &= \text{tr}(\mathbf{V}) - \text{tr}(\mathbf{W} \mathbf{C} \mathbf{W} \mathbf{V}) \\ &= \text{tr}(\mathbf{Z}_a \mathbf{Z}_a - \mathbf{Z}_a \mathbf{W} \mathbf{C} \mathbf{W} \mathbf{Z}_a) \frac{2}{a} + \text{tr}(\mathbf{Z}_m \mathbf{Z}_m - \mathbf{Z}_m \mathbf{W} \mathbf{C} \mathbf{W} \mathbf{Z}_m) \frac{2}{m} + \\ &\quad \text{tr}(\mathbf{Z}_a \mathbf{Z}_m + \mathbf{Z}_m \mathbf{Z}_a - \mathbf{Z}_m \mathbf{W} \mathbf{C} \mathbf{W} \mathbf{Z}_a - \mathbf{Z}_a \mathbf{W} \mathbf{C} \mathbf{W} \mathbf{Z}_m) \frac{2}{am} + \\ &\quad \text{tr}(\mathbf{Z}_p \mathbf{Z}_p - \mathbf{Z}_p \mathbf{W} \mathbf{C} \mathbf{W} \mathbf{Z}_p) \frac{2}{p} + \text{tr}(\mathbf{I} - \mathbf{W} \mathbf{C} \mathbf{W}) \frac{2}{e}. \end{aligned}$$

If we let the value of these quadratic forms equal their expectation and set up these equations, we can solve them to get estimates of each variance and the covariance,  $\hat{\mathbf{C}}_{am}$ .

For **REML**, following iterative equations will be used,

$$\hat{\mathbf{C}}_e^{-2} = (\mathbf{Y} \mathbf{Y} - \hat{\mathbf{b}} \mathbf{X} \mathbf{Y} - \hat{\mathbf{u}} \mathbf{Z}_a \mathbf{Y} - \hat{\mathbf{m}} \mathbf{Z}_m \mathbf{Y} - \hat{\mathbf{p}} \mathbf{Z}_p \mathbf{Y}) / (N - r(\mathbf{X}))$$

$$\hat{\sigma}_a^2 = (\hat{\mathbf{u}} \hat{\mathbf{u}} + \hat{\sigma}_e^2 \text{tr} \mathbf{C}_{11})/q$$

$$\hat{\sigma}_m^2 = (\hat{\mathbf{m}} \hat{\mathbf{m}} + \hat{\sigma}_e^2 \text{tr} \mathbf{C}_{22})/q$$

$$\hat{\sigma}_{am} = (\hat{\mathbf{u}} \hat{\mathbf{m}} + \hat{\sigma}_e^2 \text{tr} \mathbf{C}_{12})/q$$

$$\hat{\sigma}_p^2 = (\hat{\mathbf{p}} \hat{\mathbf{p}} + \hat{\sigma}_e^2 \text{tr} \mathbf{C}_{33})/r(p)$$

Where, q= the number of levels of  $\mathbf{u}$  = the number of levels of  $\mathbf{m}$ ,

$r(p)$  = the number of levels of  $\mathbf{p}$ ,

$r(x)$  = the column rank of matrix x, and

$N$  = total number of observations

### 2.3.3. Across-trait Covariance Estimation between Growth Traits and Litter Size in Sheep

The general representation for the complete bivariate animal model for growth and litter size in our study can be expressed as:

$$\begin{matrix} \mathbf{y}_1 \\ \mathbf{y}_2 \end{matrix} = \begin{matrix} \mathbf{X}_1 & \mathbf{0} \\ \mathbf{0} & \mathbf{X}_2 \end{matrix} \begin{matrix} \mathbf{b}_1 \\ \mathbf{b}_2 \end{matrix} + \begin{matrix} \mathbf{Z}_1 & \mathbf{0} \\ \mathbf{0} & \mathbf{Z}_2 \end{matrix} \begin{matrix} \mathbf{u}_1 \\ \mathbf{u}_2 \end{matrix} + [\mathbf{Z}_{m1} \mathbf{m}_1] + \begin{matrix} \mathbf{Z}_{p1} & \mathbf{0} \\ \mathbf{0} & \mathbf{Z}_{p2} \end{matrix} \begin{matrix} \mathbf{c}_1 \\ \mathbf{c}_2 \end{matrix} + \begin{matrix} \mathbf{e}_1 \\ \mathbf{e}_2 \end{matrix}$$

Where  $\mathbf{y}_i$  is a  $s_i \times 1$  vector of records, the subscripts, 1, 2, representing growth traits and litter size, respectively.  $\mathbf{b}_i$  denote the vector of fixed effects (contemporary groups in this case);  $\mathbf{X}_i$  is the matrix that associates  $\mathbf{b}_i$  with  $\mathbf{y}_i$ ;  $\mathbf{u}_i$  is the vector of breeding values for direct effects;  $\mathbf{Z}_i$  is the matrix that associates  $\mathbf{u}_i$  with  $\mathbf{y}_i$ ;  $\mathbf{m}_1$  is the vector of breeding values for maternal genetic effects for growth traits;  $\mathbf{Z}_{m1}$  is the matrix that associates  $\mathbf{m}_1$  with  $\mathbf{y}_1$ ;  $\mathbf{c}_1$  is the vector of permanent environmental plus nonadditive genetic effects contributed by dams to records of their progeny;  $\mathbf{Z}_{p1}$  is the matrix that associates  $\mathbf{c}_1$  with  $\mathbf{y}_1$ ;  $\mathbf{c}_2$  is the vector of permanent environmental effects contributed by animals;  $\mathbf{Z}_{p2}$  is the matrix that associates  $\mathbf{c}_2$  with  $\mathbf{y}_2$ . For this model,

$$\mathbf{E} \begin{matrix} \mathbf{y}_1 \\ \mathbf{y}_2 \end{matrix} = \begin{matrix} \mathbf{X}_1 \mathbf{b}_1 \\ \mathbf{X}_2 \mathbf{b}_2 \end{matrix}, \quad \mathbf{E} \begin{matrix} \mathbf{u}_1 \\ \mathbf{u}_2 \end{matrix} = \mathbf{E} \begin{matrix} \mathbf{m}_1 \\ \mathbf{c}_1 \\ \mathbf{c}_2 \end{matrix} = \begin{matrix} \mathbf{0} \\ \mathbf{0} \\ \mathbf{0} \end{matrix},$$

and the variance-covariance matrix for genetic effects is,

$$\mathbf{V} [\mathbf{u}_1', \mathbf{u}_2', \mathbf{m}_1'] = \mathbf{G} \quad \mathbf{A} ,$$

$$\mathbf{G} = \begin{matrix} & g_{11} & g_{12} & g_1 m_1 \\ & g_{12} & g_{22} & g_2 m_1 \\ & g_1 m_1 & g_2 m_1 & m_{11} \end{matrix}$$

The variance-covariance matrix for permanent environmental effect is as follows:

$$\mathbf{V} [\mathbf{c}_1', \mathbf{c}_2'] = \mathbf{P} \mathbf{e} \quad \mathbf{I}_e, \quad \text{where,}$$

$$\mathbf{P} \mathbf{e} = \begin{matrix} c_{11} & c_{12} \\ c_{12} & c_{22} \end{matrix}$$

As the  $\mathbf{c}_1, \mathbf{c}_2$  are located in different fields in the data structure, covariance ( $c_{12}$ ) between the two effects is not allowed, and thus was set to zero (Boldman et al., 1993).

The variance-covariance matrix for residual effects is

$$\mathbf{V} [\mathbf{e}_1', \mathbf{e}_2'] = \mathbf{R} \quad \mathbf{I}_e, \quad \text{where}$$

$$\mathbf{R} = \begin{matrix} r_{11} & r_{12} \\ r_{12} & r_{22} \end{matrix}$$

$$\text{Let } \mathbf{y} = \begin{matrix} \mathbf{y}_1 \\ \mathbf{y}_2 \end{matrix}, \quad \mathbf{X} \mathbf{b} = \begin{matrix} \mathbf{X}_1 \mathbf{b}_1 \\ \mathbf{X}_2 \mathbf{b}_2 \end{matrix}, \quad \mathbf{u} = \begin{matrix} \mathbf{u}_1 \\ \mathbf{u}_2 \\ \mathbf{m}_1 \end{matrix}, \quad \text{and } \mathbf{c} = \begin{matrix} \mathbf{c}_1 \\ \mathbf{c}_2 \end{matrix}, \quad \text{thus,}$$

$$\mathbf{y} \sim \mathbf{N} [\mathbf{X} \mathbf{b}, \mathbf{Z}_a' (\mathbf{G} \quad \mathbf{A}) \mathbf{Z}_a + \mathbf{P} \mathbf{e} \quad \mathbf{I}_e + \mathbf{R} \quad \mathbf{I}_e]$$

### 2.3.3.1. DF-REML

In the derivative-free REML approaches, there is no closed form for estimation of covariance nor iteration formula for different dispersion parameters. Instead, the derivative-free method, very simply, is to try different  $\mathbf{R}^*$  and  $\mathbf{G}^*$  until the combination that maximizes the log likelihood, or minimizes  $-2 \ln L$ , is found for the data,  $\mathbf{Y}$ , where

$$-2 \ln L = \text{const} + \log |\mathbf{R}^*| + \log |\mathbf{G}^*| + \log |\mathbf{C}| + \mathbf{y}' \mathbf{P} \mathbf{y} .$$

In derivative-free REML, the permanent environmental matrix ( $\mathbf{P} \mathbf{I}$ ) is combined with the genetic matrix ( $\mathbf{G} \mathbf{A}$ ) to form the expanded matrix  $\mathbf{G}^*$

EM-REML (EM = Expectation-Maximization) can be considered as a special case of EM-Bayesian methodologies, which we will discuss in next section.

### 2.3.3.2. Bayes Framework

Methods to estimate dispersion parameters have been developed from a Bayesian background for different data structures. Procedures for a single polychotomous trait have been described by Harvill and Mee (1984) and Hoeschele et al. (1987) and by Hoeschele and Tier (1995). Methods for multivariate binary traits were suggested by Foulley et al (1987a), Janss and Foulley (1993), and Hoeschele et al (1995) and extended to joint analyses of categorical and continuous data. Gianola et al (1986) discussed multivariate continuous data in detail

Essentially, most researchers in this area recommend an algorithm analogous to the EM algorithm (Dempter et al, 1977) for REML and its multitrait extension.

Assume that  $\mathbf{b}$  has a flat prior distribution (uniform distribution in this case) and  $\mathbf{u}$  and  $\mathbf{c}$  are multivariate normal distributed and independent each other. Thus,

$$P(\mathbf{b}) = \text{constant},$$

As for priors for  $\mathbf{R}$ ,  $\mathbf{P} \mathbf{e}$  and  $\mathbf{G}$ , we assume inverted Wishart distribution. For example, the distribution of priors of  $\mathbf{R}$  is,

$$P(\mathbf{R} | v_e, V_e) = |\mathbf{R}|^{-\frac{(v_e+p+1)}{2}} \exp\left[-\frac{\text{tr}(\mathbf{R}^{-1} V_e^{-1})}{2}\right]$$

$v_e$  and  $V_e$  are hyperparameters of the distributions, which we assume known. The distributions of priors for  $\mathbf{P} \mathbf{e}$  and  $\mathbf{G}$  can be expressed similarly.

The joint posterior distribution of all the parameters is given by

$$P(\mathbf{b}, \mathbf{u}, \mathbf{c}, \mathbf{R}, \mathbf{P} \mathbf{e}, \mathbf{G} | \mathbf{y}) = P(\mathbf{y} | \mathbf{b}, \mathbf{u}, \mathbf{c}, \mathbf{R}) P(\mathbf{c} | \mathbf{P} \mathbf{e}) P(\mathbf{P} \mathbf{e}) P(\mathbf{u} | \mathbf{G}) P(\mathbf{G}) P(\mathbf{R})$$

In context of (co)variance component estimation by EM, the joint distribution of  $\mathbf{D}$  can be maximized with respect to  $\mathbf{G}$  and  $\mathbf{Pe}$  by maximizing  $E\{\ln P(\mathbf{c}|\mathbf{Pe})\}$ ,  $E\{P(\mathbf{u}|\mathbf{G})\}$  at each iterate, the resulting iterative scheme for the  $[t+1]$  th round is,

$$g_{ii}^{[t+1]} = \left[ \left[ \hat{\mathbf{u}}_i \mathbf{A}^{-1} \hat{\mathbf{u}}_i + tr(\mathbf{A}^{-1} \mathbf{C}_{ii}) \right] / q_{ii} \right]$$

where  $tr(\cdot)$  is the trace operator.

Similarly,

$$c_{ii}^{[t+1]} = \left[ \left[ \hat{\mathbf{c}}_i \hat{\mathbf{c}}_i + tr(\mathbf{C}_{ii}) \right] / p_{ii} \right]$$

and,

$$\mathbf{r}^{[t+1]} = (\hat{\mathbf{y}} \hat{\mathbf{y}} - \hat{\mathbf{b}} \mathbf{X} \hat{\mathbf{y}} - \hat{\mathbf{u}} \mathbf{Z} \hat{\mathbf{y}} - \hat{\mathbf{c}} \mathbf{Z} \hat{\mathbf{y}}) / (N - r(\mathbf{X})), \text{ where,}$$

$$\mathbf{r}^{[t+1]} = \begin{matrix} r_{11} & r_{12} \\ r_{12} & r_{22} \end{matrix}^{[t+1]} \text{ and } r(\mathbf{X}) \text{ is column rank of } \mathbf{r}(\mathbf{X})$$

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# **CHAPTER 3. Estimation of Covariances between Fertility and Litter Size in Fall-lambing Sheep: A Simulation Study I. Models and Phenotypic Parameter Estimation**

## **Abstract**

## **3.1. Introduction**

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## **CHAPTER 3**

### **Estimation of Covariances between Fertility and Litter Size in Fall-lambing Sheep: A Simulation Study**

#### **I. Models and Phenotypic Parameter Estimation**

#### **Abstract**

Methodologies used in a Monte Carlo simulation study of reproductive traits were described. Reproductive outputs were simulated as functions of assumed underlying phenotypes. Realized expressions of fertility (0 vs 1) with a mean of .37 and of multinomial litter size (1, 2, 3, 4) with mean of 2.12 were created by truncation of the underlying phenotypic distributions. Four genetic models were used to simulate underlying phenotypic variates, which were derived as the sum of independent, normally distributed additive genetic and environmental effects (Model 1A and 1B) or additive genetic and permanent and temporary environmental effects (Model 2A and 2B). Four data sets were simulated for each of Model 1A and 1B and ten data sets for each of Model 2A and 2B. Each contained 5000 ewes by 500 sires and 5000 dams and with up to five records per ewe. Heritabilities for underlying fertility and litter size were .25 and

.1225, respectively, for Models 1A and 1B and .15 and .1225, respectively, for Models 2A and 2B. Permanent environment as a proportion of underlying phenotypic variance was .10 for both traits in Models 2A and 2B. Also the randomness of the SAS pseudo-random number generator was tested by simulating 20 independent variates. On the basis of t-tests for estimates of mean and variance as well as Pearson correlation analyses for the 20 variates, the SAS random generator can be efficiently applied in the large data simulation. Results of simulated phenotypic values in the underlying normal and the categorical scales indicated that correlated responses from phenotypic selection on fertility increased the mean of litter size and reduced its phenotypic variance when the two traits were correlated.

Key words: Sheep, Reproduction, Monte Carlo, Simulation, Phenotypic values, Litter size, Fertility.

### **3.1. Introduction**

Improving female reproductive performance is an important objective for increasing the profitability of sheep (Abdulkhaliq et al., 1989 ), especially in lamb production. There is much greater potential for increasing both biological and economic efficiency of lamb production through genetic improvement in reproductive rate than through improvement in growth rate or body composition ( Dickerson , 1978 ). Total production costs accounted for by replacement and maintenance of breeding females are proportionately much higher for sheep and beef cattle than for other meat-producing

species, mainly because of their relatively low reproductive rate. Ewe productivity, defined as number ( or total weight ) of lambs weaned per ewe exposed, is dependent upon the component traits of fertility, litter size, lamb survival and growth (Fogarty et al., 1985 ).

Fertility is generally high and further improvement may not have a large effect on profitability in fall breeding systems. However, for out of season breeding in late spring and early summer when conception rates are often low, improving fertility could be quite important to successful accelerated breeding systems.

Another important trait is litter size. An increase in the number of lambs weaned per ewe per year offers the greatest single opportunity for increasing the efficiency of lamb meat production. More studies have addressed genetic improvement of this trait than any other sheep reproductive trait. Genetic variation for litter size exists both among and within breeds. It is generally accepted that selection to improve litter size is effective (Bradford, 1985). The results published were in reasonably good agreement with each other with an expected response of 1 to 2% or more per year. However, Waldron and Thomas ( 1992 ) thought that although selection for litter size has been successful, the rate of improvement has been limited because the trait is only observable in females of reproductive age that conceive and maintain their pregnancy.

Selection experiments for reproductive traits of sheep to date have all been with wool or dual-purpose breeds except for the selection experiment for fertility at Virginia Polytechnic Institute and State University. Al-Shorepy and Notter (1996) summarized the results of that experiment. They applied mixed-model methodology to estimate

genetic and environmental trends for spring fertility and fall litter size in a composite sheep flock containing 50% Dorset, 25% Rambouillet and 25% Finnsheep inheritance. Genetic trends were  $1.32 \pm .11\%$  in the selected line compared with  $.57 \pm .19\%$  in the environmental control for spring fertility and  $.0065 \pm .0015$  lambs/yr in the selected line compared with  $.0024 \pm .0022$  lambs/yr in the environmental control line. Estimates of permanent environmental trends for spring fertility were similar in the selected and environmental control flocks ( $.21 \pm .7\%$  vs  $.22 \pm .13\%$ ).

Estimates of heritability for reproductive traits generally have been low (Abdulkhalig et al., 1989). Literature estimates for heritability of litter size in sheep published before 1982 were summarized by Gonzalez (1982; cited by Bradford, 1985). There were about 30 estimates in his review for different breeds or methods of estimation, ranging from .15 to .35 and with a mean of .10. Three estimates of realized heritability averaged approximately .07. Published results in the past 15 years were generally in the same range (Abdulkhalig, 1989; Atkins, 1986; Bunge, 1990; Clarke and Hohenboken, 1983; Gabina, 1989; Gama et al., 1991; Fahmy, 1990; Fogarty et al., 1985; Fossceco and Notter, 1995; Iniquez et al., 1986; Long and Thomas, 1989; Mohd-Yusuff et al., 1992; Owen et al., 1986; Shelton and Menzies, 1970; Shrestha and Heaney, 1987; Waldron and Thomas, 1992). The largest value reported is .41 (Gabina, 1989). Few estimates of heritability for litter size in fall lambing are available. Al-Shorepy and Notter (1996) reported a heritability estimate of .10, which was higher than the estimate of .05 using data from all seasons for the same flock.

Fertility is also lowly heritable. Most reported estimates are less than .1 ( Atkins, 1986; Bunge et al., 1990; Clarke and Hohenboken, 1983; Fogarty et al., 1985; Gibina, 1989; Long and Thomas, 1989; Mohd-Yusuff et al., 1992; Shelton and Menzies, 1970; Shrestha and Heaney, 1987 ). The only estimate for out-of-season fertility is from Al-Shorepy and Notter (1996 ) with a mean heritability of .09 and a range of .07 to .11. In addition, a heritability of .09 was obtained by Fossceco and Notter ( 1995 ) for fertility of fall-bred 7-month old ewe lambs used to form the base population for the same study.

Few estimates of the genetic correlation between fertility and litter size have been reported. Fogarty et al.( 1985 ) reported a genetic correlation of  $-.34 \pm .28$  between fertility and litter size and a phenotypic correlation of  $.03 \pm .02$  for ewes mated in the normal breeding season. However, Al-Shorepy and Notter (1996) obtained a much stronger genetic correlation of .56 between spring fertility and fall litter size, suggesting that selection for multiple births in an out-of-season breeding system should result in genetic improvement in spring fertility. Bradford ( 1985 ) noted an increase in fertility (decrease in barrenness ) in several selection experiments for litter size. A positive correlated response thus appears to be a general pattern, and is consistent with the decline in fertility of the line selected against twinning in another experiment (Bradford, 1985).

Repeatability theoretically should represent the upper limit of heritability, assuming that that the traits being considered at different times are genetically identical ( Falconer, 1989 ). Although not as useful as heritability, repeatability provides information on the joint magnitude of genetic and permanent environmental effects. Repeatability of litter size and fertility are generally low, ranging from  $-.56$  to  $.15$  for fertility and from  $.08$  to

.24 for litter size( Abdulkhalig, 1989; Atkins, 1986; Bunge, 1990; Clarke and Hohenboken, 1983; Gabina, 1989; Fahmy, 1989, 1990; Fogarty et al., 1985; Long and Thomas, 1989; Shelton and Menzies, 1970 ). These results imply that the permanent environmental component for reproductive traits is also small.

Methods to estimate variance components for normal, continuous data are well understood. However, approaches for ordinal, categorical data such as litter size and fertility are not as well understood. An understanding of the behavior of the threshold traits is crucial to derive reliable genetic parameter estimates and to provide a sound basis for designing selection programs. Therefore, the objective of this study was to simulate reproductive data for sheep in an out-of-season breeding program and to study their statistical properties as well as to evaluate the genetic parameter and (co)variance component estimation methods using mixed model methodology.

### **3.2. Material and Methods**

A stochastic simulation program was created to allow simulation of reproductive traits. Reproductive outputs were generated by simulating two normally distributed traits representing underlying phenotypic potential for fertility and litter size. Corresponding expression of binomial fertility ( 0 vs 1 ) and multinomial litter size (1, 2, 3, 4) were then created by truncation of the underlying phenotypic distributions. These variables were chosen because they provide a minimal set for predicting the reproductive traits of interest in out-of-season breeding of sheep. A similar approach was used by King ( 1991 ), Johnson and Notter ( 1987a, b ), Notter and Johnson ( 1987, 1988 ) and



Van Vleck and Gregory ( 1992 ) to simulate reproductive trait such as litter size, ovulation rate, fertility and postpartum interval for mice and beef cattle.

### **3.2.1. Population Structure**

Data were generated using a nested design. All the data sets were created assuming 500 sires and 10 dams per sire. Lambs produced from these mating were simulated as male or female by assigning a random number with a sex ratio of 50:50. Five thousand ewe lambs were then randomly selected as the foundation flock. If fewer than 5,000 ewe lambs were simulated, then all were assigned to the foundation flock. Ewes were mated at random to service sires from same population at a ratio 25:1 for up to 5 years. A new set of service sires was simulated for each mating year. A binomial fertility value was simulated for each ewe and litter size was simulated for each ewe that conceived. No effects of service sire on fertility or litter size were simulated. For each year, a random death loss of .12 was assumed in the ewe flock. If a ewe was open in any year, no records were generated for either underlying and realized litter size. It was assumed that all variance components were constant on underlying scale among years, generations and sexes.

### **3.2.2. Simulation Methodology**

The Monte Carlo method was used to simulate underlying phenotypic values. Programming statements were written in SAS language ( SAS, 1989 ). Several preliminary analyses were used to evaluate the randomness of the pseudo-random number generator.

#### **3.2.2.1. Model Description**

Model 1:  $Y = G + E$

In this model, only genetic (G) and environmental (E) effects were included for both fertility and litter size, which can be written as:  $Y_{ij} = G_i + E_j$ ,  $G_i \sim N(\mu, \sigma_g^2)$ ,  $E_j \sim N(0, \sigma_e^2)$ ,  $\sigma_{ge} = 0$  and  $Y_{ij} \sim N(\mu, \sigma_g^2 + \sigma_e^2)$ , where  $Y_{ij}$  is the phenotypic value for the trait of interest on the normal scale,  $G_i$  is the additive direct genetic value,  $E_j$  is the temporary environmental value,  $\sigma_g^2$  is the additive genetic variance,  $\sigma_e^2$  is the temporary environmental variance and  $\sigma_{ge}$  is the additive genetic by temporary environmental covariance.

To simulate phenotypic values for the daughters (ewes), the model applied was:

$$X_{ijk} = 1/2 BV_i + 1/2 BV_j + M_{ij} + E_k$$

where,  $BV_i$  and  $BV_j$  were breeding values of the sire  $i$  and dam  $j$ , respectively, which were simulated as:

$$BV_i = R_i \sigma_g, \text{ where } R_i \text{ is a random normal variate.}$$

The  $M_{ij}$  is the Mendelian sampling value, equal to  $R_{ij} * \text{Sqrt}(1/2 \sigma_g^2)$ , where,  $R_{ij}$  is a random normal variate, and  $E_k$ , the residual value, is simulated as:

$$E_k = R_k * \sigma_e, \text{ where, } \sigma_e \text{ is the standard deviation of the environment effect.}$$

The variance  $V$  of  $X_{ijk}$  was thus equal to:

$$V(X_{ijk}) = 1/4 \sigma_{BV_s}^2 + 1/4 \sigma_{BV_d}^2 + \sigma_M^2 + \sigma_e^2, \text{ where, } \sigma_{BV_s}^2 = \sigma_{BV_d}^2 = \sigma_g^2 = 2 \sigma_M^2$$

Contributions of sire, dam, Mendelian sampling and error was assumed to be independent. Categorical fertility and litter size were assigned phenotypic values by truncation of these underlying variates.

In the model 1A, the two underlying phenotypic variables for fertility and litter size were assumed to be independent whereas in model 1B, underlying fertility and litter size were assumed to be correlated. The algorithm to simulate normal fertility was the same as in model 1A, whereas data for normal litter size were derived from conditional probabilities given simulated values for fertility. For example, the BV for litter size on the underlying normal scale [ BV(L) ] was derived from simulated BV for fertility [BV(F)] as :

$$BV_F(L) = r_g * ( \sigma_{gl} / \sigma_{gf} ) * BV(F) + R_i * \text{Sqrt} [ (1-r_g^2) ] * \sigma_{gl}$$

where  $r_g$  was the genetic correlation between normal fertility and litter size, and  $\sigma_{gl}$  and  $\sigma_{gf}$  were genetic standard deviations of litter size and fertility, respectively. The additive genetic variance of litter size that was dependent on fertility was:

$$V [ BV(L)|BV(F) ] = ( 1 - r_g^2 ) * \sigma_{gl}^2$$

The same methodology was applied to simulate Mendelian sampling and environmental components. The phenotypic values for categorical variates were transformed from the underlying scale by the threshold methodology.

Model 2:  $Y = G + PE + E$

A new, independent permanent environmental component was introduced for model 2. For model 2A, fertility and litter size again were assumed to be uncorrelated. The formulas used to generate BV and environmental components were the same as for Model 1. Permanent environmental deviates were simulated as:

$$PE_i = R_i * \sigma_{pe}$$

where  $\sigma_{pe}$  is the permanent environmental standard deviation for the trait being simulated. Data for the two categorical traits were then generated by threshold methodology from normal fertility and litter size.

For Model 2B, the two reproductive traits were assumed to be potentially correlated because of genetic, permanent environmental, and temporary environmental correlations. Data for normal fertility were generated by the same algorithm used in Model 2A. For normal litter size, the random components were simulated as in Model 1B.

In summary, for independent trait simulation, the following methods were used:

1. All direct genetic (G), permanent environmental (PE) and temporary environmental (E) components for underlying traits were assumed to be additive and normally distributed. No higher order genetic-genetic, genetic-environmental, or environmental-environmental interactions were simulated. The distribution parameters for the components can be expressed as :  $G_i \sim N(\mu, \sigma_g^2)$ ,  $Pe_j \sim N(0, \sigma_{pe}^2)$ ,  $E_l \sim N(0, \sigma_e^2)$ , and were used as input parameters to the simulation.
2. A standard normal variate was randomly generated and multiplied by the square root of the additive genetic variance to obtain the breeding value of the sire.
3. A second standard normal variate was randomly generated and multiplied by the square root of the additive genetic variance to obtain the breeding of the dam.
4. Mendelian sampling variances were generated by simulating a third random normal variate which was multiplied by the square root of one half the additive genetic variance. The breeding value of offspring was simulated by summing of the average breeding value of sire and dam and the Mendelian sampling term.

5. A fourth standard normal variate was generated and multiplied by the square root of the permanent environmental variation to obtain the random permanent environmental effect of Model 2.
6. A fifth standard normal variate was simulated and multiplied by the square root of the residual variation to obtain the random temporary environment of the daughter.
7. The breeding value and the environmental components (temporary or both temporary and permanent) were added to the mean of the trait to obtain the underlying phenotype of the daughter.
8. Phenotypes of categorical traits (fertility and litter size) were obtained from the corresponding underlying traits by applying a set of threshold values.
9. Service sires were assumed to not contribute to a ewe's reproductive performance.

For correlated models (Model 1B and Model 2B), normal deviates for fertility were simulated as shown above. For litter size, breeding values and permanent and temporary environmental values were then derived from the conditional distribution of litter size given the correlated fertility deviates.

#### **3.2.2.2. Population Parameters and Assumptions**

The simulation study was based on the result of an out-of-season breeding program (Al-Shorepy and Notter, 1996). The main characteristics of the program include a typical high prolificacy lowland meat breed or composite as the breeding flock. The fertility of ewes in the out-of-season breeding program often was low.

Threshold values and resulting expected means and distributions for fertility and litter size for each of five years are listed in table 3.1. The expected mean and variance for the underlying scale were zero and one with the same other expected properties of the standard normal distribution. However, when correlation between the two traits was introduced, the mean of litter size would represent a correlated response to selection because only ewes that conceive would subsequently lamb. The expected means for categorical fertility for the five years were .149, .309, .652, .564 and .201, respectively, with an overall pooled mean of .375. For litter size, expected means for the five years were 1.83, 2.06, 2.21, 2.06 and 2.35, respectively, with a mean of 2.12, which is higher than the value reported by Al-Shorepy and Notter (1996) from field data. However, the overall mean for spring fertility generally agreed with their data (.41). The distribution of realized litter sizes of 1, 2, 3 and 4 over all five years was 21.1, 51.3, 21.3 and 6.3%, respectively, which showed a skewed discrete distribution with a longer right tail.

Table 3.2 gives the specific input variance components and genetic parameters used in this study. Heritability of fertility on the underlying scale was assumed to be .25 when a permanent environmental component was not included in the models (Model 1A and 1B) but was reduced to .15 when a permanent environmental component accounting for 10% of phenotypic variation was included in Model 2. Anticipated heritabilities for binomial fertility were derived using the method of Falconer (1989) and were .137 and .082, respectively, for underlying heritabilities of .25 and .15 using a mean incidence of fertility of .37. Input heritabilities of litter size on underlying scale for all models were .1225. The corresponding transformed value (Gianola, 1979) was .1025 for a litter size

distribution of 21.0% singles, 51.3% twins, 21.3% triplets and 6.3% quadruplets. The permanent environmental component was assumed to account for 10% of phenotypic variance for litter size in model 2. Genetic, permanent and temporary environmental correlations between underlying normal fertility and litter size were all initially set to .5 for Model 1B and 2B. In supplemental analyses using Model 1, genetic and temporary environmental correlations between fertility and litter size were also set to 0 and .5 (Model 1B-X) or .5 and 0 (Model 1B-Y).

### **3.2.3. Evaluation of simulation results**

Overall, 28 data sets were initially simulated for this study, representing initial evaluations of models 1A, 1B, 2A and 2B, and 25 additional simulated data sets were created to address special issues. Software for multiple trait derivative-free restricted maximum likelihood (MTDFREML) developed by Boldman et al. (1993) was used to estimate (co)variances and genetic parameters for underlying and realized categorical traits.

Simulated phenotypic means and standard deviations across replicates were used to test the null hypothesis that the mean =  $\mu$ , where  $\mu$  was an input parameters with assumption of no selection. Every replicate data set was considered as a random sample from a population with location parameters and data structure listed in tables 3.1 and 3.2. The estimates derived from MTDFREML analyses were assumed to be consistent with normal distribution with an unknown population variance. The test statistic was  $t = (X - \mu) / (S / \sqrt{n})$ , where  $X$  is the mean of the phenotypic parameter estimate and  $\mu$  is the population parameter which was equivalent to the input parameter value,  $S$  is the

standard deviation for the estimates and  $n$  is sample size. The  $t$  statistic is conformable to a  $t$  distribution with  $n-1$  degrees of freedom. Throughout the study, two-tailed  $t$  tests were used. The significant levels (two-tailed) of .05 and .01 were applied as the testing criteria.

### **3.3. Result and Discussion**

#### **3.3.1. Testing of Randomness of SAS Pseudo-random Number Generator**

Before simulation of the actual data for this study, twenty independent variates were simulated by SAS using the standard normal deviate function with mean zero. The first 10 variates were simulated with input standard deviation of 1.00; the final 10 variates had input standard deviations of .35, .50, 2.10, 2.50, 3.50, 5.00, 6.80, 12.50, 100, and 1000, respectively; Ten thousand records for each variate were created. Theoretically, these variate are conformable to normal distributions with  $N(0, \sigma_x^2)$  where  $\sigma_x$  is the input standard deviation. The range of the means for the twenty variates was .0007 to -1.2634. As expected, variates with a larger input standard deviation had larger deviation of the estimated mean from the input value. When observed means of twenty variates were tested using  $t$  tests against the null hypothesis that  $\mu = 0$ , two means were significantly different from 0 at  $\alpha$  of .05 with the remaining eighteen variate means not being significant different from zero. The pooled mean of twenty variates was -.0394 and was significantly different from zero by  $t$  test. The first ten standard normal variates had a mean .0103 and standard deviation 1.0011, which was not significant different from the input population parameters. A Pearson correlation analysis was carried out for the



twenty independent variates. The absolute range of 90 correlation coefficients was from .0002 to .0214. No single correlation coefficient was significantly different from the expected value. Although the frequency with which sample means differed from their input value of 0 was slightly larger than expected (2/20 versus 1/20), this random number generator was judged to be satisfactory for conduct of this study.

### **3.3.2. Phenotypic Statistics and Testing**

Summary statistics for simulated data sets of two models are listed in tables 3.3 and 3.4. The number of data sets for model 1A, 1B, 2A and 2B were 4, 4, 10, and 10 respectively. Generally, means and standard deviations for four traits were close to expectations. Coefficients of variation for underlying variates were meaningless due to the extremely small means of the variates. The range in values for the data sets were consistent with the normal distribution.

All means and standard deviations except for those noted were tested against their expected value ( input parameters ) by t test. The existence of correlations between the two normal variates in some models tended to reduced the phenotypic variance of litter size. The t test showed that phenotypic standard deviations of underlying litter size in models 1B and 2B were highly significantly (  $P < .01$  ) smaller than the expected values of 1.0. Moreover, the mean binomial fertility for all models also significantly differed from the input parameter, which may be due to unbalanced data structure among the five years. The data in the first year had the most observations but a much lower expected mean of 14.9%. The correlated response from selection on fertility increased the means of

categorical litter size from the expected value of 2.13 to 2.47 for model 1B and 2B, respectively. Thus ewes that conceived were inherently more prolific than those that did not conceive for these models. The binomial fertility theoretically should be conformable to all-or-none distribution with mean =  $p$  (0.375) and variance =  $pq$  (0.484). It seems that binomial fertility in this study was underestimated. All means for binomial fertility in the four models differed from the mean input value ( $P < 0.05$  or  $P < 0.01$ ), which suggested that estimates of fertility would be vulnerable to unbalanced data.

### **3.4. Implications**

1. The SAS random generator can be efficiently applied in large data set simulation although some sampling variations still exist.
2. Phenotypic selection for fertility increased the mean of litter size and reduced its phenotypic variance when the two traits were genetically correlated.
3. Binomial fertility was more vulnerable to unbalanced data than multinomial litter size.

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Table 3.1. Threshold values on the standard, normally distributed scale and proportions of observations in classes on the discrete scale for fertility and litter size by year

Year	Trait <sup>a</sup>	Threshold	Probability	Category	Expectation
1	NF	1.0365	14.9%	0,1	.149
	NL	X < .2533	40.1%	1	
		X < .8418	39.3%	2	
		X < 2.0540	18.0%	3	
		X > 2.0540	2.0%	4	
2	NF	.5000	30.9%	0,1	.309
	NL	X < -.6745	25.1%	1	
		X < .6745	49.8%	2	
		X < 1.5342	18.8%	3	
		X > 1.5342	6.3%	4	
3	NF	-.3854	65.2%	0,1	.652
	NL	X < -1.0365	14.9%	1	
		X < .5244	55.0%	2	
		X < 1.5550	24.2%	3	
		X > 1.5550	5.9%	4	
4	NF	-.1256	56.4%	0,1	.564
	NL	X < -.6745	25.1%	1	
		X < .6745	49.8%	2	
		X < 1.5342	18.8%	3	
		X > 1.5342	6.3%	4	
5	NF	.8418	20.1%	0,1	.201
	NL	X < -1.2817	9.9%	1	
		X < .3854	55.3%	2	
		X < 1.2817	24.8%	3	
		X > 1.2817	10.0%	4	
All	NF		37.5%	0,1	.375
			21.1%	1	
			51.3%	2	
			21.3%	3	
			6.3%	4	

<sup>a</sup> : NF and NL are underlying fertility and litter size, respectively.

Table 3.2. Input genetic parameters for fertility and litter size

Parameter <sup>a</sup>	Model			
	1A	1B	2A	2B
<u>Fertility</u>				
$h^2$	.25	.25	.15	.15
$pe^2$	-	-	.10	.10
$t_N$	.25	.25	.25	.25
$h_B^2$	.137	.137	.082	.082
$g$	.500	.500	.387	.387
$pe$	.000	.000	.316	.316
$e$	.866	.866	.866	.866
<u>Litter size</u>				
$h^2$	.1225	.1225	.1225	.1225
$pe^2$	-	-	.10	.10
$t_N$	.1225	.1225	.2225	.2225
$h_B^2$	.1025	.1025	.1025	.1025
$g$	.350	.350	.350	.350
$pe$	.000	.000	.100	.100
$e$	.937	.937	.882	.882
<u>Fertility - litter size</u>				
$r_g$	.00	.50	.00	.50
$r_{pe}$	-	-	.00	.50
$r_e$	.00	.50	.00	.50

<sup>a</sup>:  $h^2$  = heritability for the underlying traits,  $pe^2$  = permanent environment variance as a proportion of the phenotypic variance,  $t_N$  = repeatability for the underlying traits,  $h_B^2$  = heritability for binomial fertility,  $g$  = direct additive genetic standard deviation,  $pe$  = permanent environmental standard deviation,  $e$  = temporary environmental standard deviation (residual standard deviation),  $r_g$  = direct genetic correlation,  $r_{pe}$  = permanent environmental correlation, and  $r_e$  = residual correlation.

Table 3.3. Summary statistics of simulation data sets for fertility and litter size: data structure.

Item	Trait	Model			
		1A	1B	2A	2B
No. Animals in A <sup>-1</sup>		9033 ± 18	9075 ± 4	9034 ± 6	9041 ± 6
No. ewes/sire		10	10	10	10
No. ewes/dam		1.4	1.4	1.4	1.4
No. records	Fertility	19629±52	19611±32	19664±31	19673±41
	Litter size	7091±59	7174±53	7080±27	7198±34
No. records/ewe	Fertility	3.9	3.9	3.9	3.9
	Litter size	1.4	1.4	1.4	1.4



Table 3.4. Summary statistics of simulation data sets for sheep fertility and litter size:  
Mean and Standard deviations<sup>a</sup>.

Models	NF	NL	BF	BL
<u>Model 1A</u>				
No. data sets	4	4	4	4
Mean	.0033	.0328*	.3613*	2.1375*
	±.0120	±.0058	±.0035	±.0030
SD	1.0022	1.0006	.4803*	.8152 <sup>d</sup>
	±.0018	±.0030	±.0010	±.0025
<u>Model 1B</u>				
No. data sets	4	4	4	4
Mean	.0139	.4683 <sup>d</sup>	.3658*	2.4653**
	±.0067	±.0018	±.0024	±.0010
SD	1.0018	.9342**	.4815*	.8136 <sup>d</sup>
	±.0022	±.0039	±.0009	±.0023
<u>Model 2A</u>				
No. data sets	10	10	10	10
mean	-.0009	.01636**	.3595**	2.1248
	±.0033	±.0034	±.0010	±.0029
SD	1.0014	1.0011	.4800**	.8130 <sup>d</sup>
	±.0023	±.0029	±.0003	.0015
<u>Model 2B</u>				
No. data sets	10	10	10	10
Mean	.0177**	.4677 <sup>d</sup>	.3659**	2.4678**
	±.0051	±.0059	±.0014	±.0047
SD	1.0030	.9329**	.4817**	.8159 <sup>d</sup>
	±.0016	±.0022	±.0004	±.0010

<sup>a</sup> : NF= underlying fertility, NL = underlying litter size, BF= categorical fertility, and BL = categorical litter size, and SD = standard deviation.

\*\* : P < .01.

\* : P < .05.

<sup>d</sup>: Not tested.

# **CHAPTER 4. Estimation of Covariances between Fertility and Litter size in Fall-lambing Sheep: A Simulation Study. II. Derived Genetic Parameters**

## **Abstract**

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## CHAPTER 4

### **Estimation of Covariances between Fertility and Litter size in Fall-lambing Sheep: A Simulation Study. II. Derived Genetic Parameters**

#### **Abstract**

A stochastic computer simulation was used to simulate reproductive traits of sheep. The objective was to compare covariances between fertility and litter size on the underlying and realized categorical scales when litter size was expressed only for ewes that conceived. Reproductive outputs were simulated as functions of assumed underlying phenotypes. Realized expressions of fertility (0 vs 1) with a mean of .37 and of multinomial litter size (1, 2, 3, 4) with mean of 2.12 were created by truncation of the underlying distributions of phenotypic potential. Four genetic models were used to simulate underlying phenotypic variates, which were derived as the sum of independent, normally distributed additive genetic and environmental effects (Model 1A and 1B) or additive genetic and permanent and temporary environmental effects (Model 2A and 2B). Four replicates were simulated for Models 1A and 1B. Ten data sets were simulated for Models 2A and 2B. Each contained 5000 ewes by 500 sires and 5000 dams and with up to five records per ewe. Heritabilities for underlying fertility and litter size were .25 and .1225, respectively, for Models 1A and 1B and .15 and .1225, respectively, for Model 2A and 2B. Permanent environment as a

proportion of underlying phenotypic variance was .10 for both traits in Models 2A and 2B. For each data set, genetic parameters and variance components were estimated by REML. Mean estimates for each model were tested against input parameters by t test. The usual transformation of heritability estimated on the categorical scale to the normal scale for fertility and litter size performed better for a simple animal model than for a repeatability model. Genetic correlation estimates between the two categorical traits for Model 1B and 2B were  $.49 \pm .01$  and  $.48 \pm .04$ , respectively, and were slightly smaller than the expected value of .50. However, permanent and temporary environmental correlations were more seriously underestimated. For Model 2B, permanent and temporary environmental correlation estimates were  $.41 \pm .05$  and  $.26 \pm .03$ , respectively. For Model 1B, the temporary environmental correlation estimate was  $.33 \pm .02$ . Failure of open ewes to produce a litter size record resulted in underestimates of true genetic, permanent and temporary environmental covariances and correlations.

Key words: Sheep, Reproduction, Covariance components, Simulation.

## **4.1. Introduction**

So-called quasi-continuous, threshold or categorical traits have the properties and numerical characteristics of discrete data and can be conformable to one or a mixture of a group of discrete distributions such as the binomial, multinomial, Poisson or negative binomial. Categorical traits have generated extraordinary levels of interest in the field of animal breeding. The possible reasons are that many important economic traits such as

reproductive traits or survival-related traits are categorical in nature, and some selection experiments for categorical traits have established the potential for their genetic improvement. Several authors (Hoeschele, 1986; Foulley, 1987; Soto-Murrillo, 1991) have presented extensive reviews on methods for analysis of discrete data in animal breeding. Generally there are two main groups of procedures for analysis of discontinuous genetic data (Matos, 1993). The distinction between the two groups depends on whether an underlying continuous distribution is assumed or not. The first group includes methods that ignore the discrete nature of categorical data, and the analysis proceeds using linear methodology as if the data were continuous, whereas the second invokes the threshold concept (Falconer, 1989) which assumes an underlying, non-observable, normal distribution for the discrete variate. The link between the observable discrete variable and the underlying continuous scale is generated by a set of fixed thresholds. The underlying variable is described by linear models, but the relationship between the underlying and the outward or observed scale is nonlinear (Gianola and Foulley, 1983).

Different methodologies for genetic analysis of discrete reproductive traits have been investigated by several authors (King, 1991; Matos, 1993). King (1991) compared the merit of different methods including those which treated the traits as if they were continuous: REML (Restricted Maximum Likelihood) and Henderson's method 3. The other methods recognized the categorical nature of the traits using Bayesian analysis with an informative prior or a generalized linear model analysis. King concluded that the Bayesian method had smaller MSE's for heritability and correlation estimates, produced similar rank correlation, and required substantially less total computer time than the pseudo expectation method.

However, nonlinear models are theoretically more complex and computationally more demanding than linear models. In another simulation study, Matos (1993) observed advantages for nonlinear models only in specific instances. For example, heritability estimates on the binomial scale become progressively smaller in relation to the constant value for heritability on the underlying continuous distribution as the frequencies of the binomial classes approached 0 and 1.

There is a dearth of information about the relationship between litter size and fertility in sheep, especially for the sheep outside the normal breeding season. Summarizing over six estimates of genetic correlation between litter size and fertility during the normal breeding season in the literature gave an mean of estimates of .31 with range of -.34 to .82 (Fogarty, 1995). Bradford (1985) noted an increase in fertility (decrease in barrenness) in several selection experiments for litter size. A positive correlated response thus appears a general pattern. Al-Shorepy and Notter (1996) obtained a much stronger genetic correlation of .56 between spring fertility and fall litter size, suggesting that selection for multiple births in an out-of season breeding system should result in genetic improvement in spring fertility.

The current study used stochastic simulation models of out-of-season sheep reproduction. The models were developed to allow simulation of categorical reproductive performance as a function of underlying genetic and environmental variation in reproductive potentials. The models included additive genetic and permanent and temporary environmental components. The two models applied were described in detail in Chapter 3. The objective of the study was to investigate the applicability of REML for (co)variance estimation for categorical sheep reproductive traits.

## 4.2. Materials and Methods

### 4.2.1. Data Simulation

The phenotypic characteristics of the simulated data for four models were discussed in Chapter 3. Overall, more than 40 data sets were simulated using pairs of heritabilities ( $h^2$ ) for underlying normal fertility and litter size of ( .25, .1225 ), ( .25, .1225 ), ( .15, .1225 ) and ( .15, .1225 ). Values of  $h^2$  and associated genetic, permanent environmental and temporary environmental standard deviations were shown in Table 3.2 of the Chapter 3.

Heritability on the underlying scale ( $h_x^2$ ) for fertility was converted to  $h^2$  on the realized binomial scale ( $h_p^2$ ) as (Falconer, 1989):

$$h_p^2 = [ z^2 / ( p * (1-p) ) ] * h_x^2 \quad [ 1 ]$$

where  $p$  is average frequency of occurrence for the trait and  $z$  is the height of the curve at the truncation point for frequency  $p$ .

Heritability on the underlying scale ( $h_n^2$ ) for litter size was converted to  $h^2$  on the realized multinomial scale ( $h_c^2$ ) as (Gianola, 1979):

$$h_c^2 = h_n^2 \frac{\sum_{i=1}^{m-1} z_i (w_{i+1} - w_i)^2}{\sum_{i=1}^m w_i^2 p_i - \left( \sum_{i=1}^m w_i p_i \right)^2} \quad [2]$$

where  $m$  is number of response categories,  $p_i$  is the expected incidence in the  $i^{\text{th}}$  category,  $\{z_i\}$  are ordinates of the standard normal density function evaluated at the abscissas to  $\{p_i\}$ , and  $\{w_i\}$  are the scores assigned to the categories, 0-1 for sheep fertility and 1-4 for litter size. No culling effect and zero correlation between fertility and litter size were assumed for the transformation.

### 4.2.2. Linear Models

Variance estimates were obtained by using MTDFREML software developed by Boldman et al. ( 1993 ). In matrix notation, the Models 2A and 2B (Chapter 3) can be written as:

$$\mathbf{Y} = \mathbf{X} + \mathbf{Z} \mathbf{a} + \mathbf{Z}_c \mathbf{c} + \mathbf{e} \quad [ 3 ]$$

Where,  $\mathbf{Y}$  is the vector of records,  $\mathbf{X}$  is the vector of the fixed effects ( year ),  $\mathbf{a}$  is the vector of random additive genetic effects with association matrix  $\mathbf{Z}$ ,  $\mathbf{c}$  is the vector of random permanent environmental effects with association matrix  $\mathbf{Z}_c$  and  $\mathbf{e}$  is the vector of residual effects. Models 1A and 1B (Chapter 3) can be written using the same equations, but without the permanent environmental effect. For all models, no random service sire effect was simulated, and the service sire effect was therefore not included in the analysis.

The variance-covariance structure for random effects was:

$$\mathbf{V} = \begin{matrix} \mathbf{a} & \mathbf{A} & \mathbf{0} & \mathbf{0} \\ \mathbf{c} & \mathbf{0} & \mathbf{I}_p & \mathbf{0} \\ \mathbf{e} & \mathbf{0} & \mathbf{0} & \mathbf{I}_e \end{matrix} \quad [ 4 ]$$

where  $\mathbf{A}$  is the numerator relationship matrix,  $\mathbf{I}_p$  is an identity matrix with order equal to the number of the ewes and  $\mathbf{I}_e$  is an identity matrix with order equal to the number of records. Estimates of heritability ( $h^2$ ) and repeatability ( $t$ ) are given by

$$h^2 = \frac{\sigma_a^2}{\sigma_p^2} \text{ and } t = \frac{\sigma_a^2}{\sigma_a^2 + \sigma_{pe}^2} \quad [ 5 ] \text{ and } [ 6 ].$$

, respectively. where  $\sigma_p^2 = \sigma_a^2 + \sigma_{pe}^2 + \sigma_e^2$  or  $\sigma_p^2 = \sigma_a^2 + \sigma_e^2$ , depending on whether or not permanent environmental effects were simulated.



### 4.2.3. REML (Co)variance Component Estimation

Variance components were initially estimated using a single trait animal model with derivative-free restricted maximum-likelihood (DFREML) procedures. Then with estimates from single trait analysis as starting values, bivariate analyses were performed. If the two traits were independent, a small starting value was utilized for the covariance, whereas for correlated traits, expected genetic, permanent and residual covariances were used as the starting values. Sometimes several runs were carried out. Only the best set of estimates, based on the log values of likelihood, was retained. If some results were not expected, several testing programs were run to address special issues for estimation of the (co)variance components and genetic parameters.

### 4.2.4. Statistical Testing

All the variance component and genetic parameter estimates were tested against their input values using two-tailed t tests. Every data set was considered to be a random sample from a population with genetic parameters listed in Table 3.2 of Chapter 3. The estimates derived from MTDFREML analyses were assumed to be conformable to normal distribution with an unknown population variance. The t statistic is, thus:

$$t = (X - E(X)) / (S / \sqrt{n}) \quad [7].$$

where  $X$  is mean genetic parameter or variance component estimate,  $E(X)$  is the expected value of the corresponding population parameter,  $S$  is the standard deviation of estimates and  $n$  is sample size. The t statistic is conformable to a  $t_{(n-1)}$  distribution. Two significance levels,

.05 and .01, were used as testing criteria. To allow statistical testing of effects of culling on fertility on variance component estimates for litter size, litter size data were simulated for all ewes and then reduced to include only data on ewes that lambed for each of 10 simulated data sets. A t statistic was constructed as:  $t = d / S_d$  [ 8 ]

where d is the mean difference of parameter estimates before and after selection and  $S_d$  is standard error of d.

### **4.3. Result and Discussion**

#### **4.3.1. Genetic Parameter and Covariance Component Estimates**

Genetic parameter and variance component estimates for each model are listed in Tables 4.1 through 4.10. For each model, data are presented for univariate and bivariate Multiple-Trait DFREML analyses.

4.3.1.1. Univariate vs Bivariate Analyses: When fertility and litter size were independent (Model 1A and 2A) , almost all estimates from univariate analyses were consistent with those from bivariate analyses, with differences only at the third decimal point (Tables 4.1, 4.2, 4.7 and 4.8). However, for correlated traits (models 1B and 2B), estimates from univariate analyses for litter size differed from those from bivariate analyses (Tables 4.3, 4.4, 4.9 and 4.10). Various genetic parameter and variance component estimates for both underlying and realized litter sizes derived from single trait analyses were generally smaller than those from bivariate analyses for these models. The mean heritabilities for litter size derived from univariate and bivariate analyses were 0.120 and 0.138 for model 1B and 0.118 and 0.126 for model 2B, respectively. On the categorical scale, the corresponding values were

.103 and .110, respectively for model 1B and .100 and .111, respectively for model 2B. These results suggested that a multiple-trait animal model should be used in case of correlated traits.

4.3.1.2. Variance Components and Derived Ratios: The differences in variance component estimates and derived ratios between underlying and realized variates were much larger for fertility than for litter size because litter size had four categories and more closely approached a normal distribution. Heritability estimates for both underlying and categorical fertility and litter size were generally in good agreement with the input values in all models except that for normal litter size in Model 2A. The t tests showed that (co)variance component and genetic parameter estimates for all four models were generally not significantly different from expectations for underlying fertility. However, t tests for underlying litter size revealed less uniform results. One important finding was a reduced variance component estimate from univariate analyses for normal litter size in Models 1B and 2B ( Table 4.3 and 4.9). A significant (  $P < 0.05$  ) reduction for all variance components in model 2B from univariate analyses was confirmed by t tests. However, most of the ratios of variance components to phenotypic variance were not significantly different from the expected values because the different variance components were proportionately reduced. The genetic, permanent environmental, residual and phenotypic variances were reduced by 19%, 26%, 14%, and 16%, respectively. However, bivariate analyses for model 2B yielded estimates of both variance components and their ratios that were of the expected magnitude. Heritability of normal litter size for model 2A was larger ( $P < 0.01$ ) than expected (0.1225) for both univariate and bivariate analyses. The pooled estimate from 15 data sets was still significantly ( $P <$

0.05) larger than the input parameter (Table 4.17), while the variance and the proportion of phenotypic variance contributed by the permanent environmental component was underestimated. The reason for these results is not clear.

For categorical fertility and litter size, only the departure of heritabilities from their transformed expectations from underlying values and of the genetic, permanent and temporary environmental correlation estimates from their corresponding input values were tested. Considering the unbalanced data structure that resulted from random death losses across years, the transformed heritability values for both fertility and litter size were derived separately for each year. The mean of the transformed heritabilities over years was used as the expected value. Heritability estimates for binomial fertility were generally very close to the expected value .137 for model 1A and 1B and .082 for model 2A. However, heritability for binomial fertility in model 2B was underestimated in both univariate and bivariate analyses. For categorical litter size, heritability estimates were in good agreement with expected values in model 1A and 1B and 2B but were overestimated in model 2A. These results indicated that transformation performed better for a simple animal model, when only a additive genetic component was included, than for a repeatability model. Several previous studies addressed the applicability of heritability transformation for categorical traits estimated by different methods (Van Vleck, 1972; Olausson and Ronnigen, 1975; Van Vleck and Gregory, 1992). All the authors agreed that such a transformation was relatively good for paternal half-sib analyses, but was less good for analyses based on progeny on parent regression when the underlying distribution was normal. Mantysaari et al. (1991, cited by Van Vleck and Gregory, 1992) using a simulated sire model (no relationship) with REML,

found close agreement between heritability on the binomial scale and heritability on the normal scale for two binomially distributed traits derived from a bivariate normal distribution. However, Van Vleck and Gregory (1992) used a simple animal model to analyze simulated data sets consisting of eight measures of ovulation rate treated as separate traits. The model also included seven birth groups (year and calving season of birth) and six calendar months of first measurement. They concluded that the usual transformation of heritabilities estimated on a binomial scale overestimated heritability on the underlying normal scale.

4.3.1.3. Covariance Components and Corresponding Correlations: Genetic and environmental covariance component estimates for correlated traits were in good agreement with input correlation values (0.5) for underlying traits. The t tests for covariance components and correlation estimates (genetic, permanent environmental and residual correlations) between the two traits on the underlying scale for all models were performed against the expected value of 0.5. Only one phenotypic covariance (see Table 3.2) differed significantly from expectation ( $P < 0.05$ ), which may be attributable to chance. These results demonstrated that the covariance components between two traits with normal distributions could be accurately estimated by REML methodology.

The genetic correlation estimates for the two categorical traits for models 1B and 2B were 0.487 and 0.475 respectively, close to the expected value of 0.5. However, estimates of permanent and temporary environmental correlations were much smaller. For model 2B,  $r_{pe}$  and  $r_e$  were 0.407 and 0.264 respectively. For model 1B,  $r_e$  was 0.330. Methods for estimation of genetic and phenotypic correlations for threshold characters have not been studied to the same extent as heritability. Van Vleck and Gregory (1992) analyzed simulated

ovulation rates by multiple-trait derivative-free REML approach and eight measures of ovulation rate were treated as separate traits. Their results showed that genetic correlations on the binomial scale seriously underestimated the correlation on the normal scale. However, Olausson and Ronnigen (1975) concluded from their simulation study for joint analysis of two correlated traits, one normally distributed and the other binomially distributed (all-or-none), that the genetic correlation between the two traits could be estimated by the half-sib correlation method in the ordinary way without transformation of the estimate except for low levels of incidence (5% and 10%) for the all-or-none trait. The estimates were almost the same as if the underlying normal distribution had been used, except for low heritability levels (.1) and low incidence levels (5% and 10%) of the all-or-none trait, where correction of the estimate made on the all-or-none data was recommended. However, the estimated phenotypic correlation between the two traits was highly biased, which implied that the residual correlation may have been seriously underestimated, similar to the result of our study.

4.1.3.4. Alternative Models: In order to evaluate the interaction between genetic and environmental covariances, four replicates using Model 1B but with different structure of covariances were simulated for Model 1B-X and Model 1B-Y, respectively. Input genetic and environmental correlations were .50 and .00, respectively for Model 1B-X while for Model 1B-Y, the corresponding values were .00 and .50. The results of genetic analyses for the two models are presented in Tables 4.5 and 4.6, respectively. In the two correlation settings, the means of genetic and environmental correlations between underlying normal fertility and litter size over 4 replicates were close to expected values. However, on the

categorical scale, both genetic and environmental correlations were significantly overestimated in Model 1B-X ( $P < .05$  or  $P < .01$ ) while in Model 1B-Y the environmental correlation was significantly underestimated ( $P < .05$ ). The REML procedures gave fairly accurate estimates for normally distributed traits irrespective of relationships between the traits. However, REML did not perform as well for categorical data, especially for estimation of covariance between categorical traits.

#### **4.3.2. Should Environmental Covariance ( $\sigma_{e1e2}$ ) Be Set to Zero ?**

Model 1B was used as a template to create two additional data sets with records of 5,000 ewes for 5 years. The results of DFREML analyses are shown in Table 4.11 and Table 4.12. Comparison between two alternatives of setting  $\sigma_{e1e2} = 0$  or not setting  $\sigma_{e1e2} = 0$  clearly showed no effect on normal or binomial fertility. However, setting  $\sigma_{e1e2} = 0$  biased variance components of normal and multinomial litter size downward by 10 -25% although genetic parameter estimates did not deviate from expected values because the different variance component were reduced proportionately.

Setting  $\sigma_{e1e2} = 0$  also significantly affected the estimates of genetic correlation and generally biased genetic covariance and genetic correlation estimates downward. For underlying variates, compared with not setting  $\sigma_{e1e2} = 0$ , setting  $\sigma_{e1e2} = 0$  reduced genetic covariance and correlation by 29 and 18%, respectively, while for categorical traits, these statistics were reduced by 67 and 63%, respectively. One noteworthy observation was that the log values of likelihoods for both approaches were almost the same for categorical traits.

The results of the study suggested that true existence of environmental sources of correlation would reduce estimates of the genetic covariation, if environmental correlation were arbitrarily set to zero. A set of starting values for environmental correlation including .01, .1, .25, .5, .75, .9, .99 were tried. Only starting values of .01 and .99 affected final converged values. In conclusion, zero and extremely small or large values for covariance should be avoided as starting values for DFREML methodology.

### **4.3.3. Effects of Selection on Fertility**

Various (co)variance component and genetic parameter estimates for five simulation data sets with or without culling litter size records of open ewes are presented in Tables 4.13 and 4.14 for model 2A and in Table 4.15 and 4.16 for model 2B. Selection resulted from random death loss and from open ewes. Only effects of selection on open ewes were studied. All the correlations were set to .5 ( $r_g = r_{pe} = r_e = .5$ ).

Clearly, there was no or an extremely small culling effect with independent traits (model 2A, Table 4.13 and 4.14). No single parameter estimate for the data without culling was significantly different from that for the data with culling. Actually, for litter size and fertility in both scales, the (co)variances and derived genetic or non-genetic parameters were essentially the same between the two groups of data which differed according to culling practice. Also small t values for the difference of the estimates derived from two groups of data sets suggested that the MTDFREML methodology can deal well with selection effect for independent traits with normal distributions (Table 4.13 and 4.15).

However, for correlated traits, failure of open ewes to produce a litter size record tended to reduce estimates of genetic, permanent and temporary environmental covariances and



correlations, especially for genetic covariance and correlation. The t tests showed highly significant ( $P < 0.01$ ) reduction for the genetic covariance and correlation in Model 2B (Table 4.16). In addition, selection based on fertility caused estimates for both genetic and environmental components for categorical litter size to be unstable. Atkin (1986) observed that estimates of both repeatability and heritability of barrenness were likely to be biased downwards by such culling so that the incorporation of barrenness as a trait for selection in British hill sheep must remain an open question. He also observed that if traditional approaches for (co)variance estimation were used, culling of ewes represents a possible source of bias in the estimation of genetic parameters. Analyses showed that barren ewes were selectively culled. A similar situation to this was also reported by McGuirk (1973) and Forest and Bichard (1974) in their data sets. The genetic, permanent environmental, residual, and phenotypic variance for categorical litter size with culling open ewes were larger than the ones without culling of open ewes by 3, 9, 9 and 8% in Model 2B (Table 4.16).

#### **4.4. Implications**

The usual transformation of heritability estimated on the categorical scale generally performed better for a simple animal model than for a repeatability model. Genetic correlations between the two categorical traits generally were close to the input value, indicating no need for transformation between the two scales. On the other hand, permanent environmental and temporary environmental correlations on categorical scales were significantly underestimated. Setting residual covariance to zero reduced genetic correlations

between fertility and litter size on both scales, especially on the categorical scale. Essentially the same log values of likelihoods were obtained with setting residual covariance to zero or not, indicating that the likelihood ratio test is not sensitive to residual covariance, i.e., this parameter is flat although its true value is .50. For correlated traits, failure of open ewes to produce a litter size record tended to reduce permanent and environmental covariances and correlations, especially for genetic covariance and correlation.

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Table 4.1. (Co)variance component and genetic parameter estimates of reproductive traits of model 1A: univariate analyses<sup>a</sup>.

Parameter <sup>b</sup>	Normal. fertility	Normal litter size	Binomial <sup>c</sup> fertility	Multinomial <sup>c</sup> litter size
$\sigma_a^2$	.2570 ±.0043	.1314 ±.0018	.0257 ±.0005	.0721 ±.0025
$\sigma_e^2$	.7323 ±.0089	.8703 ±.0073	.1667 ±.0010	.5747 ±.0067
$\sigma_p^2$	1.0034 ±.0044	1.0017 ±.0060	.1925 ±.0007	.6467 ±.0047
$h^2$	.255 ±.0029	.133 ±.0025	.135 ±.0029	.110 ±.0041
$e^2$	.745 .0029	.868 ±.0025	.865 .0029	.890 ±.0041

<sup>a</sup>: The sample size is 4.

<sup>b</sup>:  $\sigma_a^2$  = direct additive genetic variance.  $\sigma_e^2$  = residual variance.  $\sigma_p^2$  = phenotypic variance.  $h^2$  = heritability.  $e^2$  = residual variance as the proportion of phenotypic variance.

<sup>c</sup>: The only parameter for categorical fertility and litter size that was tested was heritability.

Table 4.2. (Co)variance component and genetic parameter estimates of reproductive traits of model 1A: bivariate analyses<sup>a</sup>.

Parameter <sup>b</sup>	Normal. fertility	Normal litter size	Covariance /correlation	Binomial fertility <sup>c</sup>	Multinomial litter size <sup>c</sup>	Covariance /correlation <sup>c</sup>
$\sigma_a^2(\sigma_{aa})$	.2572 ±.0043	.1320 ±.0019	.0049 .0076	.0257 ±.0005	.0723 ±.0025	.0002 ±.0019
$\sigma_e^2(\sigma_{ee})$	.7461 ±.0051	.8700 ±.0074	-.0093 ±.0049	.1667 ±.0010	.5745 ±.0068	.0002 ±.0005
$\sigma_p^2(\sigma_{pp})$	1.0032 ±.0047	1.0021 ±.0060	-.0044 ±.0118	.1924 ±.0007	.6468 ±.0030	.0004 ±.0029
$h^2(r_g)$	.255 ±.0029	.133 ±.0025	.023 ±.0409	.135 ±.0029	.110 ±.0041	.003 .0446
$e^2(r_e)$	.745 ±.0029	.868 ±.0025	-.0125 ±.0048	.865 ±.0029	.890 .0041	.000 ±.000

<sup>a</sup>: The sample size is 4.

<sup>b</sup>:  $\sigma_a^2(\sigma_{aa})$  = direct additive genetic variance (covariance).  $\sigma_e^2(\sigma_{ee})$  = residual variance (covariance).  $\sigma_p^2(\sigma_{pp})$  = phenotypic variance (covariance).  $h^2(r_g)$  = heritability (genetic correlation).  $e^2(r_e)$  = residual variance as the proportion of phenotypic variance (residual correlation).

<sup>c</sup>: All the variances component and parameters for categorical fertility and litter size were not tested except heritability and correlations.

\*: p<0.05.

\*\* : p<0.01

Table 4.3. (Co)variance component and genetic parameter<sup>a</sup> estimates of reproductive traits of model 1B: univariate analyses<sup>a</sup>.

Parameter <sup>b</sup>	Normal. fertility	Normal litter size	Binomial <sup>c</sup> fertility	Multinomial <sup>c</sup> litter size
$\sigma_a^2$	.2528 ±.0036	.1002 ±.0123	.0256 ±.0006	.0653 ±.007
$\sigma_e^2$	.7530 ±.0052	.7413 ±.0065	.1679 ±.0008	.5768 ±.0057
$\sigma_p^2$	1.0058 ±.0042	.8415 ±.0068	.1935 ±.0006	.6421 ±.0042
$h^2$	.253 ±.0048	.120 ±.0135	.133 ±.0025	.103 ±.0111
$e^2$	.748 ±.0048	.880 ±.0135	.868 ±.0025	.898 ±.0111

<sup>a</sup>: The sample size is 4.

<sup>b</sup>:  $\sigma_a^2$  = direct additive genetic variance.  $\sigma_e^2$  = residual variance.  $\sigma_p^2$  = phenotypic variance.  $h^2$  = heritability.  $e^2$  = residual variance as the proportion of phenotypic variance.

<sup>c</sup>: All the (co)variances component and parameters for categorical fertility and litter size were not tested except heritabilities.

Table 4.4. (Co)variance component and genetic parameter estimates of reproductive traits of model 1B: bivariate analyses<sup>a</sup>.

Parameter <sup>b</sup>	Normal. fertility	Normal litter size	Covariance /correlation	Binomial fertility <sup>c</sup>	Multinomial litter size <sup>c</sup>	Covariance /correlation <sup>c</sup>
$\sigma_a^2(\sigma_{aa})$	.2537 ±.0037	.1376 ±.0169	.0927 ±.0065	.0255 ±.0007	.0822 ±.0080	.0217 ±.0010
$\sigma_e^2(\sigma_{ee})$	.7526 ±.0053	.8644 ±.0088	.4059 ±.0056	.1680 ±.0008	.6481 ±.0110	.1088 .0050
$\sigma_p^2(\sigma_{pp})$	1.0064 ±.0042	1.0020 ±.0082	.4985 ±.0068	.1935 ±.0006	.7302 ±.0052	.1305 ±.0042
$h^2(r_g)$	.253 ±.0048	.138 ±.0170	.500 ±.0181	.133 .0025	.110 ±.0108	.478 ±.0111
$e^2(r_e)$	.748 .0048	.863 ±.0170	.503 ±.0063	.868 ±.0025	.890 .0108	.330 <sup>**</sup> ±.0123

<sup>a</sup>: The sample size is 4.

<sup>b</sup>:  $\sigma_a^2(\sigma_{aa})$  = direct additive genetic variance (covariance).  $\sigma_e^2(\sigma_{ee})$  = residual variance (covariance).  $\sigma_p^2(\sigma_{pp})$  = phenotypic variance (covariance).  $h^2(r_g)$  = heritability (genetic correlation).  $e^2(r_e)$  = residual variance as the proportion of phenotypic variance (residual correlation).

<sup>c</sup>: All the (co)variances component and parameters for categorical fertility and litter size were not tested except heritability and correlations.

\*: p<0.05.

\*\* : p<0.01

Table 4.5. (Co)variance component and genetic parameter estimates of reproductive traits of model 1B-X: bivariate analyses<sup>a</sup>

Parameter <sup>b</sup>	Normal. fertility	Normal litter size	Covariance /correlation	Binomial fertility <sup>c</sup>	MultinomialCovariance litter size <sup>c</sup>	/correlation <sup>c</sup>
$\sigma_a^2(\sigma_{aa})$	.2501 ±.0056	.1113 ±.0098	.0857 ±.0057	.0263 ±.0006	.0833 ±.0063	.0332 ±.0024
$\sigma_e^2(\sigma_{ee})$	.7480 ±.0048	.8944 ±.0065	.0010 ±.0059	.1653 ±.0026	.6437 ±.0052	.0757 ±.0089
$\sigma_p^2(\sigma_{pp})$	.9982 ±.0024	1.0057 ±.0071	.0867 ±.0089	.1916 ±.0009	.7270 ±.0114	.1205 ±.0197
$h^2(r_g)$	.250 ±.0063	.112 ±.0037	.514 ±.0275	.136 ±.0040	.114 ±.0075	.698** ±.0306
$e^2(r_e)$	.750 ±.0063	.888 ±.0037	.000 ±.0084	.864 ±.0040	.886 ±.0075	.232** ±.0252

<sup>a</sup>: The sample size is 4.

<sup>b</sup>:  $\sigma_a^2(\sigma_{aa})$  = direct additive genetic variance (covariance).  $\sigma_e^2(\sigma_{ee})$  = residual variance (covariance).  $\sigma_p^2(\sigma_{pp})$  = phenotypic variance (covariance).  $h^2(r_g)$  = heritability (genetic correlation).  $e^2(r_e)$  = residual variance as the proportion of phenotypic variance (residual correlation).

<sup>c</sup>: All the (co)variances component and parameters for categorical fertility and litter size were not tested except heritability and correlations.

\*: p<0.05.

\*\* : p<0.01



Table 4.6. (Co)variance component and genetic parameter estimates of reproductive traits of model 1B-Y: bivariate analyses<sup>a</sup>.

Parameter <sup>b</sup>	Normal. fertility	Normal litter size	Covariance /correlation	Binomial fertility <sup>c</sup>	MultinomialCovariance litter size <sup>c</sup>	/correlation <sup>c</sup>
$\sigma_a^2(\sigma_{aa})$	.2496 ±.0027	.1195 ±.0053	-.0064 ±.0025	.0249 ±.0004	.0751 ±.0039	.0014 ±.0022
$\sigma_e^2(\sigma_{ee})$	.7535 ±.0038	.8634 ±.0140	.3987 ±.0104	.1674 ±.0004	.6836 ±.0316	.1333 ±.0180
$\sigma_p^2(\sigma_{pp})$	1.0031 ±.0051	.9829 ±.0125	.3923 ±.0111	.1923 ±.0005	.7587 ±.0322	.1347 ±.0199
$h^2(r_g)$	.248 ±.0020	.122 ±.0058	-.038 ±.0150	.130 ±.0032	.098 ±.0058	.030 ±.0487
$e^2(r_e)$	.752 ±.0020	.878 ±.0058	.494 ±.0103	.870 ±.0032	.902 ±.0058	.388 ±.0454

<sup>a</sup>: The sample size is 4.

<sup>b</sup>:  $\sigma_a^2(\sigma_{aa})$  = direct additive genetic variance (covariance).  $\sigma_e^2(\sigma_{ee})$  = residual variance (covariance).  $\sigma_p^2(\sigma_{pp})$  = phenotypic variance (covariance).  $h^2(r_g)$  = heritability (genetic correlation).  $e^2(r_e)$  = residual variance as the proportion of phenotypic variance (residual correlation).

<sup>c</sup>: All the (co)variances component and parameters for categorical fertility and litter size were not tested except heritability and correlations.

\*: p<0.05.

\*\* : p<0.01

Table 4.7. (Co)variance component and genetic parameter estimates of reproductive traits of model 2A: univariate analyses<sup>a</sup>.

Parameter <sup>b</sup>	Normal. fertility	Normal litter size	Binomial <sup>c</sup> fertility	Multinomial <sup>c</sup> litter size
$a^2$	.1541 ± .0072	.1514** ± .0072	.0160 ± .0006	.0824 ± .0056
$c^2$	.0966 ± .0066	.0698** ± .0061	.0097 ± .0008	.0382 ± .0075
$e^2$	.7532 ± .0032	.7811 ± .0046	.1661 ± .0005	.5216 ± .0050
$p^2$	1.0039 ± .0041	1.0023 ± .0058	.1918 ± .0004	.6422 ± .0028
$h^2$	.154 ± .0071	.150** ± .0065	.083 ± .0030	.126* ± .0081
$c^2$	.096 ± .0069	.071** ± .0060	.0520 ± .0044	.059 ± .0123
$e^2$	.750 ± .0033	.781 ± .0028	.866 ± .0027	.811 ± .0057

<sup>a</sup>: The sample size is 4.

<sup>b</sup>:  $a^2$  = direct additive genetic variance.  $e^2$  = residual variance.  $p^2$  = phenotypic variance.  $h^2$  = heritability.  $e^2$  = residual variance as the proportion of phenotypic variance.

<sup>c</sup>: All the (co)variances component and parameters for categorical fertility and litter size were not tested except heritabilities.

\*:  $p < 0.05$ .

\*\* :  $p < 0.01$ .

Table 4.8. (Co)variance component and genetic parameter estimates of reproductive traits of model 2A: bivariate analyses<sup>a</sup>.

Parameter <sup>b</sup>	Normal. fertility	Normal litter size	Covariance /correlation	Binomial fertility <sup>c</sup>	Multinomial litter size <sup>c</sup>	Covariance /correlation <sup>c</sup>
$\sigma_a^2(\sigma_{aa})$	.1531 ± .0023	.1545** ± .0087	-.0010 ± .0033	.0151 ± .0008	.0805 ± .0049	.0015 ± .0011
$\sigma_c^2(\sigma_{cc})$	.0980 ± .0064	.0656** ± .0070	-.0013 ± .0024	.0106 ± .0007	.0376 ± .0077	-.0005 ± .0009
$\sigma_e^2(\sigma_{ee})$	.7529 ± .0033	.7826 ± .0044	.0007 ± .0022	.1664 ± .0006	.5260 ± .0050	.0032 ± .0051
$\sigma_p^2(\sigma_{pp})$	1.0036 ± .0042	1.0031 ± .0061	-.0017 ± .0034	.1920 ± .0003	.6441 ± .0030	.0038 ± .0054
$h^2(r_g)$	.152 ± .0071	.155** ± .0081	-.013 ± .0213	.079 ± .0046	.123* ± .0073	.04 ± .0364
$c^2(r_c)$	.098 ± .0065	.066** ± .0072	-.021 ± .0290	.055 ± .0040	.058 ± .0125	-.027 ± .0492
$e^2(r_e)$	.750 ± .0033	.781 ± .0035	.000 ± .0026	.867 ± .0030	.816 ± .0054	.010 ± .0174

<sup>a</sup>: The sample size is 4.

<sup>b</sup>:  $\sigma_a^2(\sigma_{aa})$  = direct additive genetic variance (covariance).  $\sigma_e^2(\sigma_{ee})$  = residual variance (covariance).  $\sigma_p^2(\sigma_{pp})$  = phenotypic variance (covariance).  $h^2(r_g)$  = heritability (genetic correlation).  $e^2(r_e)$  = residual variance as the proportion of phenotypic variance (residual correlation).

<sup>c</sup>: All the (co)variances component and parameters for categorical fertility and litter size were not tested except heritability and correlations.

\*: p<0.05.

\*\* : p<0.01

Table 4.9. (Co)variance component and genetic parameter estimates of reproductive traits of model 2B: univariate analyses<sup>a</sup>.

Parameter <sup>b</sup>	Normal. fertility	Normal litter size	Binomial <sup>c</sup> fertility	Multinomial <sup>c</sup> litter size
$a^2$	.1485 ±.0053	.0991** ± .0051	.0140 ±.0008	.0648 ± .0040
$c^2$	.1026 ± .0041	.0745** ± .0075	.0113 ± .0008	.0459 ± .0055
$e^2$	.7492 ± .0031	.6658** ± .0037	.1674 ± .0073	.5347 ± .0015
$p^2$	1.0008 ± .0031	.8395** ± .0036	.1858 ± .0073	.6454 ± .0015
$h^2$	.148 ± .0055	.118 ± .0059	.071* ± .0038	.100 ± .0061
$c^2$	.103 ± 0.0042	.089 ± 0.0091	.058 ± 0.0047	.069 ± 0.0086
$e^2$	.747 ± .0026	.794 ± .0040	.867 ± .0021	.827 ± .0037

<sup>a</sup>: The sample size is 4.

<sup>b</sup>:  $a^2$  = direct additive genetic variance.  $e^2$  = residual variance.  $p^2$  = phenotypic variance.  $h^2$  = heritability.  $e^2$  = residual variance as the proportion of phenotypic variance.

<sup>c</sup>: All the (co)variances component and parameters for categorical fertility and litter size were not tested except heritabilities.

\*:  $p < 0.05$ .

\*\* :  $p < 0.01$ .

Table 4.10. (Co)variance component and genetic parameter estimates of reproductive traits of model 2B: bivariate analyses<sup>a</sup>.

Parameter <sup>b</sup>	Normal. fertility	Normal litter size	Covariance /correlation	Binomial fertility <sup>c</sup>	Multinomial litter size <sup>c</sup>	Covariance /correlation <sup>c</sup>
$a^2( aa)$	.1486 ± .0054	.1248 ± .0049	.0664 ± .0064	.0141 ± .0007	.0771 ± .0039	.0155 ± .0015
$c^2( cc)$	.1030 ± .0040	.1033 ± .0056	.0545 ± .0041	.0114 ± .0008	.0531 ± .0057	.0096 ± .0010
$e^2( ee)$	.7493 ± .0031	.7732 ± .0050	.3758 ± .0034	.1674 ± .0004	.5877 ± .0079	.0809 ± .0108
$p^2( pp)$	1.0008 ± .0031	1.0012 ± .0071	.4967 ± .0052	0.1928 ± .0004	.7102 ± .0107	.1076 ± .0101
$h^2(r_g)$	.148 ± .0055	.126 ± .0052	.484 ± .0410	.071* ± .0038	.111 ± .0062	.475 ± .0383
$c^2(r_c)$	.103 ± .0042	.102 ± .0057	.536 ± .0440	.058 ± .0047	.075 ± .0076	.407 ± .0452
$e^2(r_e)$	.747 ± .0026	.773 ± .0040	.495 ± .0034	.867 ± .0021	.817 ± .0040	.264** ± .0293

The sample size is 4.

<sup>b</sup>:  $a^2( aa)$  = direct additive genetic variance (covariance).  $e^2( ee)$  = residual variance (covariance).  $p^2( pp)$  = phenotypic variance (covariance).  $h^2(r_g)$  = heritability (genetic correlation).  $e^2(r_e)$  = residual variance as the proportion of phenotypic variance (residual correlation).

<sup>c</sup>: All the (co)variances component and parameters for categorical fertility and litter size were not tested except heritability and correlations.

\*:  $p < 0.05$ .

\*\* :  $p < 0.01$

Table 4.11. Effect of “ set  $\text{cov}_{e12} = 0$  “ on the estimation of ( co ) variance components for underlying variates

	Fert <sup>(1)</sup>	Fert <sup>(2)</sup>	DIFF	LS <sup>(1)</sup>	LS <sup>(2)</sup>	DIFF	COV <sup>(1)</sup>	COV <sup>(2)</sup>	DIFF
$\sigma_a^2(\sigma_{aa})$	.2572	.2550	.0022	.1549	.1160	.0389	.0950	.0674	.0276
	±.0053	±.0058		±.0170	±.0094		±.0119	±.0081	
$\sigma_e^2(\sigma_{ee})$	.7498	.7507	-.0009	.8439	.7375	.1064	.3977	.000	.3977
	±.0024	±.0022		±.0074	±.0022		±.0064	±.00	
$\sigma_p^2(\sigma_{pp})$	1.0070	1.0057	.0013	1.0089	.8535	.1554	.4927	.0674	.4253
	±.0077	±.0080		±.0096	±.0072		±.0055	±.0081	
$h^2(r_g)$	.255	.255	.000	.155	.140	.015	.475	.390	.085
	±.005	±.005		±.015	±.010		±.025	±.030	
$e^2(r_e)$	.745	.745	.000	.845	.860	-.015	.495	.000	.495
	±.005	±.005		±.015	±.010		±.005	±.000	
-2LogL							22916.6	23672.7	-756.1
							±70.2	±31.6	

Note: (a). <sup>(1)</sup> is estimates of REML when  $\text{cov}_{12}$  is not set to be zero. <sup>(2)</sup> is estimates of REML when  $\text{cov}_{12}$  is set to be zero.

(b).Fert = normal fertility. LS = normal litter size. DIFF = difference between estimates with and without setting residual covariance to zero. COV = covariance components and correlations between the normal fertility and litter size.

(c).  $\sigma_a^2(\sigma_{aa})$  = direct additive genetic variance (covariance).  $\sigma_e^2(\sigma_{ee})$  = residual variance (covariance).  $\sigma_p^2(\sigma_{pp})$  = phenotypic variance (covariance).  $h^2(r_g)$  = heritability (genetic correlation).  $e^2(r_e)$  = residual variance as the proportion of phenotypic variance (residual correlation).

(d).The sample size is 2.

Table 4.12. Effect of “ set  $\text{cov}_{e12} = 0$  “ on the estimation of (co) variance component for categorical variates.

	Fert <sup>(1)</sup>	Fert <sup>(2)</sup>	DIFF	LS <sup>(1)</sup>	LS <sup>(2)</sup>	DIFF	COV <sup>(1)</sup>	COV <sup>(2)</sup>	DIFF
$\sigma_a^2(\sigma_{aa})$	.02246	.0246	.0000	.0907	.0719	.0188	.0228	.0073	.0155
	$\pm 0.0002$	$\pm 0.0002$		$\pm 0.0058$	$\pm 0.0048$		$\pm 0.0014$	$\pm 0.0025$	
$\sigma_e^2(\sigma_{ee})$	.1690	.1690	.0000	.6441	.5768	.0673	.1063	.0000	.1063
	$\pm 0.0014$	$\pm 0.0014$		$\pm 0.0117$	$\pm 0.0004$		$\pm 0.0094$	$\pm 0.0000$	
$\sigma_p^2(\sigma_{pp})$	.1936	.1936	.0000	.7348	.6487	.0861	.1291	.0073	.1218
	$\pm 0.0012$	$\pm 0.0012$		$\pm 0.0059$	$\pm 0.0044$		$\pm 0.0080$	$\pm 0.0025$	
$h^2(r_g)$	.130	.130	.000	.120	.110	.010	.480	.175	.305
	$\pm 0.000$	$\pm 0.000$		$\pm 0.010$	$\pm 0.010$		$\pm 0.0100$	$\pm 0.055$	
$e^2(r_e)$	.870	.870	.000	.880	.890	-.010	.325	.000	.325
	$\pm 0.000$	$\pm 0.000$		$\pm 0.010$	$\pm 0.010$		$\pm 0.025$	$\pm 0.000$	
-2LogL							-9173.3	-9173.3	
							$\pm 159.35$	$\pm 159.35$	

Note: (a). <sup>(1)</sup> is estimates of REML when  $\text{cov}_{e12}$  is not set to be zero. <sup>(2)</sup> is estimates of REML when  $\text{cov}_{e12}$  is set to be zero.

(b).Fert = categorical fertility. LS = categorical litter size. DIFF = difference between estimates with and without setting residual covariance to zero. COV = covariance components and correlations between the categorical fertility and litter size.

(c).  $\sigma_a^2(\sigma_{aa})$  = direct additive genetic variance (covariance).  $\sigma_e^2(\sigma_{ee})$  = residual variance (covariance).  $\sigma_p^2(\sigma_{pp})$  = phenotypic variance (covariance).  $h^2(r_g)$  = heritability (genetic correlation).  $e^2(r_e)$  = residual variance as the proportion of phenotypic variance (residual correlation).

(d).The sample size is 2.

Table 4.13. The culling effect on variance component estimation of underlying scale of sheep reproduction for model 2A.

	Alldata N. Fert.	Sdata N.Fert.	DIFF	Alldata N.LS.	Sdata N.LS.	DIFF	Alldata COV	Sdata COV	DIFF
$a^2(a_a)$	.1613 ±.0053	.1612 ±.0058	.0001	.1196 ±.0079	.1120 ±.010	.0076	-.0055 ±.0030	-.0076 ±.0038	.0021
$c^2(c_c)$	.0904 ±.0069	.0904 ±.0073	.0000	.0953 ±.0066	0.0966 ±.0093	-.0043	.0057 ±.0038	.0028 ±.0034	.0028
$e^2(e_e)$	.7503 ±.0050	.7480 ±.0051	.0003	.7794 ±.0040	.7828 ±.0080	-.0034	-.0004 ±.0014	-.0026 ±.0042	.0022
$p^2(p_{pp})$	1.0020 ±.0053	1.0016 ±.0052	.0005	.9943 ±.0051	.9943 ±.0098	-.0001	-.0003 ±.0027	-.0073 ±.0086	.0071
$h^2(r_g)$	.160 ±.005	.160 ±.004	.002	.120 ±.008	.110 ±.010	.006	-.040 ±.021	-.062 ±.031	.022
$c^2(r_{pe})$	.090 ±.007	.090 ±.007	.000	.100 ±.007	.100 ±.009	.002	.060 ±.040	.036 .042	.020
$e^2(r_e)$	.750 ±.004	.750 ±.003	-.002	.780 ±.004	.790 ±.004	-.004	-.000 ±.002	-.004 ±.007	.002

Note: (a). Alldata was the group of data sets without culling open ewes. Sdata was the group of data sets with culling open ewes.

(b). N. Fert = normal fertility. N. LS = normal litter size. COV = covariance components and correlations between the normal fertility and litter size.

(c).  $a^2(a_a)$  = direct additive genetic variance (covariance).  $c^2(c_c)$  = permanent variance (covariance).  $e^2(e_e)$  = residual variance (covariance).  $p^2(p_{pp})$  = phenotypic variance (covariance).  $h^2(r_g)$  = heritability (genetic correlation).  $c^2(r_c)$  = permanent variance as the proportion of phenotypic variance (residual correlation).  $e^2(r_e)$  = residual variance as the proportion of phenotypic variance (residual correlation).

(d). The sample size is 5.

\*: p<0.05.

\*\* : p<0.01.



Tab 4.14. The culling effect on variance component estimation of categorical traits of sheep reproduction for model 2A.

	Alldata	SDATADIFF	Alldata	SDATADIFF	Alldata	SDATADIFF			
	C.Fert.	C.Fert.	C.LS.	C.LS.	COV.	COV.			
$a^2(_{aa})$	.0165	.0166	.0001	.0688	.0618	.0076	.0000	-.0004	.0021
	±.0008	±.0008		±.0047	±.0055		±.0008	±.0006	
$c^2(_{cc})$	.0098	.0091	.0000	.0491	.0533	-.0043	-.0005	.0128	.0028
	±.0010	±.0011		±.0043	±.0066		±.0004	±.0131	
$e^2(_{ee})$	.1662	.1665	.0003	.5320	.5322	-.0034	.0009	.0063	.0022
	±.0007	±.0009		±.0024	±.0038		±.0009	±.0020	
$p^2(_{pp})$	.1925	.1924	.0001	.6498	.6474	-.000	.0005	.0069	.0071
	±.0007	±.0007		±.0016	±.0037		±.0011	±.0022	
$h^2(r_g)$	.080	.090	.000	.106	.098	.006	-.0020	-.0120	.022
	±.005	±.006		±.006	±.009		±.0231	±.0183	
$c^2(r_{pe})$	.050	.050	.000	.080	.080	.000	-.012	.042	.0200
	±.005	±.005		±.007	±.011		±.020	±.059	
$e^2(r_e)$	.850	.870	.002	.820	.820	-.004	.002	.020	.002
	±.013	±.004		±.005	±.006		±.004	±.007	

Note: (a).Alldata was the group of data sets without culling open ewes. Sdata was the group of data sets with culling open ewes.  
 (b). C. Fert = categorical fertility. C. LS = categorical litter size. COV = covariance components and correlations between the categorical fertility and litter size.  
 (c).  $a^2(_{aa})$  = direct additive genetic variance (covariance).  $c^2(_{cc})$  = permanent variance (covariance).  $e^2(_{ee})$  = residual variance (covariance).  $p^2(_{pp})$  = phenotypic variance (covariance).  $h^2(r_g)$  = heritability (genetic correlation).  $c^2(r_c)$  = permanent variance as the proportion of phenotypic variance (permanent environmental correlation).  $e^2(r_e)$  = residual variance as the proportion of phenotypic variance (residual correlation).  
 (d).The sample size is 5.  
 \*: p<0.05.  
 \*\*: p<0.01.

Table 4.15 . The culling effect on variance component estimation of underlying normal variates of sheep reproduction for model 2B.

	Alldata Fert	Sdata Fert	DIFF	Alldata LS	Sdata LS	DIFF	Alldata COV	Sdata COV	DIFF
$\sigma_a^2(\sigma_{aa})$	.1479 ±.0020	.1471 ±.0020	.0008	.1154 ±.0049	.1127 ±.0092	.0027	.0666 ±.0110	.0648 ±.0051	.0018
$\sigma_c^2(\sigma_{cc})$	.1011 ±.0027	.1020 ±.0025	-.0005	.1099 ±.0049	.1111 .0098	-.0012	.0511 ±.0039	.0518 ±.0067	-.0007
$\sigma_e^2(\sigma_{ee})$	.7552 ±.0027	.7551 ±.0026	.0001	.7773 ±.0026	.7731 ±.0095	.0042	.3835 ±.0013	.3808 ±.0052	.0027
$\sigma_p^2(\sigma_{pp})$	1.0043 ±.0027	1.0042 ±.0026	.0001	1.0026 ±.0098	.9970 ±.0068	.0056	.5016 ±.0030	.4974 ±.0041	.0042
$h^2(r_g)$	.147 ±.002	.148 ±.002	-.001	.115 ±.0050	.112 ±.0097	.003	.513 ±.0201	.504 ±.0246	.009
$c^2(r_{pe})$	.100 ±.002	.103 ±.003	-.003	.110 ±.0054	.107 ±0.0091	.003	.481 ±.0283	.477 ±.0465	.004
$e^2(r_e)$	.753 ±.002	.754 ±.002	-.001	.775 ±.002	.775 ±.006	.000	.500 ±.002	.498 ±.005	.002

Note: (a).Alldata was the group of data sets without culling open ewes. Sdata was the group of data sets with culling open ewes.

(b). N. Fert = normal fertility. N. LS = normal litter size. COV = covariance components and correlations between the normal fertility and litter size.

(c).  $\sigma_a^2(\sigma_{aa})$  = direct additive genetic variance (covariance).  $\sigma_c^2(\sigma_{cc})$  = permanent variance (covariance).  $\sigma_e^2(\sigma_{ee})$  = residual variance (covariance).  $\sigma_p^2(\sigma_{pp})$  = phenotypic variance (covariance).  $h^2(r_g)$  = heritability (genetic correlation).  $c^2(r_c)$  = permanent variance as the proportion of phenotypic variance (permanent environmental correlation).  $e^2(r_e)$  = residual variance as the proportion of phenotypic variance (residual correlation).

(d).The sample size is 10.

\*:  $p < 0.05$ .

\*\* :  $p < 0.01$ .

Table 4.16. The culling effect on variance component estimation of categorical variates of sheep reproduction for model 2B.

	Alldata C.Fert	Sdata C.Fert	DIFF	Alldata C.LS	Sdata C.LS	DIFF	Alldata COV	Sdata COV	DIFF
$a^2(a_a)$	.0155	.0152	.0003	.0649	.0652	-.0003	.0171	.0132	.0039**
	±.0035	±.0004		±.0031	±.0055		±.0008	±.0016	
$c^2(c_c)$	.0100	.0103	-.0003	.0591	.0643	-.0052	.0110	.0107	.0003
	±.0004	±.0005		±.0030	±.0051		±.0009	±.0016	
$e^2(e_e)$	.1673	.1673	.0000	.5261	.5796	-.0535**	.0944	.0868	.0076
	±.0003	±.0004		±.0022	±.0081		±.0008	±.0035	
$p^2(p_{pp})$	.1927	.1927	.0000	.6501	.7091	-.0590**	.1225	.1107	.0118*
	±.0011	±.0004		±.0028	±.0058		±.0010	±.0036	
$h^2(r_g)$	.082	.079	.003	0.101	.092	.009	.539	.410	0.129**
	±.001	.002		±.005	.008		±.021	±.039	
$c^2(r_{pe})$	.052	.052	.000	.090	.090	.000	.454	.413	.041
	±.003	±.003		±.005	±.008		±.029	±.056	
$e^2(r_e)$	.868	.868	.000	.809	.817	.008	.317	.273	.044**
	±.001	±.001		±.003	±.006		±.003	±.013	

Note: (a).Alldata was the group of data sets without culling open ewes. Sdata was the group of data sets with culling open ewes.  
 (b). C. Fert = categorical fertility. C. LS = categorical litter size. COV = covariance components and correlations between the categorical fertility and litter size.  
 (c).  $a^2(a_a)$  = direct additive genetic variance (covariance).  $c^2(c_c)$  = permanent variance (covariance).  $e^2(e_e)$  = residual variance (covariance).  $p^2(p_{pp})$  = phenotypic variance (covariance).  $h^2(r_g)$  = heritability (genetic correlation).  $c^2(r_c)$  = permanent variance as the proportion of phenotypic variance (permanent environmental correlation).  $e^2(r_e)$  = residual variance as the proportion of phenotypic variance (residual correlation).  
 (d).The sample size is 10  
 \*:  $p < 0.05$ .  
 \*\*:  $p < 0.01$ .

Table.4.17. The pooled (co) variance component and genetic parameter estimates of reproduction trait for model 2A.

	N.Fert	N.LS	COV	B.Fert	P.LS	COV
$a^2( aa)$	.1558	.1403	.0033	.0743	.0156	.0006
	±.0052	±.0084	±.0026	±.0043	±.0006	±.0007
$c^2( cc)$	.0955	.0770**	.0001	.0428	.0101	.0040
	±.0049	±.0069	±.0020	±.0058	±.0006	±.0044
$e^2( ee)$	.7520	.7826	-.0004	.5281	.1665	.0042
	±.0028	±.0038	±.0020	±.0036	±.0005	±.0034
$p^2( pp)$	1.0029	1.0002	-.0036	.6452	.1922	.0048
	±.0032	±.0051	±.0035	±.0023	±.0003	±.0036
$h^2(r_g)$	.154	.141*	-.023	.115**	.081**	.0227
	±.005	±.008	±.0187	±.006	±.004	±.025
$c^2(r_c)$	.095	.078**	-.002	.066	.053	-.004
	±.005	±.007	±.024	±.009	±.003	±.038
$e^2(r_e)$	.750	.783*	-.001	.818	.867	.013
	±.002	±.003	±.003	±.004	±.002	±.012

Note: (a).N. Fert = normal fertility. N. LS = normal litter size. B. Fert = binomial fertility. P. LS = multinomial litter size. COV1 = covariance components and correlations between the normal fertility and litter size. COV2 = covariance components and correlations between the categorical fertility and litter size.  
 (b).  $a^2( aa)$  = direct additive genetic variance (covariance).  $c^2( cc)$  = permanent variance (covariance).  $e^2( ee)$  = residual variance (covariance).  $p^2( pp)$  = phenotypic variance (covariance).  $h^2(r_g)$  = heritability (genetic correlation).  $c^2(r_c)$  = permanent variance as the proportion of phenotypic variance (permanent environmental correlation).  $e^2(r_e)$  = residual variance as the proportion of phenotypic variance (residual correlation).  
 (c).The sample size is 15.  
 (d).Binomial Fert. and multinomial LS as well as their covariance are not tested by T test except heritability of categorical fertility.  
 \* : p < 0.05.  
 \*\* : p < 0.01.

# **CHAPTER 5. Genetic Variation and Covariation for Growth, Fleece Characteristics and Reproduction in Three Sheep Breeds**

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## **CHAPTER 5**

### **Genetic Variation and Covariation among Growth, Fleece Characteristics and Reproduction in Three Sheep Breeds**

#### **Abstract**

Bivariate genetic analyses of litter size with growth and fleece traits were carried out by REML for three breeds, Suffolk, Targhee and Polypay. Likelihood ratio tests were employed to evaluate the importance of different (co)variance components in various animal models. Heritabilities for weaning weights at 60 and 90 d and for 60- to 120-d cumulative postweaning gain for Suffolk sheep were .19, .12, and .17, respectively. Heritabilities for weaning weights at 60 and 120 d, and for 60- to 120-d and 120- to 365-d cumulative postweaning gains for Targhee sheep were .14, .16, .27 and .19, respectively. Heritabilities for birth weight, weaning weights at 60 and 90 d, and 60- to 120 d cumulative gain for Polypay sheep were .19, .11 and .10 and .22, respectively. Maternal genetic and maternal permanent environmental effects were important for all body weights of the three breeds except for weaning weight at 90 d for Polypay sheep, indicating that explicitly considering these effects should result in more genetic improvement in growth traits. Estimates of heritability and permanent environmental effects for litter size were close to each other among the three breeds and ranged from .09 to .12 and .00 to .05, respectively. The heritabilities for grease fleece weight were the

same (.44) for both Targhee and Polypay sheep. The heritability estimate for fiber diameter for Targhee sheep was .50. Direct genetic correlations between various growth traits and litter size were favorable for Suffolk and Targhee sheep but weak for Polypay sheep, indicating that growth and litter size can be selected simultaneously without marked adverse effects. Genetic correlations between maternal effects for growth and direct effects for litter size for all three breeds were generally small and not significantly different from zero, and thus do not present a serious problem for simultaneous genetic improvement of litter size and maternal performance for growth traits. Within-trait maternal-direct genetic correlations for growth in the three breeds were variable and generally negative. Strong and significant negative estimates were obtained for weaning weight at 60 d for Targhee sheep (-.89 to -.90), and for Polypay sheep (-.53 to -.56). Grease fleece weight and fleece diameter were unfavorably related with litter size; the corresponding estimates were -.09 and .29 to .30, respectively, for Targhee sheep. In contrast, grease fleece weight was favorably related with litter size ( $r_g = .21$ ) for Polypay sheep. Some dependence between estimates of two across-trait genetic correlations between litter size and growth traits were detected, suggesting that the two parameters were confounded. Generally, fixing residual covariance between growth, fleece traits and litter size to zero did not affect the estimates of other components in the models although the residual correlations often were be large. Statistical tests indicated that these correlations were not significantly different from zero. From a sampling viewpoint, the observation that none of the residual correlations between litter size and other traits from different models for all three breeds differed significantly from zero would force us to



carefully reconsider environmental covariance component. Further studies on effects of data structure, REML methodology, and the Simplex iteration process will be needed to verify these strong correlations. The flat ridge for two across-trait genetic correlation estimates may be attributed to high sampling correlations. To overcome this obstacle would be a major task for covariance estimation in future studies.

Keywords: Sheep, Litter Size, Growth, Fleece Traits, Maternal Effects, Genetic Correlations, (Co)variance Components

## **5.1. Introduction**

Genetic improvements for reproductive, growth and fleece traits are major goals for sheep breeding because the efficiency of sheep production depends primarily upon three functions: female production, reproduction, and growth of lambs (Dickerson, 1970). Improving reproductive performance is likely to increase both the biological and economic efficiency of animal production enterprises (Dickerson, 1970). Among these reproductive traits, litter size is of major interest because an increase in the number of lambs marketed per ewe per year offers the greatest single opportunity for economic gain (Shelton, 1971). Turner (1969) concluded that litter size seemed to be the most useful selection criterion for genetic improvement of reproduction. Although selection for litter size has been successful (Clark, 1972; Turner, 1978), the rate of improvement has not been large, partly because the trait has a low heritability, is categorical in nature and is expressed only in females of reproductive age that conceive and maintain pregnancy.

Knowledge of genetic relationships between litter size and other economically important traits is generally lacking. However, development of breeding objectives and effective genetic improvement programs requires simultaneous consideration of the three kinds of economically important traits mentioned above. Knowledge of genetic variation for economically important traits and genetic covariances among these traits is prerequisite. Traditional practices in wool and dual-purpose sheep breeding seldom took reproductive traits, such as litter size, into account. Recently, possible reductions in fitness including reproduction performance associated with current and past breeding programs have been a concern to many animal breeders. Therefore, Fogarty (1995) suggested that for genetic improvement in lamb breeding enterprises, the important traits associated with reproduction and wool production of the ewe and survival, growth and carcass characteristics of the lamb should be included.

Fogarty (1995) summarized published genetic parameters for live weights, fat and muscle measurements, wool production, and reproduction in sheep. Estimates of heritabilities for weaning weight in the literature range from .08 to .41 (9 estimates) for wool breeds, .03 to .45 (43 estimates) for dual-purpose breeds and .05 to .57 (14 estimates) for meat breeds (Fogarty, 1995). The weighted means of literature estimates for the three types of breeds are  $.33 \pm .10$ ,  $.21 \pm .11$ , and  $.21 \pm .18$ , respectively. The heritabilities of weaning weight, postweaning live weight and yearling live weight for Targhee were .16, .12 and .25 (Ercanbrack and Price, 1972), respectively. In Fogarty's review, no heritability estimates were available for Polypay sheep (a composite breed consisting of 25% each of Dorset, Targhee, Rambouillet and Finnsheep inheritance). Al-

Shorepy and Notter (1996) reported that heritability estimates for weights from birth to 120 d ranged from .04 to .19 in a composite sheep population containing 50% Dorset, 25% Rambouillet and 25% Finnsheep breeding.

Few reported estimates of heritabilities for postweaning gain are available, especially for cumulative postweaning gain. Thrift (1973) obtained a heritability of  $.23 \pm .12$  for rate of gain from 70 days to market in a Dorset  $\times$  Western ewe flock, which was lower than a previous estimate of  $.38 \pm .13$  for postweaning gain by Harrington et al. (1962). Fogarty (1995) summarized 42 estimates of heritabilities for postweaning weight up to 9 months of age for dual-purpose breeds and 15 estimates for meat breeds. The ranges and means were .03 to .49 and  $.26 \pm .09$  for the dual-purpose breeds and .06 to .41 and  $.28 \pm .09$  for meat breeds. The heritabilities for growth traits tended to increase with increasing age, from birth to weaning to postweaning measurements. Analysis of different weights allows a breeder to choose the most appropriate weight to use as a selection criterion to improve growth to weaning. A common finding is that more progress in weaning weight can be made by selection on postweaning weight than on weaning weight itself, due to the higher direct heritability of the postweaning weight and its high genetic correlation with direct components of weaning weight.

Heritabilities for fleece characters are generally medium to high. The mean heritabilities from 81 estimates for grease fleece weight and 43 estimates for mean fiber diameter were .35 and .51, respectively (Fogarty, 1995).

It is generally accepted that litter size has low heritability and repeatability. However, there is a considerable range in heritability estimates for litter size in sheep. Gonzalez (1982; cited by Bradford, 1985) reviewed 30 estimates of heritability of litter size for different breeds or methods of estimation. The range in the estimates was from -.15 to .35 with a mean of .10. A more recent review by Fogarty (1995) gave a range of <0 to .54, with a weighted mean of  $.08 \pm .08$  for lambs born per ewe joined. Basuthakur et al. (1973) reported a heritability of  $.12 \pm .09$  for number of lambs born per ewe joined for Targhee sheep. Al-Shorepy and Notter (1996) reported a heritability of .10 for number of lambs born for the composite population mentioned above. There are high standard errors associated with many of the estimates, and many reports do not include standard errors. Designing adequate methods, especially to account for the discrete or multinomial nature of the data still is a challenging issue for genetic analyses of reproductive traits. The restricted maximum likelihood procedure (REML) is considered an appropriate means of estimating genetic parameters for litter size. Hence Fogarty(1995) thought that animal model REML procedures might provide more reliable estimates than earlier ones for reproductive traits. Although heritability for litter size was quite low, the coefficient of variation (CV) was high. The mean CV for lambs born was 58% (Fogarty, 1995), which indicates the possibility of genetic improvement in litter size in sheep.

Additive direct genetic correlations between live weights at various ages and the components of ewe reproduction are also highly variable. The weighted average genetic and phenotypic correlations between live weights and litter size were .41 ( range from -.46 to .78) and .15, respectively (Fogarty, 1995). The correlations, especially genetic,

between wool and reproductive traits were also highly variable, but the average of estimates in the literature was close to zero for most fleece traits and litter size. For litter size, the weighted average genetic and phenotypic correlations were .12 and .07 respectively for grease fleece weight, and -.07 and .12 for fiber diameter (Fogarty, 1995). The only correlation estimate between wool and reproduction for Targhee was that between grease fleece weight and number of lambs born per ewe joined, with a genetic correlation of  $.09 \pm .48$  and a phenotypic correlation of .07 (Basuthkar et al., 1973). Al-Shorepy and Notter (1996) obtained genetic correlations of litter size with birth weight and 90-day weight of .17 and .33, respectively in a 1/2-Dorset crossbred population.

The importance of maternal effects on growth of lambs is well known. Such effects arise from the ability of the mother to produce the milk needed for growth and from other maternal behavior. In the NSIP (National Sheep Improvement Program), both additive and maternal EPD for growth traits are reported. For Polypay and Targhee sheep in western flocks, lambs are usually weaned at four months of age and maternal influences are often expected to be more pronounced than in cattle or swine (Bradford, 1972). Accounting for maternal effects would increase accuracy of selection (Robinson, 1996a, b). Results from earlier studies have shown that maternal effects have explained much of the variation in lamb weight (Nasholm and Danell, 1996; Burfening and Kress, 1993; Maria et al, 1993; Notter and Hough, 1996). Notter and Hough (1996) reported that additive maternal genetic and maternal permanent environmental effects as a proportion of phenotypic variance were .10 and .09, respectively, for 60 d weaning weight and .05 and .08 for 120 d weaning weight for Targhee sheep. However, relatively

few estimates of the within-trait direct-maternal genetic correlation are available. Frequently, unreasonably large negative correlations have been obtained in sheep (Al-Shorepy and Notter, 1996; Burfening and Kress, 1993; Maria et al, 1993; Nasholm and Danell, 1996; Notter and Hough, 1996) and in cattle (Koots et al., 1994a, 1994b; Robinson., 1996a, 1996b) . Maria et al. (1993), for example, reported an additive direct-maternal correlation of  $-.98$  for weaning weight. In the presence of such a strong correlation, estimate of additive direct and (or) maternal variance may be large and can be accepted only if the user also accepts and incorporates the additive maternal covariance into any resulting analyses (Notter and Hough, 1996). Nasholm and Danell (1996) observed that when maternal effects for mature ewe weight were included in the model, the direct genetic variance decreased and was partly replaced by maternal variance and direct-maternal covariance. Therefore, interpretation of genetic parameters for maternally influenced traits from animal models is critically dependent upon the model(s) fitted to the data. There is a dearth of estimates on across-trait direct-maternal correlations between growth and litter size, which could be important for multitrait genetic evaluation of livestock.

The present paper studied the genetic relationships of growth of lambs, maternal ability, and fleece characteristics with litter size for three breeds, Suffolk, Targhee and Polypay, with intent to evaluate the relative importance of different (co)variance components, especially three within-trait and across-trait genetic covariances between growth and litter size, and to construct appropriate multitrait animal models for the U.S. National Sheep Improvement Program (NSIP).

## 5.2. Materials and Methods

### 5.2.1. Data Structure

Body weight, fleece data and litter size records from NSIP were obtained from 125 Suffolk, 20 Targhee, and 53 Polypay flocks. Data were collected from 1984 through 1996.

5.2.1.1. Weight Data. Body weights were recorded at 30, 60, 90, 120, 180 and 365 d of age for NSIP sheep flocks. For this study, preweaning weights were treated as weaning weights, since a preweaning weight can be interpreted as a potential weaning weight (Notter and Hough, 1996). From these weights, 60- (WW60) and 90- (WW90) weaning weights and 60-120 d (PWG) postweaning gain were chosen for genetic analyses for Suffolk sheep. The characteristics of the data structure for the three growth traits was shown in Table 5.1. Numbers of records in the complete data set for these traits for Suffolk sheep were 12746, 2853 and 5621, respectively. For Targhee sheep, 60- (WW60) and 120- (WW120) day weaning weights and 60 to 120 d (PWG) and 120 to 360-d (YG) postweaning gains were used in the final genetic analyses (Table 5.2). Numbers of records for the four traits were 4650, 7428, 1406, 3241, respectively. Birth weight (BW), 60- (WW60) and 90-(WW90) weaning weight, and 60 to 120-d postweaning gain (PWG) were chosen for genetic analyses for Polypay sheep (Table 5.3). Numbers of records for the four weights were 7452, 6561, 1690, 3046, respectively.

Weaning weights were adjusted to a standard age of  $t$  days by adding  $t$  times the preweaning ADG to birth weight when birth weight was reported or as  $t$  times the preweaning weight per day of age when birth weight was not reported. Age-adjusted weaning weights were then further adjusted for dam age, type of birth and rearing and lamb sex using multiplicative factors from NSIP. The most variable trait for Suffolks was PWG, with a coefficient of variation of 32.90% and a range of .54-68.64 kg. The most variable trait for Targhees was YG, with a coefficient of variation of 57.46% and a range of 1.36-95.79 kg. Next was PWG, with a coefficient of variation of 26.41% and a range of 2.72-34.87 kg. The most variable trait for Polypays was PWG, with a coefficient of variation of 32.45% and a range of .27 to 43.31 kg. All the extreme values (outliers that were larger than  $\text{mean} \pm 4\text{SD}$ ) for each trait were excluded in the final genetic analyses.

Contemporary groups for body weights were formed based on flock, management code, date of weighing, and a producer-supplied location code. Contemporary groups for cumulative postweaning gain also included the weaning contemporary groups. The four management codes for weaning weights discriminated between lambs that were or were not creep fed and between dams that were all feed alike or fed according to the number of lambs being nursed. The management codes for postweaning weights discriminated between animals fed as market lambs and those fed on a postweaning gain tests. Animals of different sexes were grouped together for weaning weight but were grouped separately for postweaning weights. Animals were excluded from the data if their contemporary group contained only a single litter, if information on ewe age or type of birth and rearing was missing, or if the lamb was reared artificially or by a foster dam. The latter



restriction accounted for most of the weaning weights that were discarded. For postweaning weights, animals were also required to have a valid weaning weight.

5.2.1.2 Fleece Data. Grease fleece weight (FWT) and fiber diameter (FD) for Targhee sheep were chosen from four NSIP fleece traits (grease or clean fleece weight, fiber diameter and staple length ); few clean fleece weights and staple lengths were reported for both Targhee and Polypay sheep. Fiber diameter was also excluded from the final Polypay data due to small number of records available. Fleece traits were to be recorded at about 1 yr of age or at one year intervals for older animals. Most grease fleece weights and fiber diameters were from yearlings. Fleece weights were linearly adjusted to either an initial shearing age of 365 d (for yearlings) or a shearing interval of 365 d (for older animals), assuming a constant rate of wool growth during the year. Post-yearling animals were required to have both current and previous shearing dates recorded. Fiber diameters were not adjusted. Fiber diameter was the least variable trait in Targhees with a coefficient of variation of 8.68% and a range of 15.20 to 30.40  $\mu\text{m}$  (which corresponding to fineness from 90's to 54's). Adjusted grease fleece weight was more variable than fiber diameter, with a coefficient of variation of 32.61% and a range of 1.32 to 12.44 kg. The adjusted mean  $\pm$  SD for FWT for Polypay sheep was higher than that for Targhee sheep. Outliers ( $>$  mean  $\pm$  4SD) for the two fleece traits were not included in the final data set. Contemporary groups for fleece data were based on date of shearing, age at shearing (yearling versus older), sex, management code and producer-supplied location codes. Animals were excluded from the data if the contemporary group contained only one

animal, if age at shearing of yearling was not between 280 and 510 d, or if shearing interval of older sheep was not between 160 and 550 d.

5.2.1.3. Litter Size. The litter size records was preadjusted according to age of dam at time of lambing. The adjusted sample mean $\pm$  SD for litter size was  $1.95\pm.70$ ,  $1.69\pm.62$  and  $2.09 \pm .78$ , respectively for the three breeds. Litter size was very variable for all three breeds with coefficients of variation of 35.87%, 36.34% and 37.18%, respectively. (Table 5.1-5.3). The adjusted records were assigned to contemporary group by the following procedures: the lamb records were sorted by lambing date, and beginning with the first lambing date, all dams lambing within 30 days were in the same contemporary group. If a lambing date was outside the initial 30 day window, that lambing date became the starting date of the next 30 day window for the next group. Any group containing only a single dam's record was eliminated.

5.2.1.4. Pedigree Data. A total of 29115, 17633 and 16795 animals in  $A^{-1}$  (numerator relationship matrix) were included in the final pedigree files for Suffolk, Targhee and Polypay, respectively. The number of inbred animals in the three breed data were 1519, 2485 and 1615, respectively. The corresponding mean inbreeding coefficients for the inbred animals in the three breeds were .076, .068 and .086 respectively.

## 5.2.2. Genetic Analyses:

### 5.2.2.1. Linear Models

The general representation for the complete bivariate animal model was as follows:

$$\begin{matrix} \mathbf{y}_1 \\ \mathbf{y}_2 \end{matrix} = \begin{matrix} \mathbf{X}_1 & \mathbf{0} \\ \mathbf{0} & \mathbf{X}_2 \end{matrix} \begin{matrix} \mathbf{b}_1 \\ \mathbf{b}_2 \end{matrix} + \begin{matrix} \mathbf{Z}_1 & \mathbf{0} \\ \mathbf{0} & \mathbf{Z}_2 \end{matrix} \begin{matrix} \mathbf{u}_1 \\ \mathbf{u}_2 \end{matrix} + [\mathbf{Z}_{m1} \mathbf{m}_1] + \begin{matrix} \mathbf{Z}_{p1} & \mathbf{0} \\ \mathbf{0} & \mathbf{Z}_{p2} \end{matrix} \begin{matrix} \mathbf{c}_1 \\ \mathbf{c}_2 \end{matrix} + \begin{matrix} \mathbf{e}_1 \\ \mathbf{e}_2 \end{matrix}$$

Where:  $\mathbf{y}_1$  = the  $s_1 \times 1$  vector of records for growth traits and  $s_1$  is the number of observations for the growth (or fleece) trait,

$\mathbf{y}_2$  = the  $s_2 \times 1$  vector of records for litter size and  $s_2$  is the number of observations for litter size,

$\mathbf{b}_j$  = the  $p_j \times 1$  vector of the contemporary groups for trait  $j$  ( $j = 1, 2$ ),

$\mathbf{u}_j$  =  $q_j \times 1$  vector of additive genetic effects for trait  $j$ ,

$\mathbf{m}_j$  =  $m_j \times 1$  vector of maternal genetic effects for trait  $j$  ( $j = 1, 2$ ),

$\mathbf{c}_j$  =  $c_j \times 1$  vector of permanent environmental effects for trait  $j$ ,

$\mathbf{e}_j$  =  $s_j \times 1$  vector of residuals for trait  $j$ ,

$\mathbf{X}_j$  =  $s \times p$  incidence matrix corresponding to  $\mathbf{b}_j$ ,

$\mathbf{Z}_j$  =  $s_j \times q_j$  incidence matrix corresponding to  $\mathbf{u}_j$ ,

$\mathbf{Z}_{mj}$  =  $s_j \times m_j$  incidence matrix corresponding to  $\mathbf{m}_j$ ,

$\mathbf{Z}_{pj}$  =  $s_j \times c_j$  incidence matrix corresponding to  $\mathbf{c}_j$ ,

$p_j$  = the number of levels of the contemporary group,

$q_j$  = the number of additive genetic effects, which could be greater or equal to  $s$

$m_j$  = the number of maternal genetic effects and

$c_j$  = the number of permanent environmental effects.

The expectations and variance-covariance matrices of random variables are:

$$\mathbf{E} \begin{bmatrix} \mathbf{y}_1 \\ \mathbf{y}_2 \end{bmatrix} = \begin{bmatrix} \mathbf{X}_1 \mathbf{b}_1 \\ \mathbf{X}_2 \mathbf{b}_2 \end{bmatrix}, \quad \mathbf{E} \begin{bmatrix} \mathbf{u}_1 \\ \mathbf{u}_2 \end{bmatrix} = \mathbf{E} [\mathbf{m}_1] = \begin{bmatrix} \mathbf{c}_1 \\ \mathbf{c}_2 \end{bmatrix} = \mathbf{0},$$

and  $\mathbf{V} [\mathbf{u}_1', \mathbf{u}_2', \mathbf{m}_1'] = \mathbf{G} \quad \mathbf{A},$

where,  $\mathbf{G} = \begin{bmatrix} g_{11} & g_{12} & g_1 m_1 \\ g_{12} & g_{22} & g_2 m_1 \\ g_1 m_1 & g_2 m_1 & m_{11} \end{bmatrix}$

and  $\mathbf{V} [\mathbf{c}_1', \mathbf{c}_2'] = \mathbf{P} \mathbf{e} \quad \mathbf{I}_c,$

where  $\mathbf{P} \mathbf{e} = \begin{bmatrix} c_{11} & c_{12} \\ c_{12} & c_{22} \end{bmatrix}$

and  $\mathbf{V} [\mathbf{e}_1', \mathbf{e}_2'] = \mathbf{R} \quad \mathbf{I}_e,$

where  $\mathbf{R} = \begin{bmatrix} r_{11} & r_{12} \\ r_{12} & r_{22} \end{bmatrix}$

where:  $\mathbf{G}$  = 3×3 additive genetic variance-covariance matrix

$\mathbf{A}$  = (q+m)×(q+m) additive genetic relationship matrix,

$\mathbf{P} \mathbf{e}$  = 2×2 permanent environmental variance-covariance matrix,

$\mathbf{R}$  = 2×2 residual variance-covariance matrix,

$\mathbf{I}_c$  = (c<sub>1</sub> + c<sub>2</sub>)×(c<sub>1</sub>+ c<sub>2</sub>) identity matrix,

$\mathbf{I}_e$  = (s<sub>1</sub> + s<sub>2</sub>)×(s<sub>1</sub>+s<sub>2</sub>) identity matrix,

g<sub>jj</sub> = additive genetic variance of trait j,

m<sub>jj</sub> = maternal genetic variance of trait j,

c<sub>jj</sub> = permanent environmental variance of trait j,

r<sub>jj</sub> = residual variance of trait j,

g<sub>ij</sub> = additive genetic covariance between trait i and j,

$g_{mj}$  = genetic covariance between direct additive effects of trait i and maternal genetic effects of trait j,

$m_{ij}$  = maternal genetic covariance between trait i and j,

$c_{ij}$  = permanent environmental covariance between trait i and j,

$r_{ij}$  = residual covariance between trait i and j.

The unknown parameters are the location parameters

$\mathbf{Q}' = \{ \mu', \mathbf{m}', \mathbf{c}' \}$  and dispersion parameters  $\mathbf{D}' = \{ \mathbf{G}', \mathbf{P}_e', \mathbf{R}' \}$ .

Contemporary groups were fitted as the only fixed effect. Including all the random genetic and environmental effects was not necessary as not all sources of (co)variance were expected to be important for all traits. Consequently a series of reduced models was fitted to evaluate the significance of the various parameters.

The complete descriptions of the fourteen models are shown in Table 5.5 and abbreviations and their corresponding definitions used in this paper are listed in Table 5.4. The (co)variance structure for additive genetic and additive maternal effects can then be described for the fourteen models as follow:

For Model B3-B5 and B7 - B14,

$$\text{Var} \begin{matrix} a_1 \\ m_1 \\ a_2 \end{matrix} = \begin{matrix} \mathbf{A}_{a_1}^2 & \mathbf{A}_{a_1 m_1} & \mathbf{A}_{a_1 a_2} \\ \mathbf{A}_{a_1 m_1} & \mathbf{A}_{m_1}^2 & \mathbf{A}_{a_2 m_1} \\ \mathbf{A}_{a_1 a_2} & \mathbf{A}_{a_2 m_1} & \mathbf{A}_{a_2}^2 \end{matrix}$$

For model B6 and B15 - B16,

$$\text{Var} \begin{matrix} a_1 \\ a_2 \end{matrix} = \begin{matrix} \mathbf{A}_{a_1}^2 & \mathbf{0} \\ \mathbf{0} & \mathbf{A}_{a_2}^2 \end{matrix}$$

In Model B3, all the additive, maternal and permanent environmental effects attributed to the dam were included for growth traits (body weights). For litter size, both additive genetic and permanent environmental components were fitted. No covariance between permanent environment attributed to dam for growth traits and permanent environment attributed to the animal for litter size was allowed. Temporary environmental covariance was fitted although there is no reason for growth traits and litter size necessarily to be influenced by the same temporary environmental effects.

Model B4 was same as Model B3 except a permanent environmental component for LS was not fitted. Depending on whether permanent environmental effects for litter size were fitted (Targhee and Polypay data) or not (Suffolk data), Model B5 differed from Model B3 or B4 by setting temporary environmental covariance to zero. The model B5 was further reduced in Model B6 with exclusion of permanent environmental components for growth traits (body weights). The alternative to this model reduction was made in Model B7 by fitting permanent maternal effects but not maternal genetic effects for growth traits. Models B8-14 were constructed to test importance of different genetic covariances or covariance combinations. Model B15 and Model B16 were used for bivariate analyses between postweaning gains or fleece traits and litter size. A simple animal model with only additive genetic and temporary environmental effects was used for both postweaning gains, fleece traits and litter size in Suffolk data but a repeatability animal model was fitted for litter size in Targhee and Polypay data. No residual covariance was allowed in Model B16.

Also noted by Meyer et al. (1991, 1994), with single records for growth traits and repeated records for litter size in bivariate analyses, fitting a ‘full’ repeatability model (i.e., fitting permanent environmental effects due to the animal for both traits, Model B1 and B2 in this study), and attempting to partition the residual variance for the traits with single records into its permanent and temporary environmental components and to estimate permanent environmental covariance will led to computational problems. Generally, variance could not be partitioned between the permanent components due to animal and dam for growth traits if both components were included in the models (B1 and B2). Also the converged likelihood value was difficult to interpret if covariance between the permanent components due to animal for growth traits and litter size was allowed. Consequently, Models B-1 and B-2 were excluded from this study.

#### 5.2.2.2. (Co)variance Component Estimation

Estimates of variance and covariance components were obtained by Restricted Maximum Likelihood (REML) using a derivative-free algorithm, fitting an animal model throughout and incorporating all pedigree information available. Maternal genetic and permanent environmental effects of dam and permanent environmental effects due to the animal (for litter size) were taken into account by including appropriate random effects into the model of analysis. All the presented estimates of (co)variance components and genetic parameters for growth and litter size were obtained from bivariate analyses of each of the growth and fleece traits together with litter size. Throughout the study, the categorical nature of litter size was ignored. All available pedigree information was included in the analysis to eliminate bias due to selection and to increase the accuracy of

estimation through additional relationship ties among animals (Table 5.1 - 5.3). All the calculations were carried out using multiple trait, derivative-free REML procedures (Boldman, et al., 1993).

The principle of the derivative-free method is to iterate different **R** and **G** until the combination that maximizes the log likelihood,  $\ln L$ , is found for the data, **Y**. Depending on the different models, the log-likelihood function was maximized with respect to direct heritability ( $h_a^2 = \sigma_a^2 / \sigma_p^2$ ), additive maternal effects ( $m^2 = \sigma_m^2 / \sigma_p^2$ ), the within-trait genetic covariance between direct and maternal effects as a proportion of the square root of the product of two variances ( $r_{a1m1}$ ), the permanent environmental variance due to the animal or dam as a proportion of phenotypic variance ( $pe_a^2$  and  $pe_m^2$ ) as well as all the other across-trait correlations ( $r_{a12}$  and  $r_{a2m1}$ ) included in the models. The error variance was estimated directly from the residual sum of squares.

In order to obtain good starting values for bivariate analyses, univariate REML analyses were carried out to provide estimates of variance and within-trait covariance components for each trait. Using these estimates as starting values, we first maximized the likelihood for bivariate analyses with respect to the covariance and across-trait covariance components only, fixing the variances to their univariate estimates. Then the likelihood was maximized with respect to the variance components, fixing the covariances to their values obtained in the first step. Finally, the maximization was performed with respect to all the (co)variances. Moreover, some evidence for convergence of multivariate animal model REML procedures to local maxima was observed. In this case, restarts were performed with different starting values to attempt to avoid local maxima. For all



analyses, the convergence criterion was considered to be reached when the variance of function values ( $-2\log L$ ) in the simplex was less than  $10^{-9}$ .

#### 5.2.2.3. Likelihood Ratio Tests.

The overall importance of each (co)variance component for each trait and each covariance component between growth traits and litter size was assessed by comparing the ratios of likelihood of sequentially reduced models. The likelihood-ratio test statistic was defined as:

$$G(\mathbf{z}) = -2 \ln (l(\mathbf{z}) / l(\mathbf{z})) = -2 (L(\mathbf{z}) - L(\mathbf{z}))$$

Where  $l(\mathbf{z})$  is the likelihood (and  $L$  the log-likelihood) evaluated at the MLE (Maximum Likelihood Estimates) at convergence and  $l(\mathbf{z})$  is the maximum of the likelihood function, subject to the restriction that  $r$  parameters that are unconstrained in the full likelihood analysis are assigned fixed values. The ratio  $-2 (L(\mathbf{z}) - L(\mathbf{z}))$  is asymptotically distributed as chi-square with degrees of freedom equal to the difference in the number of parameters in models  $i$  and  $j$  given sufficiently large sample size, where  $L(\mathbf{z})$  is the value of the maximum likelihood function for the model following achievement of the convergence criterion.

## **5.3. Results and Discussion**

### **5.3.1. Suffolk Sheep**

#### **5.3.1.1 60-d Weaning Weight and Litter Size:**

The estimates of (co)variance components and genetic parameters for 60-d weaning weight and litter size for Suffolk sheep are presented in Table 5.6, 5.7 and 5.8. As the study was mainly focused on the behavior and properties of various location and dispersion parameters by multivariate REML approaches, the univariate estimates are not shown here. Also due to length limitations, only the converged results from four models are shown, which consist of the ‘full model’ (B3), ‘best variance model’ (B4), ‘standard model’ (B5) and ‘best covariance model’ (B10 in this case). For bivariate analyses of 60-d weaning weight and litter size, 12 models(B3-B14) were constructed and each of the other models was tested against B5 (Table 5.9). It was obvious that model construction influenced estimates of (co)variance components and genetic parameters. Heritabilities for both traits seemed to be more stable than other estimates across different models. The heritability estimates ranged from .17 to .19 for 60-d weaning weight and .09 to .10 for litter size from the four models and were in good agreement with literature estimates (Fogarty, 1995; Fossceco and Notter, 1995).

The additive genetic correlation estimates ranged from .37 to .39, and were also in good agreement with literature estimates. This correlation suggested that larger animals at weaning would be more likely to produce more lambs per lambing in later life. The genetic correlation between maternal genetic effects on growth traits and direct additive effects on litter size ranged from .25 to .35. No unfavorable across-trait genetic correlations were observed between 60-d weaning weight and litter size. However, unfavorable within-trait genetic correlations between direct and maternal effects on 60-d weaning weight were obtained and ranged from -.24 to -.33 for the four models..

According to likelihood values, Model B5 was the ‘best’ model, in which additive genetic, maternal genetic and permanent environmental components were fitted for 60-d weaning weight and only an additive genetic component was allowed for litter size. No temporary environmental covariance between 60-d weaning weight and litter size was assumed. Thus, Model B5 was considered the ‘best or standard model’. A series of sequential reduced models was constructed to test the importance of different components by likelihood ratio tests.

Testing Model B3 against B5 indicated that the permanent environmental component for litter size was not important ( $P > .05$ ). The converged value for variance of these effects was essentially zero, irrespective of the model used. Thus, the component was dropped in subsequent models. Whether or not the residual covariance was fitted, no marked differences (B4 vs B5) in likelihood value were observed, indicating the two traits shared no temporary environment. The converged values for different (co)variances and parameters for B4 and B5 also were essentially the same, suggesting the two were statistically equivalent although B5 was biologically more meaningful. In models after B5,  $e_{12}=0$  was assumed.

Models B6 and B7 were constructed to test for a permanent environmental component due to dam and a maternal genetic component (including associated genetic covariances,  $a_{2m1}$  and  $a_{1m1}$ ). Likelihood ratio tests against B5 indicated that both maternal components were important ( $P < .01$  and  $P < .05$ ) and should remain in the model.

A series of models was constructed to test importance of individual covariances (B8-B10) and their joint effects (B11-B14). Exclusion of additive direct genetic covariance between the two traits reduced the likelihood value significantly ( $P < .05$ ), suggesting that it is necessary in the model. However exclusion of genetic covariances between direct and maternal effects for 60-d weaning weight (B10) or between direct genetic effects for litter size and maternal genetic effects for 60-d weaning weight (B9) did not result in significant reduction in likelihood value ( $P > .05$ ), compared with B5 in which the two components were included. Thus, including either did not add meaningful information.

However, all the joint effects of different combinations of three covariances were significant, suggesting that the three covariances were not all independent of each other. Testing B11 against B9 or B10 indicated that within-trait and across-trait genetic covariances between maternal and direct effects were jointly significant ( $P < .05$ ), which was contradictory to individual covariance likelihood ratio tests. However, Model B12 (tested against B8) indicated that within-trait genetic covariance between maternal and direct effects for the growth trait was not significant ( $P > .05$ ), which was further justified by testing B14 against B13. All the joint tests showed that additive direct covariance or genetic covariance between direct additive effects on litter size and maternal genetic effects on 60-d weaning weight were important.

In the models after B3, only direct additive effects were fitted for litter size. Generally estimates of (co)variance components and genetic parameters from bivariate

analyses for litter size were more stable than those for 60-d weaning weight, irrespective of the models used for the other trait

#### 5.3.1.2. 90-d Weight and Litter Size:

Results from bivariate analyses between 90-d weight and litter size for four models for Suffolk sheep are presented in Table 5.10, 5.11 and 5.12, respectively. The models were the same as the models for 60-d weaning weight and litter size except that the 'best covariance model' was B12. The likelihood ratio tests are listed in Table 5.13. Estimates of heritabilities for 90-d weight from different models were slightly lower than those for 60-d weaning weight, with the range of .12 to .15. The calculated total heritabilities ranged from .15 to .19. Heritabilities for litter size were stable with a range of .09-.10. Phenotypic and environmental variances generally were less sensitive to the models selected than for WW60.

It is generally believed that no temporary environmental correlation exists between litter size and 90-d weight. Exclusion of  $e_{12}$  in B5 did not result in much loss in likelihood over that in B4. Permanent environmental effects of litter size were not important (B3 vs B4) and the estimate was essentially zero.

Failure to fit either permanent maternal environmental or additive maternal effects (B6 and B7) reduced the likelihood significantly over that for model B5 when the two components were included ( $P < .01$  and  $P < .05$ ). Results from likelihood ratio tests (B5 vs B6, B7) indicated that the environmental influence of the dam was more important than additive maternal genetic influences on this trait.

Estimates of the genetic correlation between direct effects of the two traits ranged from .43 to .51. However, exclusion of the covariance did not change the likelihood (B8 vs B5) markedly. The genetic correlation between maternal genetic effects for weaning weight and direct genetic effects for litter size ranged from .95 to 1.00. Results from model B9 indicated that excluding the covariance decreased the likelihood value significantly ( $P < .01$ ). Exclusion of this component (B9) also increased additive genetic variance and reduced maternal genetic variance for 90-d weight by too much to be acceptable. The strong correlation implied that ewes with good maternal performance on 90-d weight tended also to have larger litter sizes. Estimates of  $a_{1m1}$  were positive except for B8, when direct genetic correlation between 90-d weight and litter size was ignored; the range of the estimates was from .16 to .25. Failure to fit  $a_{1m1}$  (B10) increased likelihood only slightly compared with B5, indicating that this component was not important. Also exclusion of  $a_{1m1}$  did not change estimates of most parameters for 90-d weaning weight or litter size, except that the additive genetic correlation was reduced. Similar results were observed by Al-Shorepy and Notter (1996).

Failure to fit two maternal genetic covariances ( $a_{1m1}$  and  $a_{2m1}$ , B11) reduced likelihood values markedly. In Comparing B11 with models B9 and B10, the two genetic covariances were essentially independent, i.e., the two covariances were additive.

The results from joint covariance tests suggested that across-trait additive direct genetic covariance and across-trait covariance between direct genetic effects for litter size and maternal genetic effects for 90-d weight were correlated because their joint effects

were not simply the sum of their individual effects. Therefore, some literature estimates of additive genetic correlation between growth traits and litter size obtained without fitting maternal components may have been inflated.

#### 5.3.1.3. Postweaning Gain and Litter size:

The results from bivariate analyses of postweaning gain (PWG) and litter size (LS) for Suffolk sheep are shown in table 5.14. The simple animal model with only additive genetic effects was used for both traits. Fitting a temporary environmental covariance ( $e_{12}$ ) did not influence the converged likelihood value (B15 vs B16). However, failure to fit  $e_{12}$  reduced the phenotypic correlation from .61 to .02; the corresponding phenotypic covariance decreased from 4.89 to .16. Genetic correlation between the two traits was inflated by 6.25%.

The estimates of direct heritability for PWG was .17, which is lower than some literature estimates (Thrift, et al., 1973; Harrington, et al., 1962). Few estimates of genetic correlation between cumulative postweaning gain and litter size were previously reported. This study gave an estimate of .16-.17, indicating that postweaning growth of the lambs would be lowly positively correlated with their subsequent lambing performance.

### **5.3.2. Targhee Sheep**

#### 5.3.2.1. 60 d weaning weight and litter size:

Variance component estimates for 60 d weaning weight and litter size and across-trait covariances for Targhee sheep are shown in Table 5.15, 5.16 and 5.17, respectively.

In this case, the 'best covariance model' was B13. The heritability estimates from the four best models for 60 d weaning weight all were .14, which is much larger than that (.01) from previous single trait analysis using part of the data set but not fitting the maternal-direct genetic covariance for the trait (Notter and Hough, 1996). However, the values were in good agreement with literature estimates (Fogarty, 1995; Fossecco and Notter, 1995).

Maternal genetic effects were large ( $m^2 = .22$ ) for all four models, and more than double the previous estimate from univariate analyses ( $m^2 = .10$ ; Notter and Hough, 1996) when within-trait direct-maternal genetic covariance was not fitted. However, the estimates of the maternal permanent environmental component (.09 to .10) from bivariate models were generally in agreement with .09 from the previous univariate analyses. Likelihood ratio tests ( B6 and B7 vs B5) indicated that both maternal components were important (  $P < .01$  and  $P < .05$ ) and should be kept in the models.

The permanent environmental contribution attributed to animals for litter size was small ( $pe^2 = .01$ ) and not significant ( $P > .05$  from B4 vs B5). However, for all the bivariate models for 60 d weaning weight and litter size except B4 the permanent environmental component for litter size was always fitted. Heritability estimates for litter size were stable, and ranged from .11 to .12 and were slightly larger than those (.09-.10) for Suffolk sheep.

The temporary environmental correlation between 60 d weaning weight and litter size was small and not important ( $P > .05$ , B3 vs B5). Estimates of variance components and derived parameters from B3 (with  $e_{12}$ ) and B5 ( without  $e_{12}$  ) were essentially the



same, suggesting that the two models were equivalent. Also, because there is no perceived reason for weaning weight and litter size to share temporary environmental influences (Notter and Hough, 1996; Waldron and Thomas, 1992), from B5 no temporary environmental covariance was assumed. The additive genetic correlation estimates were low, ranging from .10 to .22, and were smaller than those for Suffolk sheep (.37-.39) but still in agreement with literature estimates. This correlation also suggested that larger animals at weaning would produce more lambs per lambing in later life. In contrast to Suffolk, the genetic correlations between maternal genetic effects on 60 d weaning weight and direct additive effects for litter size were unfavorable and ranged from -.18 to -.23. Also, strong unfavorable within-trait genetic correlations (-.89 to -.90) between direct and maternal effects for 60-d weaning weight were obtained.

According to likelihood values, Model B5 was the 'best' model, in which additive genetic, maternal genetic and permanent environmental components were fitted for 60-d weaning weight while additive genetic and permanent environmental components were fitted for litter size. Temporary environmental covariance between 60-d weaning weight and litter size was not fitted. Thus, Model B5 was considered the 'best' or 'standard model'. A series of sequential reduced models was constructed to test importance of individual covariances ( B8-B10) and their joint effects (B11-B14). Exclusion of additive direct genetic covariance between the two traits did not reduce the likelihood value significantly ( $P>.05$ ), suggesting that including the covariance did not add meaningful information. Also exclusion of genetic covariance between direct genetic effects for litter size and maternal genetic effects for 60-d weaning weight (B9) did not result in significant

reduction in the likelihood value ( $P > .05$ ) if compared with B5 in which the component was included. However, exclusion of genetic covariances between direct and maternal effects for 60-d weaning weight (B10) caused significant reduction of the likelihood value ( $P < .01$ ), indicating the genetic correlation was statistically real although perhaps biologically not meaningful (Nasholm and Danell, 1996).

Likelihood ratio tests for the joint effects of different combinations of three genetic covariances generally agreed with tests for individual covariance tests. The joint effects of  $a_{1m1}$  and  $a_{2m1}$ , or  $a_{1m1}$  and  $a_{12}$  or all three covariances together were highly significant ( $P < .01$ ), while that of  $a_{12}$  and  $a_{2m1}$  was not. In contrast to the Suffolk data, association between the estimates of the three genetic covariances was not detected.

#### 5.3.3.2. 120-d Weaning Weight and Litter Size:

Results from bivariate analyses between 120 d weaning weight and litter size for four representative models for Targhee data are presented in Table 5.19, 5.20 and 5.21. The models were the same as the models used for bivariate analyses of 60-d weaning weight and litter size for Targhee sheep except for the 'best covariance model', which was B11. The likelihood ratio tests are shown in Table 5.22. For 120 d weaning weight, estimates of heritabilities from different models were .15 to .16 and slightly larger than that (.14) for 60-d weaning weight for this breed, but much larger than the previous estimate (.10) from a single trait model (Notter and Hough, 1996). Additive maternal effects were correspondingly reduced ( $m^2 = .05-.06$ ) while maternal permanent environmental effects (.08) were of same magnitude as those observed at 60 d, indicating that the environmental influence of the dam was more important than maternal genetic

influence at 120 d of age. Failure to fit either maternal permanent environmental or additive maternal effects (B6 or B7) reduced the likelihood significantly over that for B5 when the two components were included ( $P < .01$  and  $P < .01$ ).

Heritability estimates for litter size from the bivariate analysis were stable with a range of .10-.12, and of the same magnitude as those from bivariate analyses of 60 d weaning weight and litter size but larger than those (.09-.10) for Suffolk sheep. The permanent environmental contribution attributed to the animal (.01-.02) for litter size was similar to that obtained from the bivariate analyses of 60 d weaning weight and litter size and still was not significant ( $P > .05$ ) (B4 vs B5)

Exclusion of  $e_{12}$  in B5 did not result in much loss in likelihood over that in B4. There were significant correlations between direct genetic effects of the two traits with the range of .46 to .48 ( $P < .05$ ) being similar to those (.43 to .51) for 90 d weaning weight and litter size for Suffolk sheep. This correlation also implied that the Targhee sheep with high performance for 120-d weaning weight would tend to have larger litter sizes later in life. The genetic correlations between maternal genetic effects for 120 d weaning weight and direct genetic effects for litter sizes ranged from -.35 to -.36 and were not significant ( $P > .05$ ). Relatively small, unfavorable within-trait genetic correlations between direct and maternal effects (-.03 to -.10) were also obtained.

Failure to fit two maternal genetic covariance components ( $a_{2m1}$  and  $a_{1m1}$ , B11) did not reduce likelihood values markedly. Testing against individual covariances (B9 and B10) further confirmed that the two covariances were not important. However, although the joint effect of  $a_{12}$  and  $a_{2m1}$  was significant ( $P < .05$ ), testing B13 against B8 and B9

resulted in the conclusion that both covariances were not significant ( $P > .05$ ). This did not agree with individual covariance tests, suggesting at least some kind of association between the two covariances involved. That is, the across-trait additive direct genetic covariance and across-trait covariance between direct genetic effects for litter size and maternal genetic effects for 120 d weaning weight were themselves correlated.

#### 5.3.2.3. 60 - 120 d Postweaning Gain (PWG) and Litter Size(LS):

The simple animal model with only additive genetic effects for PWG and the repeatability model for litter size was used. Heritabilities for 60-120 d cumulative postweaning gain ( Table 5.23) indicated that additive effects were more important (.27) than those for the two weaning weights at 60 and 120 d. Also the  $h^2$  estimate was larger than that for Suffolk sheep, but in good agreement with some literature estimates (Thrift, et al., 1973; Harrington, et al, 1962). Fitting a temporary environmental covariance ( $e_{12}$ ) did not influence the value of the converged likelihood (B12 vs B13) nor the parameter estimates. The additive direct genetic correlation for this breed was .44, much larger than that (.16-.17) for Suffolk sheep, indicating that selection on postweaning growth of the lambs should result in genetic improvement of litter size.

#### 5.3.2.4. 120 -365 d Postweaning Gain (YG) and Litter Size(LS):

The same models as those for PWG and LS were used. As shown in Table 5.24, heritability for YG was smaller(.19) than that for PWG, which may reflect the fact that yearling weights came primarily from western flocks whereas 120 d postweaning weights came primarily from eastern flocks (Notter and Hough, 1996). These authors reported that additive effects for postweaning gain were more important in relatively well-fed

eastern lambs ( $h^2 = .33$ ) than in the more extensively managed western lambs ( $h^2 = .20$ ). Maternal effects on postweaning gains were tested in preliminary analyses but were not significant (Notter and Hough, 1996). Therefore, maternal components were dropped in the study. Setting residual covariance to zero also did not result in any marked changes in the converged likelihood value and parameter estimates. A weak direct genetic correlation (.08 to .09) between YG and LS was obtained.

#### 5.3.2.5. Fleece Traits and Litter Size:

For both grease fleece weight (FWT) and fiber diameter (FD), a simple model with only direct additive components was used, while for litter size, a repeatability model was used (Table 5.25 and Table 5.26). Heritability for FWT (.41) was the same as the previous estimate from univariate analysis, but heritability for FD (.50) was smaller than the previous estimate (.58) (Notter and Hough, 1996). The heritability estimate for litter size was .11, larger than that obtained for Suffolk sheep. Unfavorable genetic correlations for FWT and FD with litter size were observed; their values were -.09 and .29 to .30, respectively. Notter and Hough (1996) also observed a genetic antagonism between fleece weight and fiber diameter. Therefore, simultaneous improvement in litter size and the two fleece traits would require explicit consideration of these antagonisms. When residual covariances between FWT, FD and litter size were allowed (B15), strong residual correlations, .84 and .62, respectively for the two pairs, were obtained. However, likelihood ratio tests showed that the two residual correlations were not significantly different from zero.

### 5.3.3. Polypay Sheep

#### 5.3.3.1. Birth Weight and Litter Size:

Estimates of variance components and their ratios for birth weight (BW) and litter size were obtained from bivariate analyses and are listed in Table 5.27 and 5.28, respectively. The covariances and corresponding correlation estimates are shown in Table 5.29. In this case, the 'best covariance model' was B14. The results of likelihood ratio tests for all twelve models are shown in Table 5.30. The heritability estimates for BW varied among different models, with a range of .15 to .23, which is well within the range of literature estimates (Fogarty, 1995). In contrast to that for Suffolk and Targhee sheep, heritability for litter size for Polypay sheep was sensitive to the models. When a permanent maternal component was not included, the heritability ( $h^2 = .12$ ) was higher than that for the other three models ( $h^2 = .09$ ). Ratios ( $m^2$ ) of variance due to maternal genetic effects to phenotypic variance for BW was .06 to .10, smaller than some literature estimates. Burfening and Kress (1993) gave estimates of .30-.45 ( $m^2$ ) from information on maternal and paternal half-sibs, full-sibs, offspring on dam and offspring on sire for Rambouillet, Targhee and Columbia sheep. Gjedrem (1967) obtained an estimate of .17 ( $m^2$ ) from a sire-maternal grandsire model for Dala and Steigar sheep. Maria et al. (1993) reported an estimate of .22 for  $m^2$  for BW of Romanov by an univariate animal model, and Nasholm and Danell (1996) observed an estimate of .30 by an animal model for Swedish Finewool sheep. The maternal environmental effects ( $c^2$ ) for BW were .21-.22 and larger

than previous estimates (Maria et al., 1993,  $c^2=.10$ , Romanov sheep). Likelihood ratio tests showed that maternal genetic and environmental effects for birth weight were highly significant ( $P<.01$ ) and significant ( $P<.05$ ), respectively, implying that the two should be kept in the bivariate model. Likelihood ratio tests showed  $PE_a$  for litter size approached significance ( $P<.05$ ). For uniformity throughout the models,  $PE_a$  for litter size was fitted.

The temporary environmental correlation between birth weight and litter size was unreasonably large, with a value of .78 when this covariance component was included in the analysis (Model 3 and Model 4). Similar values were also observed for other growth traits with litter size in Suffolk and Targhee sheep. Biologically these values are not interpretable. Likelihood ratio tests showed that the covariance was not important ( $P>.05$ ), which further places the large values into question. Therefore, from model B5 on,  $r_e$  was fixed to zero. Fortunately, excluding  $r_e$  did not influence the converged estimates of other components and the values were essentially the same for the two alternative models (Model B3 and Model B5). The covariance ( $c_{12}$ ) between maternal permanent effects for BW and permanent effects of animal for LS was not estimable by MTDFREML software because the two effects were on different fields in the data structure (Boldman et al., 1993). Throughout the remaining models,  $c_{12}$  was set to zero. The additive genetic correlation estimates were variable, ranging from .14 to .27. Likelihood ratio tests indicated that this covariance was not significant ( $P>.05$ ). Both maternal-direct genetic correlations ( $r_{a1m1}$  and  $r_{a2m1}$ ) were negative. Within-trait correlations ( $r_{a1m}$ ) for birth weight were relatively stable, with values of -.34 to -.45.

Literature estimates of  $r_{alm1}$  were highly variable ranging from .11 to -.99 (Nasholm and Danell, 1996; Burfening and Kress, 1993; Maria et al., 1993). Likelihood ratio tests showed that neither of the two maternal-direct genetic covariances or their joint effects were significant ( $P > .05$ ), suggesting that BW and LS were basically genetically independent.

#### 5.3.3.2. 60 d Weaning Weight (WW60) and Litter Size (LS):

Variance component estimates for 60 d weaning weight and litter size and across-trait covariances are shown in Table 5.31, 5.32 and 5.33, respectively. The 'best covariance model' was B13. For bivariate analyses of 60-d weaning weight along with litter size, twelve models (B3-B14) were constructed and tested against B5 (Table 5.34). As observed in Targhee sheep, heritabilities for both traits seemed robust to different models. The heritability estimates for WW60 for Polypay sheep were .10-.11, slightly smaller than .14 for Targhee, but still were in agreement with literature estimates (Fogarty, 1995; Fossceco and Notter, 1995). As observed in a previous section,  $h^2$  for LS was larger in Model 4 when  $PE_a$  for LS was not fitted.

Maternal additive effects ( $m^2 = .11-.12$ ) were smaller than those for Targhee sheep ( $m^2 = .22$ ), while the reverse was true for the maternal permanent environmental component ( $pe_m^2 = .15$  vs  $pe_m^2 = .09-.10$ ), indicating that non-genetic maternal effects at weaning are more important for Polypay than for Targhee sheep. Al-Shorepy and Notter (1996) obtained  $m^2$  of .10 and  $pe_m^2$  of .09 for a crossbred sheep population containing 50% Dorset, 25% Rambouillet and 25% Finnsheep breeding. Failure to fit



either of the maternal components caused significant reduction in likelihood (Model B6 and B7 vs B5).

The temporary environmental correlation between 60 d weaning weight and litter size was small ( $r_e = .09$ ) and not important ( $P > .05$ , B3 vs. B5). Estimates of (co)variance components and derived parameters from B3 (with  $e_{12}$ ) and B5 (without  $e_{12}$ ) were essentially the same. From model B5 on, no temporary environmental covariance was assumed. The unfavorable additive genetic correlation estimates ranged from  $-.12$  to  $-.15$ , which was not in agreement with that for Targhee (.10 to .22) or Suffolk, (.37-.39), but still were within the range of literature estimates. Likelihood Ratio tests for individual and joint covariances indicated that additive direct covariance was not important ( $P > .05$ ), suggesting that the corresponding correlation between WW60 and LS is not real or very weak. Also, variable and weak genetic correlations between maternal genetic effects for 60 d weaning weight and direct additive effects for litter size were observed (.17 to .23) and were not significant ( $P > .05$ ). It was also found that if one covariance estimate was flat, the other would also tend to be flat, suggesting that the two covariances were not independent due to sampling correlations. However, the within-trait genetic correlations ( $-.53$  to  $-.55$ ) between direct and maternal effects for 60-d weaning weight for Polypay were negative, large, and significant ( $P < .05$ ).

#### 5.3.3.3. 120-d Weaning Weight and Litter Size:

Results from bivariate analyses between 120 d weaning weight and litter size for four models are presented in Table 5.35, 5.36 and 5.37, respectively. The ‘best covariance model’ was B14. The likelihood ratio tests are shown in Table 5.38. For 90 d weaning

weight, estimates of heritabilities from different models were variable and ranged from .05 to .13. The estimates seemed to be influenced by the large sampling variances and correlations between the estimates of three genetic covariances, indicating that the estimate of additive variance was not only dependent on the magnitude of the true value, data structure, and choice of quadratic forms, but also on the estimates of some, if not all, other components. Additive maternal effects at 90 d were markedly reduced ( $m^2 = .01-.02$ ) and essentially not different from zero by LR tests on joint effects of  $m^2$ ,  $a_{1m1}$  and  $a_{2m1}$ . Maternal permanent environmental effects (.21-.22) became larger, indicating that the environmental influence of the dam was more important than the additive maternal influence at 90 d of age. Failure to fit maternal permanent environmental effects (B6) reduced the likelihood significantly over that for model B5 ( $P < .01$ ).

Patterns of heritability estimates for litter size from different models were the same as observed during the bivariate analyses with WW60 and BW, i.e., failure to fix the permanent environmental contribution attributed to the animal ( $pe^2=.04$ ) for litter size inflated  $h^2$  by 20-30%. Essentially the same value for  $pe^2$  for litter size was obtained from all three pairs of bivariate analyses. However, only effects obtained from this analysis were significant ( $P < .05$ ).

An unreasonably high temporary environmental correlation between litter size and 90 d weaning weight was obtained ( $r_e=.80$ ), Exclusion of  $e_{12}$  in B5 did not result in significant reduction in the likelihood. The additive direct genetic correlation between the two traits was highly variable (ranging from .09 to .44) as was the genetic correlation between maternal genetic effects for 90 d weaning weight and direct genetic effects for

litter size ( $r_{a2m1}$ ) with a range of .18 to .98. A negative relationship between  $r_{a12}$  and  $r_{a2m1}$  was detected, i.e., a constant sum of the two correlation estimates was obtained across the four models. Within-trait genetic correlation ( $r_{a1m1}$ ) was small and not significantly different from zero. LR ratio tests confirmed that all three genetic covariances were not significant and not necessary to retain in the model.

#### 5.3.3.4. 60 - 120 d Postweaning Gain (PWG) and Litter Size(LS):

Heritabilities for 60-120 day cumulative postweaning gain ( Table 5.39) indicated that additive effects were more important ( $h^2=.22$ ) than for body weights. Temporary environmental covariance ( $e_{12}$ ) between the two traits was not significantly different from zero, although the corresponding correlation estimate was .78. The additive direct genetic correlation were essentially zero, smaller than those for Targhee ( $r_{a12}=.44$ ) and Suffolk sheep ( $r_{a12} = .16-.17$ ).

#### 5.3.3.5. Fleece Weight and Litter Size

Heritability for FWT ( $h^2=.44$ ) was similar to that ( $h^2 = .41$ ) for Targhee sheep. However, a positive genetic correlation ( $r_{a12} = .21$ ) between fleece weight and litter size was obtained for Polypay sheep (Table 5.40), indicating that unlike Targhee sheep, selection on fleece weight would not impose adverse effects on litter size. When residual covariances between FWT and litter size were allowed (B15), a strong residual correlations ( $r_e =.87$ ) was obtained. Likelihood ratio tests showed that the residual covariance was not significantly different from zero.

### **5.3.4. General Discussion**

#### 5.3.4.1. Models and Parameter Estimation:

In the 'standard' bivariate model (B5) between body weights (BW, WW60, WW90 and WW120) and litter size for the three breeds, all four of the potentially important variance components (additive, additive maternal, permanent maternal environmental, and temporary environmental) were fitted for body weights. However, none of other traits (LS, PWG, YG, FWT and FD) required fitting all the variance components. The decision on whether to include a maternal genetic or permanent environmental component in the animal models depends on empirical knowledge about the biological impact of these random effects on the traits studied and likelihood ratio tests from univariate or bivariate analyses. When information about these parameters is lacking, a sire model instead of an animal model would be preferred. Otherwise the estimates of heritabilities for the trait may be inflated in the presence of large maternal genetic effects and large maternal-genetic covariance.

Direct heritability estimates for body weights in the three breeds were low to medium and were in good agreement with previous literature estimates (Fogarty, 1995; Maria, et al, 1993; Notter and Hough, 1995). However, maternal genetic and maternal permanent environmental effects were relatively large and important for all body weights except for weaning weight at 90 d for Polypay sheep, indicating that explicitly considering these effects should result in more genetic improvement in growth traits. Also, permanent maternal environmental effects on the lamb tended to increase with age, while the reverse trend was observed for genetic maternal effects.

Estimates of heritability and permanent environmental effects for litter size across various bivariate animal models were close to each other among the three breeds and ranged from .09 to .12 and .00 to .05, respectively, suggesting that the genetic basis underlying litter size was essentially the same for all three breeds.

For PWG, YG, FWT and FD, no maternal genetic or permanent environmental effects were fitted because the results from this and other studies (Maria et al, 1993; Waldron and Thomas, 1992; Notter and Hough, 1995; Mortimer and Atkins, 1994; Swan and Hickson, 1994) indicated the two effects were generally small and not important. Swan and Hickson (1994) thought that there was no immediate need to consider maternal effects on fleece traits in a Merino breeding program. Genetic analyses with Model B15, in which a simple animal model was fitted for PWG, YG, FWT and FD and a simple animal model (for Suffolk data) or a repeatability model (for Targhee and Polypay data) was fitted for litter size, gave estimates of direct heritability of 60-120 d cumulative postweaning gain (PWG) of .17, .44 and .22, respectively for Suffolk, Targhee and Polypay sheep. The heritability estimate for 120-360 d cumulative postweaning gain for Targhee sheep was .19. These values are generally larger than those for weaning weights for the three breeds. Thus, postweaning gains would provide alternative measures to improve growth rate in sheep. The heritabilities for grease fleece weight were the same (.44) for Targhee and Polypay sheep. Heritability estimates for fiber diameter for Targhee sheep was .50. These large values suggest that mass selection would be effective to improve fleece traits in the three breeds.

#### 5.3.4.2. Residual Covariance ( $\sigma_{e12}$ ) and Corresponding Correlation ( $r_{e12}$ )

Whether or not a residual covariance between growth traits or fleece traits with litter size should be fitted was tested throughout the three breeds. Frequently temporary environmental covariance between growth traits and litter size have been assumed to be zero (Waldron and Thomas, 1992). The reasoning for this assumption is that records for the two traits are taken at quite different times: before 1 year of age for most growth traits, and after 12 months of age for litter size. The temporary environmental effects on growth traits are not expected to be the same as those for litter size.

For all three breeds, likelihood ratio (LR) tests of model B4 (or B3) against model B5 for bivariate analyses of body weights at birth, 60 d, 90 d and 120 d with litter size and model B15 against B16 for other traits (PWG, YG, FWT and FD) with litter size indicated that temporary environmental covariances of growth traits, and of fleece traits with litter size were not important, although some kind of statistical correlations existed. Also, the estimates of other variance components and genetic parameters generally were not affected by fixing the temporary environmental covariance to zero.

However, large estimates of residual correlations were found between litter size and BW, WW90, PWG and FWT with values of .78, .80, .78 and .78 for Polypay sheep. Also very strong temporary environmental correlations were obtained in bivariate genetic analyses of the other two breeds. Interpreting these correlations is difficult. From LR tests, these large values seemed unreal. However, in terms of estimation, what are the sources of these covariances? Also from a sampling viewpoint, it would not be likely that none of 14 residual correlations for the 14 pairs of traits from various bivariate models were significantly different from zero. Permanent environmental carry-over effects could

cause common temporary environment between litter size and other traits but were unlikely to explain such strong correlations. Further studies on effects of data structure, REML methodology and the Simplex iteration process will be needed to verify these correlations.

#### 5.3.4.3. Three Within-Trait And Across-trait Genetic Covariances and Correlations (

$r_{a1m1}$ ,  $r_{a2m1}$  and  $r_{a12}$ ):

Theoretically within-trait genetic correlation ( $r_{a1m1}$ ) contributes to the phenotypic variance of the trait. Maternal-direct genetic correlations for growth traits in three breeds were variable and ranged from -.90 to .25, while most of them were small and negative. Large and significant negative estimates were obtained between litter size and weaning weight at 60 d for Targhee sheep (-.89 to -.90,  $P < .01$ ) and for Polypay sheep (-.53 to -.56,  $P < .05$ ). Many authors have reported unrealistically high negative estimates of  $r_{a1m1}$  for various growth traits for sheep (Nasholm and Danell, 1996; Tosh and Kemp, 1994; Maria et al. 1993; Notter and Hough, 1996) and cattle (Robinson, 1996a, b; Swalve, 1993; Canter, et al. 1993). However, interpreting these high negative correlations is difficult. Robison (1972) proposed that negative direct-maternal genetic correlations may be environmentally induced. Swalve (1993) and Meyer et al (1993) concluded that negative covariances could be amplified by the management system.

Robinson (1996a,b) did a detailed study to trace the reasons for the high negative genetic correlations between maternal and direct genetic effects in beef cattle. By examination of the correlations between estimated breeding values and the fitting of alternative models, she thought that such correlations were a consequence of other effects

in the data, rather than evidence of a true negative genetic relationship. Her simulation study established that sire  $\times$  year variation and negative dam-offspring covariance could be responsible, in addition to genetic antagonisms. These causes will often be difficult to distinguish from true negative genetic correlations. Therefore Robinson (1996b) suggested that the best method of detection is to fit alternative models and assess their significance using likelihood ratio tests. As the correlations involve additive genetic variance ( $\sigma_a^2$ ) and maternal genetic variance ( $\sigma_m^2$ ) and one covariance ( $\sigma_{am}$ ), the correlation depends on the accurate partition and convergence of the three parts. Meyer (1989) observed that for data including 3 generations, sufficient comparisons between and within generations were available to estimate  $\sigma_a^2$  and  $\sigma_m^2$  virtually independent of each other, while estimates of  $\sigma_{am}$  were highly variable and showed a strong negative association with  $\sigma_m^2$ .

Al-Shorepy and Notter (1996) also found that partition of maternal genetic and permanent environmental effects was often difficult due to confounding of these effects. For animal breeding data, six kinds of relationships often are used, i.e. individual(Ind), sire-offspring(S-O), dam-offspring (D-O), paternal half-sibs (PHS), maternal half-sibs(MHS) and full sibs (FS), to estimate various parameter and (co)variance components. Meyer, in an unpublished paper, gave expectations of (co)variance components for different models and data structure. For example, if additive genetic ( $\sigma_a^2$ ), maternal direct ( $\sigma_m^2$ ) and environmental ( $\sigma_c^2$ ) components are fitted and Ind, S-O, D-O, PHS and MHS relationships are included, the estimates of  $\sigma_a^2$  and  $\sigma_{am}$  are



unbiased. However,  $\sigma_m^2$  is upward biased by  $2\sigma_{ec}$  (covariance between permanent and temporary environmental effects) and  $\sigma_c^2$  is downward biased by  $2\sigma_{ec}$ .

Another important effect is REML iteration. Given  $\mu_i$  and  $u_i$  ( $i=1, \dots, s$ ) known, the (co)variances are estimated by the following iteration formula:

$$\sigma_e^2 = (\mathbf{y}'\mathbf{y} - \mathbf{X}'\mathbf{y} - \sum u_i z_i y) / (N - r(\mathbf{X})) \text{ and}$$

$$\sigma_i^2 = (\mathbf{u}_i' \mathbf{u}_i + \sigma_e^2 \text{tr} \mathbf{C}_{ii}) / q_i$$

where  $\mathbf{C}_{ii}$  is sub matrix of  $\mathbf{C}$  and

$$\mathbf{C} = \begin{bmatrix} \mathbf{X}'\mathbf{X} & \mathbf{X}'\mathbf{Z}_1 & \cdots & \mathbf{X}'\mathbf{Z}_s \\ \mathbf{Z}_1'\mathbf{X} & \mathbf{Z}_1'\mathbf{Z}_1 + \mathbf{I}_{q_1} & \cdots & \mathbf{Z}_1'\mathbf{Z}_s \\ \vdots & \vdots & \ddots & \vdots \\ \mathbf{Z}_s'\mathbf{X} & \mathbf{Z}_s'\mathbf{Z}_1 & \cdots & \mathbf{Z}_s'\mathbf{Z}_s + \mathbf{I}_{q_s} \end{bmatrix}$$

Note that  $\mathbf{C}_{11} = (\mathbf{X}'\mathbf{X})$  and  $\mathbf{C}_{ii} = (\mathbf{Z}_i'\mathbf{Z}_i + \mathbf{I}_{q_i})$ , i.e.  $\mathbf{C}_{ii}$  is function of  $\mathbf{Z}_i$ ,  $\mathbf{Z}_j$  ( $j \neq i$ ),  $q_i$ , and  $q_j$ . Therefore,  $\sigma_i^2$  is not independent on  $\sigma_j^2$ , because of the iteration process itself and because of confounded effects through the  $\mathbf{Z}$  matrix. The converged values of  $\sigma_i^2$  are dependent on  $u_i$  and  $\sigma_j^2$  ( $j \neq i$ ). If one parameter is flat, the other ( $s$ ) will also tend to be flat, although not both of them are necessarily flat. In terms of the likelihood surface, this implied a maximum along a flat ridge, i.e. an area where for a constant sum of the two parameters, the value of the likelihood changes very little with changes in the parameter values (Meyer, 1989).

There is very little literature on theoretical considerations about estimation of covariances, especially across-trait covariances, which are vital for multitrait genetic evaluation. Also, we are not clear about the expectation of these covariances in different models and in field data. However, general methodology for variance components should

apply for estimation of covariances, although covariance estimation needs much more data and a suitable data structure. Additive genetic covariances theoretically are more robust than other estimates because they have the largest degrees of freedom. So are additive direct genetic correlations, which consist of three components ( $a_1^2$ ,  $a_2^2$  and  $a_{12}$ ), all of which are robust with small Simplex sampling errors. However, it should be noted that this covariance is affected by  $a_{2m1}$  and  $pe_m^2$  for growth traits. The results from genetic analyses of Suffolk and Targhee data clearly indicated that additive genetic covariance between growth traits and litter size was confounded with additive genetic covariance between maternal genetic effects for growth and additive direct effects for litter size. Failure to fit either one would increase the value of the other. For example, additive genetic correlations between 60-d WW and LS for Suffolk sheep were increased from .38 (model B5) to .54 (model B9). Likelihood ratio tests showed that the joint effects of the two corresponding genetic covariances was larger than the sum of their individual effects. Similar results also were observed in genetic analyses of WW60 and LS for Targhee sheep.

Inclusion or exclusion of some variance components affected estimation of genetic covariance. Failure to fit permanent environmental effects due to the dam for 90-d weaning weight decreased the additive genetic correlation with LS from .43 (model B5) to .24 (model B6). All these results showed that estimates of additive genetic covariance not only depend on the presence of other genetic covariances such as  $a_{2m1}$ , but also on variance components, such as permanent environmental variance of the dam for growth traits.

Additive genetic correlation estimates (or ranges) of litter size with BW, WW60, WW90, PWG and FWT for Polypay were .14 to .27, -.12 to -.15, .00 to .44, -.05 and .21, respectively. Substantial variation was observed. Across-trait genetic-maternal correlation ( $r_{a2m1}$ ) estimates were also variable, with estimates (or ranges) of -.13 to -.23, .17 to .23, and .18 to .98 for BW, WW60, WW90 with LS. The general dynamic trend was an increase in one covariance accompanying decreases in the other, which indicated some kind of association, called a flat ridge by Meyer (1989). Therefore, accurate estimates for the two covariances would be hindered during the REML Simplex process. Unlike results from the other two breeds, LR tests failed to reveal any dependence between the two covariance components in Polypay, i.e., individual effect tests agreed with two-component joint and three-component joint tests. The reason was that individual effects were so small that we did not detect the association between the two components by joint effect tests. Dependence between  $a_{1m1}$  and the other two genetic covariances was not detected in any of the breeds. Moreover, partition of these covariances was affected by additive genetic variance. Meyer (1992) concluded in her simulation study that estimates of (co)variance components due to maternal effects were subject to large sampling error and high sampling correlations, even for a “reduced” model ignoring dominance effects and for family structures providing numerous types of covariances between relatives which have been specifically designed for the estimation of maternal effects. She found that for small data sets and models of analysis fitting both genetic and maternal environmental effects and a direct-maternal covariance, this frequently induced the need to constrain estimates to the parameter space. Consequently,

large sample theory predictions of sampling errors and correlation estimates do not agree with empirical results. She suggested that further research is required to evaluate the implications of such large sampling (co)variances on the accuracy of selection indexes including both direct and maternal effects, i.e. the expected loss in selection response because of inaccurately estimated parameters used to derive index weights.

## **5.4. Implications**

Heritabilities for growth traits for Suffolk, Targhee and Polypay were low to medium and smaller than average values of previous literature estimates. On the other hand, maternal genetic and maternal environmental effects for all body weights in the three breeds were large and important, implying that explicitly considering these effects should result in more genetic improvements in the growth traits. Mass selection should be effective to improve fleece characteristics for Targhee and Polypay sheep due to high direct heritabilities. Genetic correlations between direct and maternal effects for growth and direct effects for litter size were generally favorable or small and negative, thus not imposing serious problems for simultaneous genetic improvement of growth and litter size as well as maternal performance for growth traits. Within-trait maternal-direct genetic correlations for growth in the three breeds were small and variable, indicating that strong, negative maternal-direct correlations for growth traits are not a universal phenomenon as implied by some scientists. Potentially unfavorable relationships between fleece traits and litter size should be taken into account. Reducing sampling

variance and correlations among different covariance estimates should be a major tasks for covariance estimation in the future studies.

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Table 5.1. Characteristics of the data structure for three growth traits and litter size in Suffolk sheep.

	WW60 (kg)	WW90 (kg)	PWG (kg)	LS
No. of records	12746	2853	5621	10295
No of animals	12746	2853	5621	5038
Animals in $A^{-1}$	29115	29115	29115	29115
Levels of fixed effects	648	165	722	658
Levels for maternal effects	29115	29115	-	-
Levels for pe	4276	1221	-	5038
Trait,				
Mean	32.18	47.18	23.51	1.95
SD	6.81	10.06	7.73	.70
CV	21.18	21.32	32.90	35.87
MIN	9.03	16.39	.54	.95
MAX	80.18	83.22	68.64	4.60

Note: WW60, WW90 = 60-d, 90-d weaning weight. PWG = 60 - 120 d cumulative postweaning gain. LS = No. of lambs born. pe = permanent environment effects. SD = standard deviation. CV = coefficient of variation. MIN = minimum value and MAX = maximum value.  $A^{-1}$  = the inverse of the additive genetic relationship matrix.



Table 5.2. Characteristics of the data structure for growth (kg), grease fleece weight (kg) and fiber diameter ( $\mu$ ), and litter size in Targhee sheep.

	WW60	WW120	PWG	YG	FWT	FD	LS
No. of records	4650	7428	1406	3241	5471	3908	7591
No of animals	4650	7428	1406	3241	5471	3908	7591
Animals in $A^{-1}$	17633	17633	17633	17633	17633	17633	17633
Contemporary groups	117	81	55	68	164	113	182
Levels for maternal effects	17633	17633	-	-	-	-	-
Levels for pe	1654	2621	-	-	-	-	3131
Trait,							
Mean	24.57	36.82	17.96	32.33	3.81	22.19	1.69
SD	5.54	7.47	4.74	18.58	1.24	1.92	.62
CV	22.53	20.29	26.41	57.46	32.61	8.68	36.34
MIN	8.54	6.81	2.72	1.36	1.32	15.20	.95
MAX	51.12	67.46	34.87	95.79	12.44	30.40	4.60

Note: WW60 = 60-d weaning weight. WW120 = 120-d weaning weight. PWG = 60-120 d cumulative post-weaning gain. YG = 120-365 d cumulative post-weaning gain. FWT= fleece weight. FD=fiber diameter. LS=No. of lambs born. pe = permanent environment effects. SD= standard deviation. CV= coefficient of variation. MIN=minimum value and MAX= maximum value.  $A^{-1}$  = the inverse of the additive genetic relationship matrix.

Table 5.3. Characteristics of the data structure for growth, fleece weight, and litter size in Polypay sheep.

	BW	WW60	WW90	PWG	FWT	LS
No. of records	7542	6561	1690	3046	1099	6061
No of animals	7542	6561	1690	3046	1099	2709
Animals in A <sup>-1</sup>	16795	16795	16795	16795	16795	16795
Contemporary groups	340	274	80	240	74	403
Levels for maternal effects	16795	16795	16795	-	-	-
Levels for pe	2507	2304	695	-	-	2709
Trait,						
Mean	5.19	26.08	29.82	19.41	4.15	2.09
SD	.99	5.50	8.02	6.30	1.26	.78
CV	19.01	21.09	26.90	32.45	30.35	37.18
MIN	1.73	7.63	15.93	.27	1.59	1.00
MAX	8.99	44.17	56.21	43.31	10.26	6.30

Note: BW = birth weight. WW60=60-d weaning weight. WW90 =90-d weaning weight. PWG = 60-120 d cumulative post-weaning gain. FWT= fleece weight. LS = No. of lambs born. pe = permanent environment effects. SD = standard deviation. CV = coefficient of variation. MIN = minimum value and MAX = maximum value. A<sup>-1</sup> = the inverse of the additive genetic relationship matrix.

Table 5.4. Abbreviations and corresponding definitions

Abbreviation	Definition
$\sigma_a^2$	Direct additive genetic variance
$\sigma_m^2$	Maternal additive genetic variance
$\sigma_{am}$	Covariance between direct and maternal genetic effects
$\sigma_{pe(m)}^2$	Permanent environmental variance due to animal ( due to dam)
$\sigma_e^2$	Residual variance
$\sigma_p^2$	Phenotypic variance
$h^2$	Direct heritability, $\sigma_a^2 / \sigma_p^2$
$m^2$	$\sigma_m^2 / \sigma_p^2$
$h_t^2$	$\sigma_a^2 + 0.5 \sigma_m^2 + 1.5 \sigma_{am}$
$r_{am}$	Correlation between direct and maternal additive genetic effects
$pe^2$	$\sigma_{pe}^2 / \sigma_p^2$
$e^2$	$\sigma_e^2 / \sigma_p^2$

Table 5.4. Abbreviations and corresponding definitions(continued).

Abbreviation	Definition
P	Phenotypic value for the trait.
A	Additive direct genetic value.
M	Additive maternal genetic value.
PE <sub>a</sub>	Permanent environmental value attributed to animal.
PE <sub>m</sub>	Permanent environmental value attributed to dam.
E	Temporary environmental value.
e <sub>12</sub>	Residual covariance between the two traits.
a <sub>12</sub>	Additive direct genetic covariance between the two traits.
a <sub>2m1</sub>	Genetic covariance between direct additive effects for litter size and maternal additive effects for the growth traits.
a <sub>1m1</sub>	Genetic covariance between additive direct and maternal additive effects for the growth traits.

1 = growth traits or postweaning gains or fleece traits; 2 = litter size.

Table 5.5. Model descriptions for bivariate analysis of some growth traits together with litter size in three breeds of sheep.

Model	Description
B-3:	For the growth traits, $P = A + M + PE_m + E$ For litter size, $P = A + PE_a + E$ . All the associated covariances are fitted.
B-4	For the growth traits, $P = A + M + PE_m + E$ For litter size, $P = A + E$ . All the associated covariances are fitted.
B-5	Same as Model B4 except fixing $cov_{e_1e_2} = .0000$ .
B-6	For the growth traits, $P = A + M + E$ For litter size, $P = A + E$ .
B-7	For the growth traits, $P = A + PE_m + E$ For litter size, $P = A + E$ .
B-8	Same as Model B5 except one additional constraint, $cov_{a_1a_2} = .0000$
B-9	Same as Model B5 except one additional constraint. $cov_{a_2m_1} = .0000$
B-10	Same as Model B5 except one additional constraint. $cov_{a_1m_1} = .0000$
B-11	Same as Model B5 except two additional constraints, $cov_{a_2m_1} = .0000$ and $cov_{a_1m_1} = .0000$ .
B-12	Same as Model B5 except two additional constraints, $cov_{a_1m_1} = .0000$ and $cov_{a_12} = .0000$ .
B-13	Same as Model B5 except two additional constraints, $cov_{a_2m_1} = .0000$ and $cov_{a_12} = .0000$ .
B-14	Same as Model B5 except for fixing all covariance to be zero.
B-15	For postweaning gain or fleece traits, $P = A + E$ , for litter size (Suffolk data) or $P = A + PE_a + E$ (Targhee and Polypay data).
B-16	Same as Model B-12 except with $cov_{e_12} = .0000$ .

Table 5.6. Estimates of (co)variance components and genetic parameters for 60-d weaning weight (kg) from bivariate analyses together with litter size in Suffolk sheep

	B-3	B-4	B-5	B-10
$\sigma_a^2$	5.42	5.63	5.71	4.95
$\sigma_m^2$	1.36	1.70	1.68	1.03
$\sigma_{am}$	-.65	-.98	-1.02	-
$\sigma_{pem}^2$	3.21	3.14	3.18	3.10
$\sigma_e^2$	20.63	20.53	20.48	20.88
$\sigma_p^2$	29.97	30.02	30.03	29.95
$h^2$	.18	.19	.19	.17
$m^2$	.05	.06	.06	.03
$h_t^2$	.17	.17	.17	.18
$r_{am}$	-.24	-.32	-.33	-
$pe_m^2$	.11	.10	.11	.10
$e^2$	.69	.68	.68	.70

Note: (a). Definitions of parameters are listed in Table 5.4.

(b). Models are described in detail in Table 5.5

Table 5.7. Estimates of (co)variance components and genetic parameters for litter size from bivariate analyses with 60-d weaning weight in Suffolk sheep

	B-3	B-4	B-5	B-10
$\sigma_a^2$	.0435	.0438	.0440	.0440
$\sigma_{pe}^2$	.0000	-	-	-
$\sigma_e^2$	.4157	.4160	.4157	.4158
$\sigma_p^2$	.4592	.4598	.4597	.4598
$h^2$	.09	.10	.10	.10
$pe^2$	.00	-	-	-
$e^2$	.91	.90	.90	.90

Note:(a). Definitions of parameters are listed in Table 5.4.

(b). Models are described in detail in Table 5.5.

Table 5.8. Estimates of covariance components<sup>a</sup> and of corresponding correlations<sup>b</sup> from bivariate analyses of 60-d weaning weight (WW60, kg) and litter size (LS) in Suffolk sheep

	B-3	B-4	B-5	B-10
a <sub>12</sub>	.189	.186	.190	.154
a <sub>2m1</sub>	.086	.089	.087	.102
e <sub>12</sub>	2.564	.998	-	-
p <sub>12</sub>	2.795	1.228	.233	.233
r <sub>a</sub>	.39	.37	.38	.39
r <sub>a2m1</sub>	.35	.33	.32	.25
r <sub>e</sub>	.88	.34	-	-
r <sub>p</sub>	.75	.33	.06	.07

<sup>a</sup> a<sub>12</sub> = direct additive covariance between WW60 and LS. a<sub>2m1</sub> = additive genetic cross-trait covariance between direct effects for LS and maternal effects for WW60.

<sup>b</sup>r<sub>a</sub> = direct, genetic correlation between WW60 and LS. r<sub>a2m1</sub> = genetic correlation between direct effects for LS and maternal effects on WW60. r<sub>e</sub> = residual correlation. r<sub>p</sub> = phenotypic correlation.



Table 5.9. Likelihood ratio tests for different models of bivariate analyses for 60-d weaning weight and litter size in Suffolk sheep.

Model	-2 log L <sup>a</sup>	tests against	X <sup>2</sup> <sup>b</sup>	Probability.
B-3	76427.60	B-5	.30	P> .05(df=2)
B-4	76427.31	B-5	.01	P> .05(df=1)
B-5	76427.30	-	-	-
B-6	76462.30	B-5	35.00	P< .01(df=1)
B-7	76437.63	B-5	10.33	P< .05(df=3)
B-8	76433.15	B-5	5.85	P< .05(df=1)
B-9	76430.19	B-5	2.89	P> .05(df=1)
B-10	76429.44	B-5	2.14	P> .05(df=1)
B-11	76434.66	B-5	7.36	P< .05(df=2)
B-12	76435.73	B-5	8.43	P< .05(df=2)
B-13	76457.10	B-5	29.80	P< .01(df=2)
B-14	76459.89	B-5	32.59	P< .01(df=2)

<sup>a</sup> Log L = log likelihood.

<sup>b</sup> X<sup>2</sup> = the difference of -2 log L between the model and the model tested against.

Table 5.10. Estimates of (co)variance components and genetic parameters for 90-d weaning weight (kg) from bivariate analyses together with litter size in Suffolk sheep

Model	B-3	B-4	B-5	B-12
$\sigma_a^2$	6.80	7.69	6.46	5.72
$\sigma_m^2$	2.14	2.12	2.00	4.08
$\sigma_{am}$	.88	.64	.92	-
$\sigma_{pem}^2$	8.31	8.56	8.73	7.93
$\sigma_e^2$	32.51	31.94	32.51	33.01
$\sigma_p^2$	50.63	50.94	50.61	50.74
$h^2$	.13	.15	.13	.11
$m^2$	.04	.04	.04	.08
$h_t^2$	.18	.19	.17	.15
$r_{am}$	.23	.16	.25	-
$pe_m^2$	.16	.17	.17	.16
$e^2$	.64	.63	.64	.65

Note: (a). Definitions of parameters are listed in Table 5.4.  
 (b). The models are described in detail in Table 5.5

Table 5.11. Estimates of (co)variance components and genetic parameters from bivariate analyses for litter size together with 90-d weaning weight in Suffolk sheep

	B-3	B-4	B-5	B-12
$\sigma_a^2$	.0418	.0430	.0431	.0448
$\sigma_{pe}^2$	.0000	-	-	-
$\sigma_e^2$	.4170	.4160	.4158	.4151
$\sigma_p^2$	.4587	.4590	.4589	.4599
$h^2$	.09	.09	.09	.10
$pe^2$	.00	-	-	-
$e^2$	.91	.91	.91	.90

Note:(a).Definitions of parameters are listed in Table 5.4.

(b).The models are described in detail in Table 5.5

Table 5.12. Estimates of covariance components<sup>a</sup> and of corresponding correlations<sup>b</sup> from bivariate analyses of 90-d weaning weight (WW90, kg) and litter size (LS) in Suffolk sheep

	B-3	B-4	B-5	B-12
a <sub>12</sub>	.272	.253	.227	-
a <sub>2m1</sub>	.285	.288	.289	.427
e <sub>12</sub>	1.555	3.643	-	-
p <sub>12</sub>	1.969	4.041	.371	.214
r <sub>a</sub>	.51	.44	.43	-
r <sub>a2m1</sub>	.95	.96	.98	1.00
r <sub>e</sub>	.42	1.00	-	-
r <sub>p</sub>	.41	.84	.08	.04

<sup>a</sup> a<sub>12</sub> = direct additive covariance between WW90 and LS. a<sub>2m1</sub> = additive genetic cross-covariance between direct effects for LS and maternal effects for WW2. e<sub>12</sub> = residual covariance. p<sub>12</sub> = phenotypic covariance.

<sup>b</sup> r<sub>a</sub> = direct, genetic correlation between WW90 and LS. r<sub>a2m1</sub> = genetic correlation between direct effects for LS and maternal effects on WW90. r<sub>e</sub> = residual correlation. r<sub>p</sub> = phenotypic correlation.

Table 5.13. Likelihood ratio tests for different models of bivariate analyses for 90-d weaning weight and litter size in Suffolk sheep.

Model	-2 log L <sup>a</sup>	tests against	X <sup>2</sup> <sup>b</sup>	Probability
B-3	21100.04	B-5	.35	P> .05(df=2)
B-4	21099.76	B-5	.10	P> .05(df=1)
B-5	21099.69			
B-6	21120.42	B-5	20.73	P< .01(df=1)
B-7	21110.40	B-5	10.71	P< .05(df=3)
B-8	21100.48	B-5	.79	P> .05(df=1)
B-9	21110.59	B-5	10.9	P< .01(df=1)
B-10	21099.42	B-5	-.27	P> .05(df=1)
B-11	21110.46	B-5	10.77	P< .01(df=2)
B-12	21099.46	B-5	-.23	P>.05(df=2)
B-13	21124.98	B-5	25.29	P< .01(df=2)
B-14	21124.98	B-5	25.29	P< .01(df=3)

<sup>a</sup> Log L = log likelihood.

<sup>b</sup> X<sup>2</sup> = the difference of -2 Log L between the model and the model tested against.

Table 5.14. Estimates of (co)variance components<sup>a</sup> and of genetic parameters ( corresponding correlations )<sup>b</sup> from bivariate analyses of post-weaning gain (PWG, kg) and litter size (LS) in Suffolk sheep

Model	B-15			B-16		
	PWG	LS	COV	PWG	LS	COV
$\sigma_a^2(\sigma_{a12})$	4.80	.041	.071	4.76	.041	.073
$\sigma_e^2(\sigma_{e12})$	23.73	.418	2.148	23.76	.418	-
$\sigma_p^2(\sigma_{p12})$	28.52	.459	2.219	28.52	.459	.073
$h^2(r_a)$	.17	.09	.16	.17	.09	.17
$e^2(r_e)$	.83	.91	.68	.83	.91	-
$r_p$	-	-	.61	-	-	.02
-2log L	33577.52			33577.53		

Note:(a). Definitions of parameters are listed in Table 5.4.

(b). The models are described in detail in Table 5.5

<sup>a</sup>  $\sigma_{a12}$  = direct additive covariance between PWG and LS.  $\sigma_{e12}$  = residual covariance.  $\sigma_{p12}$  = phenotypic covariance.

<sup>b</sup>  $r_a$  = direct, genetic correlation between PWG and LS.  $r_e$  = residual correlation.  $r_p$  = phenotypic correlation.

Table 5.15. Comparison of Estimates of (co)variance components and genetic parameters for 60-d weaning weight from bivariate analyses, together with litter size in Targhee sheep.

	B-3	B-4	B-5	B-13
$\sigma_a^2$	2.37	2.40	2.38	2.42
$\sigma_m^2$	3.76	3.82	3.83	3.77
$\sigma_{am}$	-2.66	-2.71	-2.71	-2.73
$\sigma_{pem}^2$	1.65	1.64	1.65	1.69
$\sigma_e^2$	12.09	12.09	12.09	12.07
$\sigma_p^2$	17.21	17.23	17.23	17.21
$h^2$	.14	.14	.14	.14
$m^2$	.22	.22	.22	.22
$r_{am}$	-.89	-.90	-.90	-.90
$pe_m^2$	.10	.09	.10	.10
$e^2$	.70	.70	.70	.70

Note: (a). Definitions of parameters are listed in Table 5.4.

(b). Models are described in detail in Table 5.5.

Table 5.16. Comparison of Estimates of (co)variance components and genetic parameters for litter size from bivariate analyses, together with 60-d weaning weight in Targhee sheep.

	B-3	B-4	B-5	B-13
$\sigma_a^2$	.0366	.0399	.0359	.0348
$\sigma_{pe}^2$	.0039	-	.0047	.0053
$\sigma_e^2$	.2902	.2915	.2901	.2899
$\sigma_p^2$	.3307	.3314	.3307	.3301
$h^2$	.11	.12	.11	.11
$pe^2$	.01	-	.01	.02
$e^2$	.88	.88	.88	.88

Note: (a). Definitions of parameters are listed in Table 5.4.

(b). Models are described in detail in Table 5.5.



Table 5.17. Estimates of covariance components<sup>a</sup> and of corresponding correlations<sup>b</sup> from bivariate analyses of 60-d weaning weight (WW1) and litter size (LS) in Targhee sheep.

	B-3	B-4	B-5	B-13
a <sub>12</sub>	.031	.065	.066	-
a <sub>2m1</sub>	-.068	-.089	-.086	-
e <sub>12</sub>	.196	-	-	-
p <sub>12</sub>	.193	.020	.023	-
r <sub>a</sub>	.10	.21	.22	-
r <sub>a2m1</sub>	-.18	-.23	-.23	-
r <sub>e</sub>	.10	-	-	-
r <sub>p</sub>	.08	.01	.01	-

<sup>a</sup> a<sub>12</sub> = direct additive covariance between WW60 and LS. a<sub>2m1</sub> = additive genetic cross-covariance between direct effects for LS and maternal effects for WW60. e<sub>12</sub> = residual covariance. p<sub>12</sub> = phenotypic covariance.

<sup>b</sup>r<sub>a</sub> = direct, genetic correlation between WW60 and LS. r<sub>a2m1</sub> = genetic correlation between direct effects for LS and maternal effects on WW60. r<sub>e</sub> = residual correlation. r<sub>p</sub> = phenotypic correlation.

Table 5.18. Likelihood ratio tests for different models of bivariate analyses for 60-d weaning weight and litter size in Targhee sheep.

Model	-2 log L <sup>a</sup>	tests against	X <sup>2</sup> <sup>b</sup>	Probability
B-3	24003.32	B-5	.19	P> .05(df=2)
B-4	24003.70	B-5	.57	P> .05(df=1)
B-5	24003.13	B-5	-	-
B-6	24020.36	B-5	17.23	P< .01(df=1)
B-7	24042.01	B-5	38.88	P< .01(df=3)
B-8	24003.72	B-5	.59	P> .05(df=1)
B-9	24005.49	B-5	2.36	P> .05(df=1)
B-10	24016.22	B-5	13.09	P< .01(df=2)
B-11	24018.76	B-5	15.63	P< .01(df=2)
B-12	24016.31	B-5	13.18	P< .01(df=2)
B-13	24006.24	B-5	3.11	P> .05(df=2)
B-14	24019.33	B-5	16.20	P<.01(df=3)

<sup>a</sup> Log L = log likelihood.

<sup>b</sup> X<sup>2</sup> = the difference between the model and the model tested against.

Table 5.19. Comparison of estimates of (co)variance components and genetic parameters for 120-d weaning weight (kg) from bivariate analyses<sup>a</sup>, together with litter size in Targhee sheep.

	B-3	B-4	B-5	B-11
$\sigma_a^2$	5.34	5.22	5.30	4.90
$\sigma_m^2$	1.74	1.68	1.80	1.77
$\sigma_{am}$	-.24	-.10	-.30	-
$\sigma_{pem}^2$	2.71	2.69	2.73	2.65
$\sigma_e^2$	22.89	22.96	22.91	23.10
$\sigma_p^2$	32.44	32.45	32.44	32.42
$h^2$	.16	.16	.16	.15
$m^2$	.05	.05	.06	.05
$r_{am}$	-.08	-.03	-.10	-
$pe_m^2$	.08	.08	.08	.08
$e^2$	.71	.71	.71	.71

Note: (a). Definitions of parameters are listed in Table 5.4.

(b). Models are described in detail in Table 5.5.

Table 5.20. Comparison of estimates of (co)variance components and genetic parameters for litter size from bivariate analyses<sup>a</sup>, together with 120-d weaning weight in Targhee sheep.

	B-3	B-4	B-5	B-11
$\sigma_a^2$	.0365	.0393	.0347	.0344
$\sigma_{pe}^2$	.0033	-	.0056	.0058
$\sigma_e^2$	.2908	.2918	.2899	.2901
$\sigma_p^2$	.3306	.3312	.3541	.3303
$h^2$	.11	.12	.11	.10
$pe^2$	.01	-	.02	.02
$e^2$	.88	.88	.88	.88

Note: (a). Definitions of parameters are listed in Table 6.2.

(b). Models are described in detail in Table 6.3.

Table 5.21. Estimates of covariance components<sup>a</sup> and of corresponding correlations<sup>b</sup> from bivariate analyses of 120-d weaning weight (WW120, kg) and litter size ( Trait 2, LS) in Targhee sheep.

	B-3	B-4	B-5	B-11
a <sub>12</sub>	.209	.206	.205	.111
a <sub>2m1</sub>	-.091	-.089	-.089	-
e <sub>12</sub>	.115	-	-	-
p <sub>12</sub>	.279	.162	.161	.111
r <sub>a</sub>	.47	.46	.48	.27
r <sub>a2m1</sub>	-.36	-.35	-.35	-
r <sub>c12</sub>	.00	-	-	-
r <sub>e</sub>	.04	-	-	-
r <sub>p</sub>	.09	.05	.05	.03

<sup>a</sup> a<sub>12</sub> = direct additive covariance between WW120 and LS. a<sub>2m1</sub> = additive genetic cross-covariance between direct effects for LS and maternal effects for WW120. e<sub>12</sub> = residual covariance. p<sub>12</sub> = phenotypic covariance.

<sup>b</sup>r<sub>a</sub> = direct, genetic correlation between WW120 and LS. r<sub>a2m1</sub> = genetic correlation between direct effects for LS and maternal effects on WW120. r<sub>e</sub> = residual correlation. r<sub>p</sub> = phenotypic correlation.

Table 5.22. Likelihood ratio tests for different models of bivariate analyses for 120-d weaning weight and litter size in Targhee sheep.

Model	-2 log L <sup>a</sup>	tests against	X <sup>2</sup> <sup>b</sup>	Probability
B-3	43700.20	B-5	0.16	P> .05(df=2)
B-4	43701.04	B-5	1.00	P> .05(df=1)
B-5	43700.04	-	-	-
B-6	43718.07	B-5	18.03	P< .01(df=1)
B-7	43713.29	B-5	13.25	P< .01(df=3)
B-8	43706.81	B-5	6.77	P< .05(df=1)
B-9	43703.60	B-5	3.56	P> .05(df=1)
B-10	43700.23	B-5	.19	P> .05(df=1)
B-11	43703.70	B-5	3.66	P> .05(df=2)
B-12	43707.07	B-5	7.03	P< .05(df=2)
B-13	43706.83	B-5	6.79	P< .05(df=2)
B-14	43707.12	B-5	7.08	P< .05(df=3)

<sup>a</sup> Log L = log likelihood.

<sup>b</sup> X<sup>2</sup> = the difference between the model and the model tested against.

Table 5.23. Estimates of (co)variance components and genetic parameters (corresponding correlations) from bivariate analyses of 60-120 d cumulative postweaning gain (kg) together with litter size in Targhee sheep

Model	B-15			B-16		
	PWG	LS	COV	PWG	LS	COV
$\sigma_a^2(r_{a12})$	3.60	.037	.156	3.54	.035	.155
$\sigma_{pe}^2(r_{c12})$	-	.005	-	-	.006	-
$\sigma_e^2(r_{e12})$	9.80	.290	.408	9.82	.290	-
$\sigma_p^2(r_{p12})$	13.40	.330	-.252	13.36	.330	.155
$h^2(r_g)$	.27	.11	.44	.27	.11	.44
$pe^2(r_{c12})$	-	.02	-	-	.02	-
$e^2(r_{e12})$	.73	.88	-.24	.73	.88	-
-2logL	6502.93			6502.93		

Note: (a).Definitions of parameters are listed in Table 6.2.

(b).The models are described in detail in Table 6.3

Table 5.24. Estimates of (co)variance components and genetic parameters (corresponding correlations) from bivariate analyses of 120-1365 d cumulative postweaning gain (kg) together with litter size in Targhee sheep

Model	B-15			B-16		
	YG	LS	COV	YG	LS	COV
$\sigma_a^2(r_{a12})$	7.88	.035	.045	7.84	.035	.042
$\sigma_{pe}^2(r_{c12})$	-	.006	-	-	.006	-
$\sigma_e^2(r_{e12})$	33.04	.290	.277	33.11	.290	-
$\sigma_p^2(r_{p12})$	40.92	.330	.322	40.96	.330	.042
$h^2(r_g)$	.19	.10	.09	.19	.11	.08
$pe^2(r_{c12})$	-	.02	-	-	.02	-
$e^2(r_{e12})$	.81	.88	.09	.81	.88	-
-2logL	19531.08			19531.08		

Note: (a).Definitions of parameters are listed in Table 5.2.

(b).The models are described in detail in Table 5.3



Table 5.25. Estimates of (co)variance components and genetic parameters (corresponding correlations) from bivariate analyses of grease fleece weight (kg) together with litter size in Targhee sheep

Model	B-15			B-16		
	FWT	LS	COV	FWT	LS	COV
$\sigma_a^2(r_{a12})$	.137	.035	-.006	.138	.035	-.006
$\sigma_{pe}^2(r_{c12})$	-	.006	-	-	.005	-
$\sigma_e^2(r_{e12})$	.198	.290	.200	.198	.290	-
$\sigma_p^2(r_{p12})$	.335	.330	.194	.335	.330	-.006
$h^2(r_g)$	.41	.11	-.09	.41	.11	-.09
$pe^2(r_{c12})$	-	.02	-	-	.02	-
$e^2(r_{e12})$	.59	.88	.84	.59	.88	-
-2logL	7159.76			7159.76		

Note: (a).Definitions of parameters are listed in Table 5.4.

(b).The models are described in detail in Table 5.5.

Table 5.26. Estimates of (co)variance components and genetic parameters (corresponding correlations) from bivariate analyses of fiber diameter together with litter size in Targhee sheep

Model	B-15			B-16		
	FD	LS	COV	FD	LS	COV
$\sigma_a^2(\sigma_{a12}^2)$	1.00	.035	.054	1.00	.035	.056
$\sigma_{pe}^2(\sigma_{c12}^2)$	-	.006	-	-	.006	-
$\sigma_e^2(\sigma_{e12}^2)$	1.00	.290	.337	1.00	.290	-
$\sigma_p^2(\sigma_{p12}^2)$	2.00	.331	.391	2.00	.331	.056
$h^2(r_g)$	.50	.11	.29	.50	.11	.30
$pe^2(r_{c12})$	-	.02	-	-	.02	-
$e^2(r_{e12})$	.50	.88	.62	.50	.88	-
$r_p$						
-2logL	5616.48			5616.48		

Note: (a).Definitions of parameters are listed in Table 5.4.  
 (b).The models are described in detail in Table 5.5.

Table 5.27. Comparison of estimates of (co)variance components and genetic parameters for birth weight from bivariate analyses, together with litter size in Polypay sheep.

	B-3	B-4	B-5	B-14
$\sigma_a^2$	.16	.13	.14	.11
$\sigma_m^2$	.07	.07	.07	.04
$\sigma_{am}$	-.05	-.03	-.03	-
$\sigma_{pem}^2$	.16	.15	.15	.16
$\sigma_e^2$	.38	.40	.40	.41
$\sigma_p^2$	.73	.72	.72	.72
$h^2$	.23	.19	.19	.15
$m^2$	.10	.09	.09	.06
$r_{am}$	-.45	-.34	-.36	-
$pe_m^2$	.22	.21	.21	.22
$e^2$	.53	.55	.55	.57

Note: (a).Definitions of parameters are listed in Table 5.4.  
 (b). Model are described in detail in Table 5.5.

Table 5.28. Comparison of estimates of (co)variance components and genetic parameters for litter size from bivariate analyses by different models, together with birth weight in Polypay sheep

	B-3	B-4	B-5	B-14
$\sigma_a^2$	.0460	.0617	.0460	.0461
$\sigma_{pe}^2$	.0211	-	.0217	.0211
$\sigma_e^2$	.4423	.4494	.4414	.4423
$\sigma_p^2$	.5095	.5111	.5092	.5096
$h^2$	.09	.12	.09	.09
$pe^2$	.04	-	.04	.04
$e^2$	.87	.88	.87	.87

Note: (a).Definitions of parameters are listed in Table 5.4.

(b). Model are described in detail in Table 5.5.

Table 5.29. Estimates of covariance components<sup>a</sup> and of corresponding correlations<sup>b</sup> from bivariate analyses of birth weight (BW) and litter size (LS) in Polypay sheep.

	B-3	B-4	B-5	B-14
$a_{12}$	.024	.012	.013	-
$a_{2m1}$	-.013	-.008	-.008	-
$e_{12}$	.321	-	-	-
$p_{12}$	.339	.008	.009	-
$r_a$	.27	.14	.17	-
$r_{a2m1}$	-.23	-.13	-.14	-
$r_e$	.78	-	-	-
$r_p$	.56	.01	.02	-

<sup>a</sup>  $a_{12}$  = direct additive covariance between BW and LS.  $a_{2m1}$  = additive genetic cross-covariance between direct effects for LS and maternal effects for BW.  $e_{12}$  = residual covariance.  $p_{12}$  = phenotypic covariance.

<sup>b</sup>  $r_a$  = direct, genetic correlation between BW and LS.  $r_{a2m1}$  = genetic correlation between direct effects for LS and maternal effects on BW.  $r_e$  = residual correlation.  $r_p$  = phenotypic correlation.

Table 5.30. Likelihood ratio tests for different models of bivariate analyses for birth weight and litter size for Polypay sheep.

Model	-2 log L <sup>a</sup>	tests against	X <sup>2</sup> <sup>b</sup>	Prob. <sup>c</sup>
B-3	18396.90	B-5	.8696	P> .05(df=2)
B-4	18399.29	B-5	3.2592	P> .05(df=1)
B-5	18396.04	B-5	-	-
B-6	18483.57	B-5	87.5341	P< .01(df=1)
B-7	18404.36	B-5	8.3378	P< .05(df=3)
B-8	18397.05	B-5	1.0177	P> .05(df=1)
B-9	18396.48	B-5	.4489	P> .05(df=1)
B-10	18398.30	B-5	2.2715	P> .05(df=1)
B-11	18398.65	B-5	2.6269	P> .05(df=2)
B-12	18398.67	B-5	2.6424	P> .05(df=2)
B-13	18396.55	B-5	.5241	P> .05(df=2)
B-14	18398.72	B-5	2.6980	P> .05(df=3)

<sup>a</sup> Log L = log likelihood.

<sup>b</sup> X<sup>2</sup> = the difference of -2 log L between the model and the model tested against.

Table 5.31. Comparison of estimates of (co)variance components and genetic parameters for 60-d weaning weight from bivariate analyses , together with litter size in Polypay sheep.

	B-3	B-4	B-5	B-13
$\sigma_a^2$	2.09	2.05	2.13	2.19
$\sigma_m^2$	2.23	2.17	2.24	2.30
$\sigma_{am}$	-1.18	-1.11	-1.21	-1.23
$\sigma_{pem}^2$	3.01	3.00	3.01	2.97
$\sigma_e^2$	13.46	13.49	13.43	13.40
$\sigma_p^2$	19.61	19.59	19.60	19.63
$h^2$	.11	.10	.11	.11
$m^2$	.11	.11	.11	.12
$r_{am}$	-.55	-.53	-.55	-.55
$pe_m^2$	.15	.15	.15	.15
$e^2$	.69	.69	.69	.68

Note: (a). Definitions of parameters are listed in Table 5.4.

(b). Model are described in detail in Table 5.5.

Table 5.32. Comparison of estimates of (co)variance components and genetic parameters for litter size from bivariate analyses, together with 60-d weaning weight in Polypay sheep.

	B-3	B-4	B-5	B-13
$\sigma_a^2$	.0438	.0611	.0452	.0458
$\sigma_{pe}^2$	.0238	-	.0222	.0214
$\sigma_e^2$	.4414	.4499	.4421	.4421
$\sigma_p^2$	.5090	.5111	.5094	.5093
$h^2$	.09	.12	.09	.09
$pe^2$	.05	-	.04	.04
$e^2$	.87	.88	.87	.87

Note: (a).Definitions of parameters are listed in Table 5.4.  
 (b). Model are described in detail in Table 5.5.



Table 5.33. Estimates of covariance components<sup>a</sup> and of corresponding correlations<sup>b</sup> from bivariate analyses of 60-d weaning weight (WW60) and litter size (LS) in Polypay sheep.

	B-3	B-4	B-5	B-13
a <sub>12</sub>	-.044	-.042	-.043	-
a <sub>2m1</sub>	.070	.063	.068	-
e <sub>12</sub>	.218	-	-	-
p <sub>12</sub>	.209	-.010	-.009	-
r <sub>a</sub>	-.15	-.12	-.14	-
r <sub>a2m1</sub>	.23	.17	.21	-
r <sub>e</sub>	.09	-	-	-
r <sub>p</sub>	.07	.00	-	-

<sup>a</sup> a<sub>12</sub> = direct additive covariance between WW60 and LS. a<sub>2m1</sub> = additive genetic cross-covariance between direct effects for LS and maternal effects for WW60. e<sub>12</sub> = residual covariance. p<sub>12</sub> = phenotypic covariance.

<sup>b</sup> r<sub>a</sub> = direct, genetic correlation between WW60 and LS. r<sub>a2m1</sub> = genetic correlation between direct effects for LS and maternal effects on WW60. r<sub>e</sub> = residual correlation. r<sub>p</sub> = phenotypic correlation.

Table 5.34. Likelihood ratio tests for different models of bivariate analyses for 60-d weaning weight and litter size for Polypay sheep.

Model	-2 log L <sup>a</sup>	tests against	X <sup>2</sup> <sup>b</sup>	Probability
B-3	37522.34	B-5	.04	P> .05(df=2)
B-4	37525.94	B-5	3.64	P> .05(df=1)
B-5	37522.30	-	-	-
B-6	37567.09	B-5	44.79	P< .01(df=1)
B-7	37540.19	B-5	17.89	P< .01(df=3)
B-8	37522.41	B-5	.11	P> .05(df=1)
B-9	37523.09	B-5	.79	P> .05(df=1)
B-10	37526.69	B-5	4.39	P< .05(df=1)
B-11	37528.11	B-5	5.81	P> .05(df=2)
B-12	37527.12	B-5	4.82	P> .05(df=2)
B-13	37523.48	B-5	1.18	P> .05(df=2)
B-14	37528.15	B-5	5.85	P> .05(df=3)

<sup>a</sup> Log L = log likelihood.

<sup>b</sup> X<sup>2</sup> = the difference of -2 log L between the model and the model tested against.

Table 5.35. Comparison of Estimates of (co)variance components and genetic parameters for 90-d weaning weight from bivariate analyses, together with litter size in Polypay sheep.

	B-3	B-4	B-5	B-14
$\sigma_a^2$	2.43	.95	1.92	1.35
$\sigma_m^2$	.17	.29	.30	.00
$\sigma_{am}$	-.51	.10	-.53	-
$\sigma_{pem}^2$	4.15	3.99	4.31	4.23
$\sigma_e^2$	13.10	14.01	13.45	13.66
$\sigma_p^2$	19.34	19.35	19.45	19.25
$h^2$	.13	.05	.10	.07
$m^2$	.01	.02	.02	.00
$r_{am}$	-.80	.19	-.69	-
$pe_m^2$	.21	.21	.22	.22
$e^2$	.68	.72	.69	.71

Note: (a).Definitions of parameters are listed in Table 5.4.  
 (b). Model are described in detail in Table 5.5.

Table 5.36. Comparison of Estimates of (co)variance components and genetic parameters for litter size from bivariate analyses, together with 90-d weaning weight in Polypay sheep.

	B-3	B-4	B-5	B-14
$\sigma_a^2$	.0463	.0617	.0500	.0430
$\sigma_{pe}^2$	.0226	-	.0179	.0244
$\sigma_e^2$	.4401	.4512	.4414	.4402
$\sigma_p^2$	.5089	.5230	.5093	.5077
$h^2$	.09	.12	.10	.08
$pe^2$	.04	-	.04	.05
$e^2$	.86	.88	.87	.87

Note: (a). Definitions of parameters are listed in Table 5.4.  
 (b). Models are described in detail in Table 5.5.

Table 5.37. Estimates of covariance components<sup>a</sup> and of corresponding correlations<sup>b</sup> from bivariate analyses of 90-d weaning weight (Trait 1, WW1) and litter size ( Trait 2, LS) in Polypay sheep.

	B-3	B-4	B-5	B-14
a <sub>12</sub>	.149	.000	.029	-
a <sub>2m1</sub>	.016	.131	.081	-
e <sub>12</sub>	1.918	-	-	-
p <sub>12</sub>	2.076	.065	.069	-
r <sub>a</sub>	.44	.00	.09	-
r <sub>a2m1</sub>	.18	.98	.65	-
r <sub>e</sub>	.80	.00	.00	-
r <sub>p</sub>	.66	.02	.02	-

<sup>a</sup> a<sub>12</sub> = direct additive covariance between WW90 and LS. a<sub>2m1</sub> = additive genetic cross-covariance between direct effects for LS and maternal effects for WW90. e<sub>12</sub> = residual covariance. p<sub>12</sub> = phenotypic covariance.

<sup>b</sup>r<sub>a</sub> = direct, genetic correlation between WW90 and LS. r<sub>a2m1</sub> = genetic correlation between direct effects for LS and maternal effects on WW90. r<sub>e</sub> = residual correlation. r<sub>p</sub> = phenotypic correlation.

Table 5.38. Likelihood ratio tests for different models of bivariate analyses for 90-d weaning weight and litter size for Polypay sheep.

Model	-2 log L <sup>a</sup>	tests against	X <sup>2</sup> <sup>b</sup>	Probability
B-3	11561.89	B-5	-1.0	P> .05(df=2)
B-4	11567.51	B-5	4.62	P< .05(df=1)
B-5	11562.89	-	-	-
B-6	1586.25	B-5	23.36	P< .01(df=1)
B-7	1561.73	B-5	-1.16	P> .05(df=3)
B-8	1563.21	B-5	.32	P> .05(df=1)
B-9	1562.96	B-5	.07	P> .05(df=1)
B-10	1562.67	B-5	-.22	P> .05(df=1)
B-11	1563.77	B-5	.88	P> .05(df=2)
B-12	1563.64	B-5	.75	P> .05(df=2)
B-13	1565.09	B-5	2.20	P> .05(df=2)
B-14	1565.44	B-5	2.55	P> .05(df=3)

<sup>a</sup> Log L = log likelihood.

<sup>b</sup> X<sup>2</sup> = the difference of -2 log L between the model and the model tested against.

Table 5.39. Estimates of (co)variance components and genetic parameters (corresponding correlations) from bivariate analyses of 60-120d cumulative postweaning gain together with litter size in Polypay sheep

Model	B-15			B-16		
	PWG	LS	COV	PWG	LS	COV
$\sigma_a^2(\sigma_{a12}^2)$	3.22	.046	-.017	3.22	.046	-.017
$\sigma_{pe}^2(\sigma_{c12}^2)$	-	.021	-	-	.021	-
$\sigma_e^2(\sigma_{e12}^2)$	11.69	.442	2.155	11.69	.442	-
$\sigma_p^2(\sigma_{p12}^2)$	14.91	.510	2.137	14.91	.510	-.017
$h^2(r_g)$	.22	.09	-.05	.22	.09	-.05
$pe^2(r_{c12})$	-	.04	-	-	.04	-
$e^2(r_{e12})$	.78	.87	.95	.78	.87	-
-2logL	17665.84			17665.84		

Note: (a).Definitions of parameters are listed in Table 5.4.

(b).The models are described in detail in Table 5.5.

Table 5.40. Estimates of (co)variance components and genetic parameters (corresponding correlations) from bivariate analyses of grease fleece weight together with litter size in Polypay sheep

Model	B-15			B-16		
	FWT	LS	COV	FWT	LS	COV
$\sigma_a^2(\sigma_{a12})$	.23	.047	.022	.23	.047	.022
$\sigma_{pe}^2(\sigma_{c12})$	-	.022	-	-	.021	-
$\sigma_e^2(\sigma_{e12})$	.30	.441	.282	.30	.442	-
$\sigma_p^2(\sigma_{p12})$	.530	.510	.304	.530	.510	.022
$h^2(r_g)$	.44	.09	.21	.44	.09	.21
$pe^2(r_{c12})$	-	.04	-	-	.04	-
$e^2(r_{e12})$	.56	.87	.78	.56	.87	-
-2logL	4594.73			4594.72		

Note: (a).Definitions of parameters are listed in Table 5.4.  
 (b).The models are described in detail in Table 5.5



## CHAPTER 6

### Summary

Most scientists agree that low heritabilities and repeatabilities and the discrete nature of expression of sheep reproductive traits are major factors limiting a faster rate of genetic improvement. Also, procedures for estimation of genetic parameters and (co)variance components for these discrete traits are more complicated than those required for other traits with normal distributions. There are two kinds of methodologies for genetic analyses of sheep discrete reproductive traits: linear models and nonlinear models. Nonlinear models take the discrete nature of data into account and thus appear to be the more adequate method. However, these models are theoretically more complex and computationally more demanding than linear models. Previous simulation and field data studies comparing the performance of linear and nonlinear models have been unable to reveal advantages of nonlinear models relative to linear models (Matos, 1993; Meijering and Gianola, 1985; King, 1991). Analyses of discrete traits using the nonlinear models in sheep breeding are scarce.

Over the last decade, restricted maximum likelihood (REML) has become the method of choice for (co)variance component estimation in animal breeding. REML has many desirable statistical properties and is especially suitable for genetic analyses of large animal breeding data sets with complex pedigree structures. However, as for other methodologies (ANOVA, Henderson's methods, MINQUE, Bayesian approaches), REML is not free of drawbacks. For example, REML does not always eliminate all biases in parameter estimation because many methods for obtaining REML estimates cannot return negative

estimates of a variance component and few guarantees can be made concerning convergence to global maxima.

This study provides some insights into the applicability of REML in genetic analyses of discrete data in sheep using simulation and field data. In Chapters 3 and 4, two categorical sheep reproductive traits, fertility and litter size in fall-lambing sheep, were chosen to study the threshold theory. Our special interests were estimation of genetic, permanent environmental, and temporary environmental correlations between the two traits on both the underlying normal and the realized categorical scales by derivative-free multitrait REML. This simulation work also provided excellent material for studying the applicability and robustness of the linear methodology in genetic analyses of normally distributed and categorical traits. The results generally supported transformation theory (Gianola, 1979) for converting between heritabilities on the two scales, although the transformation performed less satisfactorily for repeatability models. Genetic correlations between the two categorical traits generally were close to the input value, indicating no need for transformation. On the other hand, permanent and temporary environmental correlations on categorical scales were significantly underestimated; thus some kind of correction is suggested.

In REML, temporary environmental covariances are directly estimated from residual sums of cross-products divided by residual degrees of freedom. Although this covariance is not so important as the genetic one, the relationship between the two could be important. Two additional data sets were simulated to evaluate the effects on genetic covariance estimation of setting the temporary environmental covariance to zero. The results clearly showed that setting the residual covariance to zero reduced the estimates of the genetic correlation between fertility and litter size on both scales. However, the same likelihood was obtained from the simulated data for both situations, indicating that the residual covariance was not sensitive to the assumed parameters.

It is generally believed that the use of mixed models can eliminate bias due to selection by taking into account relationships among animals as well as effects of cumulative selection and nonrandom mating, provided that all information related to the selection is included in the analysis (Henderson, 1975). However, few studies have examined if these properties apply for categorical data. Thus, the repeatability models, with two independent traits or two correlated traits with corresponding input genetic, permanent and temporary environmental correlations of .5, were used to study effects of selection. The conclusion was that REML can provide accurate estimates of (co)variance components for normal data with selection. However, for correlated categorical traits, failure of open ewes to produce a litter size record tended to reduce genetic, permanent environmental, and temporary environmental covariances and correlations. Therefore, other methodologies involving nonlinear approaches should be investigated for covariance estimation in future studies.

In Chapter 5, the genetic analyses were extended to the joint analyses of litter size with one of several continuous growth or fleece traits. The field data were collected from Suffolk, Targhee and Polypay flocks participating in the National Sheep Improvement Program. Summaries of results are shown in Tables 6.1 and 6.2. Heritabilities for various growth traits were slightly smaller than the average values of literature estimates (Fogarty, 1995) and fairly consistent across the breeds. Maternal genetic and maternal permanent environmental effects were important for all body weights except for weaning weight at 90 d for Polypay sheep, indicating that explicitly considering these effects should result in more genetic improvements in growth traits. Heritabilities for litter size were similar for the three breeds and ranged from .09 to .11. Permanent environmental effects for litter size were small and not important. In contrast, the heritabilities for the two fleece traits were high.

In contrast to many previous studies (Al-Shorepy and Notter, 1996; Burfening and Kress, 1993; Maria et al., 1993; Nasholm and Danell, 1996), strong negative genetic correlations between maternal and direct effects for growth traits for the three breeds were not always obtained, indicating that a strong negative correlation is not a universal phenomenon as implied by some scientists. However, distinguishing other effects in the data, such as sire  $\times$  year variation, negative dam-offspring covariance, or environmental effects, from a true genetic antagonism would often be difficult (Robinson, 1996 a,b). There was some evidence indicating that direct genetic variance was often confounded with maternal variance and direct-maternal covariance, so that interpretation of genetic parameters for maternally influenced traits from animal models is critically dependent upon the model(s) fitted to the data (Meyer, 1992; Notter and Hough, 1996).

Generally no genetic antagonisms between direct effects or maternal effects for growth and direct effects for litter size were observed. Most of the estimates for these cross-trait genetic correlations were positive or weakly negative, and thus do not impose serious problems for simultaneous genetic improvement of litter size and growth.

Three issues related to (co)variance estimation and likelihood ratio tests were also investigated. Some scientists have assumed no temporary environmental covariance between growth and litter size because records for the two traits are taken at quite different times: before 1 year of age for most growth traits and after 12 months of age for litter size. Thus, a value of zero was used for the component (Waldron and Thomas, 1992). The effect of this assumption was investigated. Generally, fixing temporary environmental covariance did not affect the converged likelihood and parameter estimates although the corresponding residual correlation (ranging from  $-.24$  to  $.95$ ) was often large. Essentially the same likelihoods were obtained irrespective of setting the covariance to zero or not, indicating that the likelihood ratio test is not sensitive to the component. From a sampling viewpoint, it was

highly unlikely that none of 14 estimates were significantly different from zero. Further studies about effects of data structure, REML methods and the Simplex process are required to account for these high correlation estimates.

Limited evidence from some bivariate analyses (for example, between weaning weights at 60 and 90 days and litter size for Suffolk) suggested that the direct genetic correlation between two traits and the genetic correlation between maternal effects for growth and direct effects for litter size were confounded. However, within-trait direct-maternal genetic correlations usually were not dependent on the other two genetic correlations.

Sampling properties are important criteria to evaluate the applicability of various methodologies in genetic analysis of animal breeding data (Hoeschele and Tier, 1995; Meyer, 1989, 1992; Templeman and Gianola, 1993). A minimum sampling variance and correlation among different parameters are desirable. In the context of REML, the sampling properties are often expressed in term of the likelihood surfaces, and high sampling correlations implies a maximum along a flat ridge, i.e., an area where a constant sum of the two parameters and the value of the likelihood change very little with changes in the parameter values (Meyer, 1989). High sampling correlations between two across-trait genetic correlations, especially between litter size and growth for Polypay, were observed. It seemed that the flat surface for the correlations often occurred when one or both parameters themselves were flat. The methodologies to obtain accurate genetic estimates, and especially accurate genetic covariances and corresponding correlations, in flat ridge conditions would be a major focus in future studies.

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Table 6.1. Genetic parameter<sup>a</sup> estimates obtained from “standard model (B5)’ or B15 for the three breeds

	$h^2$	$m^2$	$pe^2$	$r_{am}$
<u>Suffolk</u>				
WW60	.19	.06*	.11**	-.33
WW90	.13	.04*	.17**	.25
PWG	.17	-	-	-
LS	.09-.10	-	-	-
<u>Targhee</u>				
WW60	.14	.22**	.10**	-.90**
WW120	.16	.06**	.08**	-.10
PWG	.44	-	-	-
YG	.19	-	-	-
FWT	.41	-	-	-
FD	.50	-	-	-
LS	.11	-	.01-.02	-
<u>Polypay</u>				
BW	.19	.09*	.21**	-.36
WW60	.11	.11**	.15**	-.55*
WW90	.10	.02	.22**	-.69
PWG	.22	-	-	-
FWT	.44	-	-	-
LS	.09-.10	-	.04	-

<sup>a</sup>:  $h^2 = \sigma_a^2 / \sigma_p^2$ ;  $m^2 = \sigma_m^2 / \sigma_{pe}^2$ ;  $pe^2 = \sigma_{pe}^2 / \sigma_p^2$ ;  $r_{am}$  = Correlation between direct and maternal additive genetic effects, where,  $\sigma_a^2$ ,  $\sigma_m^2$ ,  $\sigma_{pe}^2$  and  $\sigma_p^2$  are genetic additive, maternal genetic, permanent environmental variance due to dam for growth traits (or due to animal for litter size) and phenotypic variance.

\*:  $P < .05$ .

\*\* :  $P < .01$



Table 6.2. Correlation<sup>a</sup> estimates of growth and fleece traits with litter size

Trait	$r_{a12}$	$r_{a2m1}$
<u>Suffolk</u>		
WW60	.37-.39*	.25-.35
WW90	.43-.51	.98-1.00**
PWG	.16-.17	-
<u>Targhee</u>		
WW60	.10-.22	-.18- -.23
WW120	.27-.48*	-.35- -.36
PWG	.44	-
YG	.08-.09	-
FWT	-.09	-
FD	.29-.30	-
<u>Polypay</u>		
BW	.14-.27	-.13 - -.23
WW60	-.12 - -.15	.17-.23
WW90	.00-.44	.18 - .98
PWG	-.05	-
FWT	.09	-

<sup>a</sup>:  $r_{a12}$  = direct additive genetic correlation of litter size with growth or fleece traits.  $r_{a2m1}$  = genetic correlation between direct effects for litter size and maternal effects for growth traits.

\*: P < .05.  
 \*\*: P < .01.

# Vita

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(signature)\_\_\_\_\_

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