SELECTION TO IMPROVE SPRING FERTILITY IN A CROSSBRED SHEEP POPULATION

by

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(Abstract)

Reproductive and productive performance of a composite sheep population, containing 50% Dorset, 25% Rambouillet and 25% Finnsheep breeding and under selection for ability to lamb in the fall, was evaluated. Traits considered were spring fertility, fall litter size, live weights at birth, weaning, and at about 90 and 120 d of age, and scrotal circumference at weaning and at about 90 and 120 d of age. Fertility was defined as 1 or 0 depending upon whether a ewe lambed or failed to lamb, respectively, in fall. Litter size was defined as the number of lambs born per ewe lambing. A total of 1,102 exposures were used. Fertility averaged .59 for adult ewes (3 years and older), .45 for second-lambing ewes and .11 for yearling ewes (12 months old). Mean litter size averaged 1.89 across seasons and ages. Scrotal circumferences (SC) and body weights (WT) were measured at means of 65, 96 and 128 d. Data were collected on 1878 lambs over 5 years; 63 sires and 420 dams were represented

Genetic parameters were estimated by restricted maximum likelihood (REML) using various animal models. Heritability estimates for spring fertility ranged from .07 to .11. Litter size heritability was .05 for fall lambing and .10 for all lambings. Heritability estimates for weights from birth to 120 d ranged from .04 to .19. Heritabilities for SC ranged from .02 to .25. Estimated genetic correlations among weights were large, and ranged from .77 to unity. The genetic correlations of litter

size with birth weight (BWT), 90-d weight (90WT) and 90-d scrotal circumference (90SC) were .17, .33 and .36, respectively. Genetic correlations of spring fertility with BWT, 90WT and 90SC were .22, -.31 and .29, respectively.

Mixed model methodology was applied to estimate genetic trends for fertility, litter size, BWT, weaning weight (WWT), 90WT and 90SC resulting from selection for fall lambing. Positive genetic gains in both spring fertility and fall litter size were observed. Rate of increase was higher for fertility than litter size, which was due to direct selection for fertility. Selection for spring fertility did not cause significant correlated changes in BWT, WWT, 90WT or 90SC. Thus, no genetic antagonisms resulted from the selection for fall lambing.

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Chapter 1

Introduction

In this chapter, the general motivation of this thesis is presented along with the specific objectives of the study. 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. Factors affecting the genetic evaluation of these components are reviewed in chapter 2. Also, considerable attention is given in chapter 2 to the methods of estimating genetic parameters for reproductive and productive traits and to mixed model procedures to estimate selection response. Variance and covariance component estimation for fertility and litter size is discussed in chapter 3. Chapter 4 includes variance and covariance component estimates for growth traits such as birth, weaning, 90-d and 120-d weights, and testicular measurements in males at weaning, 90-d and 120-d. Genetic and phenotypic correlations between reproductive and productive traits are also discussed in chapter 4. Genetic and environmental trends in spring fertility and fall litter size are discussed in chapter 5, using mixed model approaches. Chapter 6 deals with correlated changes in birth, weaning and 90-d weights, and 90-d scrotal circumference resulting from selection for fall lambing ability.

General Background

The efficiency of lamb production systems may be greatly improved by increasing the lambing frequency. To increase the frequency of lambing, a large proportion of the ewes in a flock must have the ability to lamb throughout the year and maintain high prolificacy in all seasons. The gestation length of the ewe is around 5 months, and within the normal fall breeding season, ewes can rebreed within 1 to 2 months after lambing. Therefore it is theoretically possible for ewes to lamb twice a year. However, the sheep is a seasonal breeder, mating only in the fall and winter months to lamb in spring and early summer. This seasonality of breeding limits the number of lambings that can occur during the year and also places major constraints upon the lamb marketing system. Lambs generally require 4 to 8 months from birth to reach market weight and condition. Thus, lambs from ewes bred during the normal breeding season (August through December) lamb between January and May and reach market weight between May and December. As a result, few lambs are available for the remaining 4 months of the year.

Mating can be induced during the anestrous period by light and (or) exogenous hormone treatment, but these practices require confinement of animals and increased inputs of labor, housing and energy. In contrast, extension of the fertile period by

utilizing between- and within-breed variation in length and timing of the breeding season would provide permanent, cumulative changes in breeding patterns. Thus, improving the genetic potential of the ewe for out-of-season lambing through selection has great potential to improve efficiency of lamb production.

Several studies have reported differences among sheep breeds and crosses in timing and duration of breeding (Dufour, 1974; Nugent et al., 1988; Notter, 1992). Among temperate breeds available in North America, the Dorset, Finnish Landrace and Rambouillet appear to have the greatest potential for use in programs to reduce seasonality of breeding (Hulet et al., 1974; Lax et al., 1979; Clarke et al., 1984; Clarke, 1985). The Dorset, in particular, is considered to have the longest breeding season of temperate breeds (Dufour, 1974; Hall et al., 1986). However, in some studies, the Rambouillet and Finnish Landrace have approached the Dorset in out-of-season breeding performance (Hulet et al., 1974; Bernard and Fahmy, 1974).

Selection for one trait is almost always associated with changes in other traits. The size of these correlated responses depends on the genetic correlation between the two traits, which measures the extent to which the two traits are influenced by the same genes (Falconer, 1989). Once the nature of the genetic associations among traits is known, information from several traits can be combined to maximize rate of genetic improvement in economically important traits. Reproductive traits such as litter size and fertility are difficult to improve because the traits are lowly heritable, expressed in categorical fashion and sex-limited. Consequently it would be helpful to identify continuous traits in the ram that are highly correlated with female reproductive traits. If such traits could be identified, distributional inconsistencies due to analyzing categorical data could be reduced, and overall accuracy of selection would be

improved. These advantages, however, cannot be documented and quantified until accurate estimates of covariance among the traits of interest are available.

A number of publications have suggested the use of testicular size, which can be best described in terms of testes weight, as a trait in the male that can be used as a selection criterion to genetically improve female reproductive performance (Land, 1973, Land and Carr, 1975; Notter et al., 1981; Notter et al., 1985; Purvis et al., 1988; Matos and Thomas, 1992). Testicular size can be easily and accurately assessed in the live ram by measuring the circumference of the testicles in the scrotum with a circular tape (Notter at al., 1985) and is a reliable indicator of testes weight (Notter et al., 1981). Ovulation rate in the female is positively related to testes growth in the male (Land and Carr, 1975), indicating that genes affecting the ovary of the female may also influence the growth of the testis in the male (Land, 1973). Although few studies have attempted to relate measures of testis growth to seasonal breeding, studies by Fossceco (1991) and Fossceco and Notter (1995) have suggested that indirect selection based on male testis size may be a useful supplement to direct selection based on female fertility in spring.

When one wishes to estimate the genetic merit , or breeding value, of an animal using information on several traits and on a number of related animals, the so-called BLUP method of estimation developed by Henderson (1949, 1973) is preferred. BLUP stands for best linear unbiased prediction, which describes the statistical properties of the estimates obtained using the procedure. The real merit of the BLUP procedure is that it is more powerful than the traditional methods of prediction such as the selection index. For example, the BLUP method can be used to provide directly by comparable estimates of the average breeding values of groups of animals born in different years, thus providing information for estimating of response to selection.

Moreover, BLUP can account for complications such as non-random mating, sires that come from more than one distinct group or population, environmental trends over time, flock differences in the average breeding value of dams, and bias due to selection and culling.

The computation of BLUP is based on a computing algorithm known as the mixed model equations (MME) (Henderson, 1973). In relatively small planned experiments, MME allow use of highly descriptive models in which all information available is used to obtain estimates of genetic parameters and subsequent breeding value predictions as well as response to selection. The most descriptive of these models is the Animal Model in which breeding values are predicted for all animal in the population. The primary advantage of the animal model is the inclusion of all relationships among the animals in the flocks. Thus, the performance of every animal is incorporated into the evaluation and contributes to the breeding value predictions of all relatives of that animal.

The prediction of breeding values, which provides a basis for selecting breeding animals, requires knowledge about the genetic parameters of the population. In particular the estimation of variance components, which describe the extent to which the observed variation in measured characteristics in the flock is attributable to genetic causes, is required prior to breeding value prediction. Historically, the estimation of variance components and the prediction of breeding values, are two main areas of analysis of interest to animal breeders. A variety of methods to estimate variance components exists. In many cases, different methods produce essentially equivalent results, but in other cases this is not true. Thus, when estimating variance components, the method used may be important. Among available methods, restricted

maximum likelihood (REML) (Meyer, 1989) has become the method of choice in animal breeding applications for variance and covariance component estimation.

A particular complication unique to studies such as this one is that many female reproductive traits such as fertility and , rebreeding success rate are expressed in a binomial, all-or-none fashion rather than as continuous variables that can assume a range of values and that can usually be assumed to follow a normal distribution. Most analyses of characters of this sort have been done using methodology developed for continuous data (Gianola, 1980; 1982), and they ignore the discrete nature of categorical data. Among different procedures to estimate variance components for these traits, Maximum Likelihood (ML) and REML are popular methods due to their desirable statistical properties such as non-negativity and asymptotic normality (Banks et al., 1985; Searle, 1989; Meyer, 1989). Some methodology for breeding value prediction for threshold characters exists (Foulley et al., 1990) but additional research is required to implement these methods.

Selection for growth has been one of the most popular selection practices in sheep, though it is not necessarily advantageous (Bradford and Meyer, 1986). The weight most frequently used as selection criteria are those which can be measured early in the animal's life, such as birth, weaning and 120-d weights.

In addition to heritability estimates for growth traits, it is important to know the relationship among growth traits and between growth and reproductive traits. In this respect the estimation of genetic and phenotypic correlations between such traits should be considered.

Objectives of this study:

Therefore, the objectives of this study are:

(i). to estimate genetic parameters (variance components and genetic correlations) for reproductive and growth traits in a composite sheep population containing 50% Dorset, 25% Rambouillet and 25% Finnsheep bred outside the normal breeding season. Emphasis will be placed on female fertility traits, male testis measurements, and animal growth.

(ii). to evaluate the genetic and environmental trends for reproductive performance (spring fertility and fall litter size) resulting from selection for fall lambing ability, and

(iii). to evaluate correlated changes in birth, weaning and 90-d weights and 90-d scrotal circumference, resulting from the selection for fall lambing ability.

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Chapter 2

Literature Review

Genetic effects on growth and reproduction

Improving the level of expression of economic traits in sheep through selection requires the effective use of genetic variation. Pertinent to the effective use of this genetic variation is an expression of its magnitude that can be described by the heritability of characters. Also, knowledge of genetic and phenotypic correlations among various traits is important in maximizing the genetic gain in a relatively short periods of time. For these reasons, knowledge of heritabilities as well as genetic correlations and of the factors that affect their estimation is important in determining how selection may be practiced for several traits simultaneously.

Growth traits

Selection for growth has been common in sheep, though it is not always advantageous (Bradford and Meyer, 1986). The weight most frequently used as selection criteria are those which can be measured early in the animal's life, such as

birth, weaning and four-month weights. The interest in different weights is simply in choosing the most adequate 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 post weaning weight and its high genetic correlation with the direct component of weaning weight. Bradford (1985) suggested that a weight collected by early months of age should be adequate for use in selecting for the direct component of weaning weight in sheep.

Heritability estimates in the literature for birth weight ranges from .07 to .47 (Butcher et al., 1964; Bradford et al., 1989; Bennett et al., 1991). It is well known that in monotocous species, emphasis on birth weight results in birthing difficulties or dystocia; however, the prevalence of multiple births in some sheep populations lowers the occurrence of dystocia. Thus, selection to increase birth weight should be considered whenever selection for prolificacy is practiced to achieve better survival rate of multiple born lambs.

A wide range of heritability estimates for weaning and postweaning weight is reported in the literature. Bennett et al. (1991) reported a value of .28 $\pm$ .11 for weaning weight. Martin et al. (1980) reported estimates of heritability for postweaning weight in a synthetic line of sheep at 12 and 16 weeks of age of .23 $\pm$ .09. Mavrogenis et al. (1980) reported relatively high heritability estimates for body weight at 10, 15 and 20 weeks of age of .63, .73 and .66, respectively.

In addition to heritability, it is important to know the relationship among growth traits. In this respect, estimates of the genetic and phenotypic correlations between such traits are needed. In general, the genetic correlation between birth and weaning weights is usually high (Martin et al., 1980). However, several studies

reported low correlations involving birth and weaning weights (Atkins, 1986; Bennett et al., 1991). A general conclusion is that the genetic correlation between weights at more closely adjacent ages are high which indicates that selection for one weight will definitely result in considerable positive change in the following or preceding weights.

Reproductive traits

It is generally accepted that reproductive traits have low heritability and repeatability. 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 and the mean was .10. Heritability estimates for fertility ranged from 0 to .11 (Table 1).

Theoretically, repeatability should set the upper limit of heritability, assuming that the traits being considered at different times are genetically identical (Falconer, 1989). Using multiple records on dams is one common way to improve the accuracy of the estimated breeding values. This improved accuracy can subsequently result in higher response to selection, but will likely also increase generation interval. The earlier lambing records of ewes commonly have lower repeatability than those of later parities (Atkins, 1986) and the heritability may also be lower (Young et al., 1963). Results for the latter assumption are not consistent, which may be due to the effects of breeds and environmental factors. Based on a general survey of the published literature, some heritability and repeatability estimates are presented in Table 1.

Genetic correlations among reproductive traits and between reproductive traits and productive traits are important in planning a selection program to improve total sheep performance. Shelton and Menzies (1968) reported genetic correlations of .03 and .18 between the number of lambs born and weaning and yearling weight,

respectively. Fogarty et al. (1985) reported a genetic correlation of .70 ±.18 between fertility and number of lambs per ewe mated and .03±.02 between fertility and litter size born.

Environmental influences

Reproductive performance can be affected by age of ewe, type of birth and rearing and season. Likewise, growth of lambs is dependent upon their age, sex, season of birth, type of birth and rearing and the age of their dams. Accounting for such environmental factors will better allow the genetically superior animals to be recognized.

Ewe traits

Age of Ewe. In analyzing the fertility of Rambouillet, Columbia, Suffolk and North County Cheviot ewes, Vesely and Peters (1974) observed that only 50% of one year old ewes that were exposed to rams conceived. They also found that prolificacy was lowest for the yearling ewes and highest for the ewes of 3 to 6 years of age. Dickerson and Glimp (1975) reported that fertility in nine different ewe breeds (Suffolk, Dorset, Targhee, Hampshire, Rambouillet, Coarse Wool, Navajo, Fine Wool and Correidale) changed curvilinearly with age at lambing, ranging from 45 to 75% at 1 year, 85 to 95% at 4 to 6 years and 60 to 80% at 9 years. Also, number of lambs per lambing increased curvilinearly with age of ewe from 1.05 at 1 year to 1.6 at 6 years and back to 135% at 9 years of age. According to Martin at al. (1980), reproductive traits in a synthetic line of sheep were influenced ($P<.01$) by age of ewe. Fertility increased with age from 78% for 1-year-old dams to 89% for 2-and 3-year-

old dams. Similarly, Notter and Copenhaver (1980) reported that conception rates among ewes 3 years old or older increased with age until ewes were 5 to 6 years old. However, McLaughlin (1970) found that age of Merino ewes had no effect on reproductive performance. He suggested that relationships between ewe age and fertility or fecundity might be explained by changes in ewe live weight as age increased.

Season. Notter and Copenhaver (1980) evaluated the reproductive performance of 1/2-Finnsheep, 1/2-Rambouillet ewes; 1/4-Finnsheep, 3/4-Rambouillet ewes; and 1/2-Suffolk, 1/2-Rambouillet ewes when all ewes were given the chance to lamb three times every 2 years. Ewes were bred in August, November and April. Overall conception rates were 90% for August, 70% for November and 53% for April matings. Also, they reported a .62 lamb decline in prolificacy between April and September. Dzakuma et al. (1982) reported conception rate of 47 %, 91% and 90% for breeding in late spring (May-June), winter (January-February) and fall (September-October), respectively.

Type of birth and rearing. It has been a matter of controversy whether twin born ewes will be more productive than single born ewes. In management system where multiple births are desired, it is important to know how multiple-born ewes perform in comparison with single-born ewes. In a study of life time production in Targhee and Columbia sheep, Basuthakur et al. (1973) reported that ewe type of birth significantly ($p < .05$) affected the number of lambs born during the ewe's lifetime. Ewes born as a single tended to produce fewer lambs in their life-time than did ewes born as twins. Dunn and Grewall (1963) concluded that twin-born ewes were superior in productivity to singles due to their higher fertility. In addition, Vakil et al. (1968) indicated that ewes and rams born as twins tended to produce more lambs than those

born as singles. In contrast, Saoud and Hohenboken (1984) reported that over five parities single-born ewes, were more efficient than twin-born ewes. The best way to study ewe type of birth and rearing would be to analyze these effects within parities and study the significance of these effects for each parity.

Lamb Growth.

Age of the dam. Lambs born out of very young ewes are handicapped. In fact, the age of dam seems to affect the growth of the lamb in a curvilinear fashion. Several researchers have described the effect of age of ewe on lamb weight. Under station conditions, Subandriyo et al. (1985) observed that the peak birth weight of lambs from Javanese ewes occurred at 40 months of age. In the same study, no significant influence was found on weaning weight (90 days). Nawaz and Meyer (1992) studying growth performance of Polypay, Coopworth and crossbred lambs, concluded that the effect of ewe age on birth weight was curvilinear as previously described by Dickerson et al. (1975) and Lewis and Burfening (1988). In contrast, Olthoff and Boylan (1991) found that age of ewe did not affect ($P < .05$) birth weight of purebred Finnsheep, Suffolk, Targhee and Dorset lambs. Also, Mavrogenis (1982) found no significant influence of age of ewe on birth weight.

Martin et al. (1980) reported that weaning weight of lambs from 3-year-old ewes exceeded those of 2-years-old ewes by 2.5 kg. The effect of ewe age on weaning weight of her lamb is mainly due to milk production. It is generally accepted that the maximum milk yield is attained in the third to the sixth lactation, which is in agreement with the most typical effect of age of dam on weaning weight.

Notter et al. (1975) found that age of ewe effects for 90-d lamb weight were significant ($P < .05$). Lamb weight was heaviest for ewes between 3 and 6 years of

age among the breeds considered. Wright et al. (1975) found no significant influence of age of dam on 4-month weight, or on rate of gain from birth to 4 months.

Type of Birth and Rearing. In general, it has been shown that single-born lambs are heavier than twin-born lambs at birth (i.e. Sidwell, 1956; Bennett et al., 1991) and at weaning (Sidwell et al. 1970; Dickerson and Laster, 1975). For example, Eikje (1975) observed that lambs born and reared as singles were 9.8 kg heavier at weaning (160 days) than those born and reared as triplets. It is a common observation however, that ewes suckling multiples tend to produce more milk than ewes with singles. In reviews of 24 estimates in the literature dealing with the relationship between milk yield and the number of lamb suckled, Treacher (1978) reported an increase of about 40% in favor of ewes suckling twins as compared to ewes suckling singles. Notter at al. (1975) reported that both type of birth and type of rearing had significant effects on 90 d lamb weight.

Sex of lamb. Sex has long been identified as a source of variation in the growth of domesticated animals. Usually males lambs are heavier than female lambs at birth, weaning and postweaning (Dickerson et al., 1972; Nawaz and Meyer, 1992). Rams and wethers have been reported to be about 11% and 3% heavier, respectively, than ewes at 90 days (Thrift and Whiteman, 1969; Notter et al., 1975).

Variance Component Estimation

A variety of methods exists to estimate variance components. In many cases different methods produce essentially equivalent results but in other cases, this is not true. Thus, when variance components are used to estimate heritabilities, the method used to estimate the variance components may be important. Common methods for variance component estimation include analysis of variance (ANOVA), which

encompasses Henderson's Method 1, 2 and 3 (Searle, 1989), minimum-norm-quadratic unbiased estimation (MINQUE) (i.e., Khuri and Sahai, 1985; Searle, 1989), maximum likelihood estimation (ML) (Harville, 1977, Khuri and Sahai, 1985) and restricted maximum likelihood estimation (REML) (Harville, 1977; Khuri and Sahai, 1985; Meyer, 1989).

Among these methods, REML is the current method of choice in animal breeding applications for estimation of variance and covariance components as well as for genetic parameter estimation. REML is marginally sufficient, consistent, efficient and asymptotically normal (Harville, 1977). Thus, all information available is utilized in an optimal way. REML requires that the likelihood function be partitioned into two parts including one which is free of fixed effects (Khuri and Sahai, 1985; Meyer, 1989). The values obtained when the partition which is free of fixed effects is maximized, are the REML variance components estimates. Conceptually, this value is achieved by replacing the data by linear functions known as error contrast which have an expectation of zero.

Consider a mixed linear model for one trait, represented by

$$\mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}\mathbf{u} + \mathbf{e},$$

with **y**, **b**, **u**, and **e** representing the vectors of observations, fixed effects, random effects and residual errors, respectively, and **x** and **z** the corresponding design matrices. Assume that $E(y) = \mathbf{X}\boldsymbol{\beta}$; $E(\mathbf{u}) = E(\mathbf{e}) = 0$; $V(\mathbf{u}) = \mathbf{G} = \mathbf{A}\sigma^2 a$, where **A** is the so-called numerator relationship matrix; $V(e) = R = I\sigma^2 e$, and cov $(u,e')=0$; then:

$V(y) = ZGZ' + R = ZAZ'\sigma^2 a + I\sigma^2 e$, and the mixed model equations (MME) are :

$$\begin{bmatrix} X'R^{-1}X & X'R^{-1}Z \\ Z'R^{-1}X & Z'R^{-1}Z \end{bmatrix} \begin{bmatrix} \beta \\ \hat{u} \end{bmatrix} = \begin{bmatrix} X'R^{-1}Y \\ Z'R^{-1}Y \end{bmatrix}$$

Variance components estimates from REML are functions of only u, which suggests estimating $\sigma^2 u$ and $\sigma^2 e$ from a function of the data (y), say K′y with K′xβ = 0. K′ is a matrix whose rows correspond to different error contrasts and there are at most n-p linearly independent error contrasts.

The method of likelihood is then applied to K′y , or equivalently to **K′(zu + e)**. For y ~(**xβ** , V), the log likelihood for the mixed linear model given above is (Harville, 1977);

$$\text{Log L} = -1/2(\text{const} + \log |V| + \log |\mathbf{x}^{*\prime} V \mathbf{x}^{*}| + (y-\mathbf{x}\beta)' V^{-1}(y-\mathbf{x}\beta),$$

where $\mathbf{x}^*$ is a full rank submatrix of **x** and β is BLUE(b).

Recently, an algorithm proposed by Smith and Graser (1986) used a derivative-free approach to evaluate the likelihood function (L) and to locate the maximum without inversion of the mixed model equations coefficient matrix. This derivative-free method is used in several programs called derivative-free restricted maximum likelihood (DFREML) that obtain REML estimates in an animal model (Meyer, 1988 and 1989; Boldman et al., 1993). These programs allow models with several random effects as well as several covariances.

REML was used to estimate variance components for a variety of traits by different authors (Wright et al., 1987; Foster et al., 1988; Harris, 1989; VanVleck et al., 1991; Waldron and Thomas, 1992, Maria et al., 1993; Tosh and Kemp, 1994). Foster et al. (1988) used REML on linear type traits of Holstein dairy cattle. Weaning weight of American Simmental cattle was the focus of Wright et al. (1987). Harris (1989) used REML to estimate heritability for survival rate of beef cattle. The

heritability estimates were on the binary scale and then were transformed to the underlying normal scale (Falconer, 1989). Waldron and Thomas (1992) used REML in sheep data to estimate heritabilities and genetic correlations among litter size, ovulation rate, scrotal circumference and body weight. Maria et al. (1993) and Tosh and Kemp (1994) used REML to estimate variance components for growth traits of sheep using animal models.

Categorical Data

ML and REML are popular methods for estimating variance components in categorical data due to their desirable statistical properties such as non-negativity and asymptotic normality (Harville, 1977; Banks et al., 1985). Both ML and REML were derived under normality conditions and require that the random part of the model, such as genetic factors and residuals, and phenotypes follow a normal distribution. Categorical traits in which the class frequencies differ greatly may cause the distribution to be skewed. Banks et al. (1985) conducted a simulation study using a one-way random model to examine the robustness of REML when applied to skewed data involving categorical traits. Observations were classified in two through six classes with separate analyses being performed on each set of classes. The responses were coded as 0 or 1 for the case of two classes. The responses were coded similarly for the other classes. The binomially distributed case had the greatest deviation of estimated variances from the true parameters. The mean estimate asymptotically approached the true parameter as the number of classes increased. Increasing the number of classes did not increase the accuracy of heritability estimates if one class had a high frequency of observations.

REML was used to estimate variance components for categorical traits by several authors (i.e., Harris, 1989; Van Vleck et al., 1991; Waldron and Thomas, 1992). Van Vleck et al. (1991) used REML to estimate heritability of ovulation rate and twinning rate as well as the genetic correlation between them in beef cattle. Litter size and ovulation rate of a flock in Rambouillet sheep was the focus of Waldron and Thomas (1992).

Theory of all-or-none Traits

Many traits of biological interest and/or economic importance vary in a discontinuous manner but are not inherited in a simple Mandelian manner. However, the inheritance of these traits when subjected to genetic analysis has been found to be analogous to that of continuous traits. According to Matos (1993), there are two main groups of procedures for analysis of discontinuous data in statistical genetics: methods analyzing the discontinuous data ignoring their categorical nature, in which the analysis proceeds using linear methodology as if the data were continuous, and methods analyzing the data on the hypothetical continuous scale by invoking the threshold concept (Wright, 1934; Falconer, 1965), which assumes an underlying, non-observable normal distribution for the discrete variate.

Threshold Concept

The concept of thresholds was originally introduced by Wright (1934). Falconer (1965) described the inheritance of threshold traits.

The threshold concept for binomial traits is based on the assumption that the phenotypic expression of the trait is associated with a continuous underlying variate which is not observed. This underlying variate has been labeled the 'liability' (Falconer,

1965), emphasizing that it is influenced by many genetic and environmental factors which modify the manifestation of the character.

Figure 1 illustrates the concept of a threshold in a single population. On the visible scale, an individual falls into one of two discrete classes, for example a ewe conceives and is scored as 1 or does not conceive and is scored as 0. At the population level, a population may exhibit a certain frequency of ewes that conceive equal to p and of ewe that do not conceive equal to 1-p as illustrated in part (a) in figure 1. Part (b) shows the fixed threshold (τ) and the unobservable liability mean (η). The liability is assumed to be the sum of a normally distributed genetic component and an independent, normally distributed environmental components. If the liability is assumed to be being normally distributed, the unit of liability is its standard deviation and standardized liability values can be obtained by subtracting the mean from the threshold.

$$\mu = (\tau - \eta)/\sigma$$

where σ is the phenotypic standard deviation of the liability, and τ. gives the point in the underlying scale at which there are probability masses equal to 1-ω to the right of threshold and ω to the left of the threshold (Gianola, 1982).

Linear approaches

Linear procedures can be used for analysis of discontinuous data, although they ignore the discrete nature of discontinuous data. If the analysis of discontinuous data is carried out on the discontinuous scale, parameters are estimated from categorical data directly, hence without referring to an underlying continuous distribution. Early estimates of heritability from binary data based on the analysis of variance were presented by Lush et al. (1948) and Robertson and Lerner (1949). They suggested that heritability of a trait be measured in terms of its probability of expression, with

values of 1 and 0 assigned to each individual that expresses or fails to express the trait, respectively. This binomial phenotypic expression has been defined as the p scale by Dempster and Lerner (1950). The use of the p scale might, however, introduce three basic problems in evaluation of all-or-non traits (Dempster and Lerner, 1950). The first of these is that considerable measurement error 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. Second, 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. Finally, 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.

The relationship between the heritability on the underlying liability scale (h^2_N) and on the p scale (h^2_B) was used by Lush et al. (1948) and proved by Robertson (in an appendix to Dempster and Lerner, 1950). This relationship, repeated below, assumes a normal distribution for the underlying scale.

$$h_B^2 = {z^2 h_N^2}/{p(1-p)} \text{ and}$$

$$h_N^2 = {h_B^2 p(p-1)}/{z^2}$$

where p is the fraction of individuals that express the character and z is the height of the ordinate at the point which truncates area **p** of the normal curve. The accuracy of this relationship between heritabilities on the p and underlying scale was studied

empirically by Van Vleck (1972). He concluded that "heritability on the normal scale generally will be slightly over-estimated by multiplying the estimate from the paternal half-sibs correlation from binomial data by $p(1-p) / z^2$ but may be over-estimated substantially if the estimate from parent offspring correlation is similarly reduced 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".

A large number of papers has been published, for instance, Pollak and Freeman, (1976), Schaeffer and Wilson (1977), Harris, (1989), Van Vleck et al. (1991), and Waldron and Thomas (1992), in which the estimation of variance components was carried out for categorical data as if the data were continuous by ignoring their heterogeneous variance structure and by applying the usual assumptions, $\mathbf{G} = \mathbf{A}\sigma^2_u$ and $\mathbf{R} = \mathbf{I}\sigma^2_e$ for genetic and residual variances.

Several problems were listed by Gianola (1980, 1982) in the use of linear models to perform genetic evaluation of categorical traits. The problems include: 1) the arbitrary assignment of scores to the response categories, 2) the dependence of the additive genetic variance in the observed scale on the mean incidence of the character in the subpopulation considered in the model, 3) the failure to incorporate restrictions on the estimation space so that the sum of the response probabilities will equal 1, and 4) the failure of linear relationships outside the range of the data, and 5)the lack of ranking optimality of best linear predictors when the conditional expectation of the predictand given the data in not linear.

Mixed model methods in analyses of selection response

The main reason for initiating selection program is to improve productivity of certain traits. Therefore, it is important to evaluate the genetic response in such

selection experiments. Prediction of response can be obtained using the following equation (Falconer, 1989),

$$\textbf{Response} = \mathbf{ih^2\sigma p},$$

where i = intensity of selection, h^2 = is the heritability of the trait and σp = phenotypic standard deviation. Although this equation is very simple computationally and it is operationally useful in describing the response to selection, it overestimates response because the following factors are not accounted for: 1) reduction of genetic variability from directional selection and inbreeding, 2) lag in initial response when generations overlap (Belonsky and Kennedy, 1984) and 3) reduction of selection intensity because of family structure (Hill, 1971).

The method most commonly used in the analyses of designed experiments is that of least-squares. Least-squares estimators provide unbiased estimates of response to selection under simple designs (Sorensen and Kennedy, 1984; Blair and Pollak, 1984). However, when the data are highly unbalanced and involve overlapping generations, least-squares estimators may not be unbiased (Blair and Pollak, 1984). .

An alternative way of estimating response to selection is to use a mixed model approach. Mixed model methodology using animal models is being used to measure selection response in farm animals (Blair and Pollak, 1984; Van Vleck et al., 1986; Parnell et al., 1986; Estany et al., 1989; Cantet et al., 1989; Southwood and Kennedy, 1991; Bhuiyan and Curran, 1993). Mixed model methods, under certain conditions, yields best linear unbiased estimators (BLUE) of fixed effects and best linear unbiased predictors (BLUP) of random effects (Sorensen and Kennedy, 1986; Henderson, 1975; Kennedy, 1988). In addition, this method accounts for the effects of selection as well as nonrandom mating if all the information related to selection is included in the analysis (Kennedy, 1988).

Belonsky and Kennedy (1988) used computer simulation of a closed 100-sow and 4-boar swine herd to compare expected response to selection based on mixed model genetic evaluations using an animal model with the more traditional practice of selection based on the individual's phenotype performance. The animals were selected over a 10-year period for a single trait with heritabilities of .10, .30 or .60. Additionally, two forms of culling existing breeding animals were considered. In the first, an animal was removed from the breeding herd only because of age or reproductive failure. In the second, removal of a breeding animal also occurred any time a potential replacement with a better estimated genetic value was available. That is, genetic culling was practiced. They found that differences in estimated selection response were considerable, particularly when heritability was low (h^2=.10). BLUP selection gave 80% and 55% greater expected response than phenotypic selection with and without genetic culling, respectively. In this simulation, the trait considered was measured in both sexes. For traits measured only in females, such as fertility, differences in response between selection on phenotypic performance and BLUP of additive genetic merit would be expected to be even greater (Kennedy, 1988). Kennedy comments that given the nature of reproductive traits, information from relatives, obtained over repeated cycles of selection with overlapping generations will be of most importance, and the only method to make maximum use of the data is mixed model methodology.

Blair and Pollak (1984) and Sorensen and Kennedy (1984) examined the properties of estimators of response to selection in animal experiments based on least squares procedures and on mixed model methodology. Blair and Pollak (1984) examined the behavior of different estimators of selection response in sheep data, and Sorensen and Kennedy (1984) studied properties of mixed model estimators of

selection response through computer simulation. Both studies concluded that mixed model methods can offer advantages over least-squares techniques.

To illustrate the use of mixed models to estimate response to selection, consider the additive genetic model:

$$\mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}\mathbf{a} + \mathbf{e},$$

where, $\mathbf{a} \sim (\mathbf{0}, \mathbf{A}\sigma^2\mathbf{a})$ is the vector of additive genetic values of animals in the population, β is the vector of fixed effects and $\mathbf{e} \sim (\mathbf{0}, \mathbf{I}\sigma^2\mathbf{e})$ is the vector of random environment effects. The vector $\boldsymbol{\beta}$ and $\mathbf{a}$ are estimated by:

$$\begin{bmatrix} \beta \\ \hat{a} \end{bmatrix} = \begin{bmatrix} X'X & X'X \\ Z'X & Z'Z + A^{-1}\lambda \end{bmatrix}^{-} \begin{bmatrix} X'Y \\ Z'Y \end{bmatrix}$$

$$= \begin{bmatrix} C_{00} & C_{01} \\ C_{10} & C_{11} \end{bmatrix} \qquad \begin{bmatrix} X'Y \\ Z'Y \end{bmatrix}$$

where $\lambda = \sigma^2_{\mathbf{e}} / \sigma^2_{\mathbf{a}} = (1-h^2)/ h^2$, and A is the matrix of additive relationships.

Under the above model, the mixed model estimator of the genetic mean of generation t is simply the average estimated genetic value of all individuals in generation **t**, i.e., $\mathbf{g_t} = \mathbf{k'_t A}$, where **A** is estimated from the above model. Henderson (1975) showed that if certain conditions hold, i.e., if the model is correct and heritability in the base population is known, then $\mathbf{g_t}$ is an unbiased estimate of the genetic mean. The variance of $\mathbf{g_t}$ is

$$\mathbf{V}\,(\,\mathbf{k`_t\,A}\,) = \{\,\mathbf{A_t h^2 - c_t(1-h^2)}\}\sigma^2,$$

where $\mathbf{A_t}$ is the average additive relationship among the individuals of generation **t**, $\mathbf{c_t}$ is the average element of the prediction error variance matrix of generation **t**, and $\mathbf{h^2}$ and σ^2 are heritability and the phenotypic variance in the base population (Sorensen and Kennedy ,1984).

As mentioned earlier, the mixed model approach resides on the assumptions that initial $\mathbf{h^2}$ in known and the model is described correctly. Questions arise as to the consequences of errors in these assumptions. What can be done if the heritability in base population is not known? Kennedy (1988) listed two approaches that can be followed: one is to use a prior based on information from the literature, the other is to obtain an estimate from the data. With respect to the second approach, he further suggested to either use MIVQUE or REML to obtain an estimate of the base population $\mathbf{h^2}$. Sorensen and Kennedy (1986) examined this approach and found that it leads to unbiased estimates of $\mathbf{g_t}$, if the model is correct.

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Table 2.1. Heritability (h^2) and repeatability (t) estimates of fertility (FERT) and litter size(LS).

Breed	Trait	h^2	t	reference
Rambouillet	FERT	.07±.09	.09	Shelton and Menzies (1970)
Crossbred	FERT	.02±.04	.15±.03	Clarke and Hohenboken (1983)
Crossbred	FERT	.06±.02	.06±.09	Fogarty et al. (1985)
Merino	FERT	.11±.05	.17±.01	Davis and Kinghorn (1986)
Scot. Blackface	FERT	.01±.03	.10±.01	Atkins (1986)
Texel	FERT	.03±.07		Sharafeldin (1960)
Rambouillet	FERT	.03±.043	.03±.035	Bunge et al. (1990)
Rasa Aragonesa	FERT	.00		Gabina (1989)
Lacaune	FERT	.04±.06		Bodin et al. (1988)
Rambouillet	FERT	.03±.043	.03±.035	Bunge et al. (1990)
Crossbred	FERT	.09±.12		Fossceco and Notter (1995)
Rambouillet	LS	.10±.11	.15	Shelton and Menzies (1970)
Crossbred	LS	.12+.06	.19±.05	Clarke and Hohenboken (1983)
Merino	LS	.19±.08	.18±.01	Davis and Kinghorn (1986)
Scot. Blackface	LS	.12±.04	.22±.02	Atkins (1986)
Crossbred	LS	.14±.04	.08±.02	Fogarty et al. (1985)
Rasa Aragonesa	LS	.12		Gabina (1989)
Columbia	LS	.35*	.17±.04	Abdulkhaliq et al. (1989)
-Suffolk	LS	.18*	.09±.04	Abdulkhaliq et al. (1989)
Targhee	LS	.23*	.12±.04	Abdulkhaliq et al. (1989)
Galway	LS	.18	.20±.04	More O'Ferrall (1976)

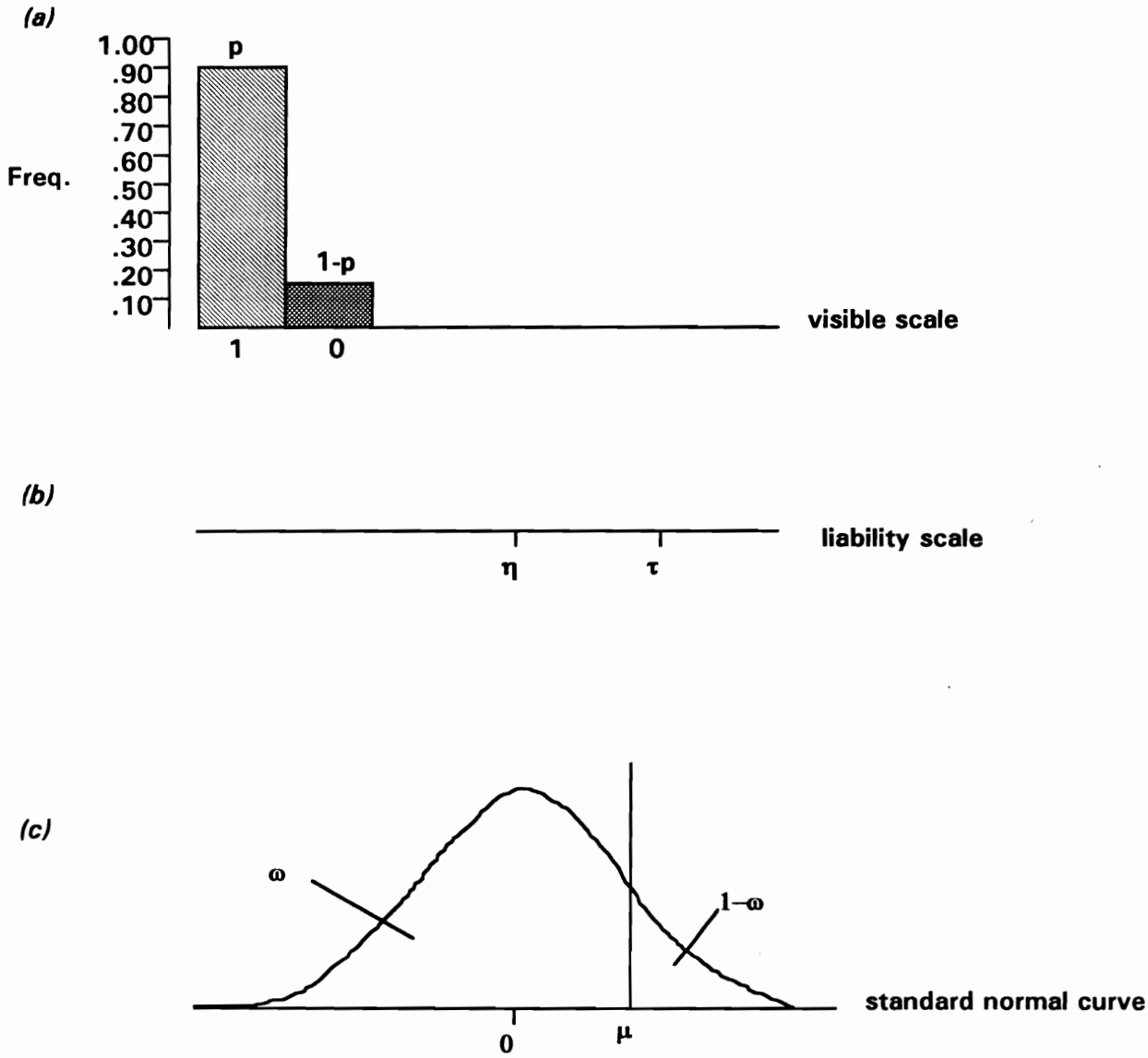

Figure 2.1: Threshold concept illustration

Chapter 3

Estimation of Genetic Parameters for Fertility and Litter Size in Crossbred Sheep Bred Outside the Normal Breeding Season.

Summary

Spring fertility and litter size were evaluated in a composite population containing 50% Dorset, 25% Rambouillet and 25% Finnsheep breeding and under selection for ability to lamb in fall. Three lines were formed: selected (S), environmental control (EC) and genetic control (GC). Fertility was defined as 1 or 0 depending upon whether a ewe lambed or failed to lamb, respectively, in fall. Litter size (LS) was defined as the number of lambs born per ewe lambing. Ewes in the S and EC lines were exposed to rams for 60 d beginning May 1 and were reexposed to rams for 30 d beginning August 1. Ewes bred in August lambed in January (winter lambing) and returned to the spring-bred flock the following May. The GC ewes were bred once per annum for 42 d beginning October 1. Replacements ewes for the EC flock came from the GC flock. First lambing therefore occurred at 12 months and 19 months of age in S and EC flocks, respectively. Records on 1,102 ewe exposures between 1988 and 1994 were used. Fertility averaged .59 for adult ewes (3 years and

older), .45 for second-lambing ewes and .11 for yearling ewes (12 months old at lambing) in the S flock. Mean litter size was 1.75 for fall lambing, 2.17 for spring lambing and 1.77 for winter lambing and averaged 1.89 across seasons and ages. Several mixed models were fitted to the data and restricted maximum likelihood (REML) estimates of heritabilities and genetic correlations were obtained. Heritability estimates for fertility varied among models but ranged only from .07 to .11 with an average of .09. Litter size heritability was .10 for fall lambing and .05 for a combination of fall, winter and spring lambings. The genetic correlation between spring fertility and fall litter size was .56.
Key words: Spring Fertility, Litter Size, REML, Heritability.

Introduction

The efficiency of lamb production systems could be greatly improved by increasing the lambing frequency. To increase the frequency of lambing, a large proportion of the ewes in a flock must have the ability to lamb throughout the year and maintain high prolificacy in all seasons. The gestation length of the ewe is around 5 months, and, within the normal fall breeding season, ewes can rebreed within 1 to 2 months after lambing, so it is theoretically possible for ewes to lamb twice a year. However, the sheep is a seasonal breeder, mating only in the fall and winter months to lamb in spring and early summer. This seasonality of breeding limits the number of lambing that can occur during the year and also places major constraints upon the lamb marketing system. Lambs generally require 4 to 8 months from birth to reach market weight and condition. Thus, lambs from ewes bred during normal breeding season (August through December) lamb between January and May and reach marketing

weight between May and December. As a result, few lambs are available in the market for the remaining 4 months of the year.

Mating can be induced during the anestrous period by light and (or) exogenous hormone treatment, but these practices require confinement of animals and increased inputs of labor, housing and energy. In contrast, extension of the fertile period by utilizing between- and within-breed variation in length and timing of the breeding season would provide permanent, cummulative changes in breeding patterns. Thus, improving the genetic potential of the ewe for out-of-season lambing through selection has great potential to improve efficiency of lamb production.

Several studies have reported differences among sheep breeds and crosses in timing and duration of breeding (Dufour, 1974; Nugent et al., 1988; Notter, 1992). Among temperate breeds available in North America, the Dorset, Finnish Landrace and Rambouillet appear to have the greatest potential for use in programs to reduce seasonality of breeding (Hulet et al., 1974; Lax et al., 1979; Clarke et al., 1984). The Dorset, in particular, is considered to have the longest breeding season of temperate breeds (Dufour, 1974; Hall et al., 1986). However, in some studies, the Rambouillet and Finnsheep have approached the Dorset in out-of-season breeding performance (Hulet et al., 1974; Bernard and Fahmy, 1974).

Few studies have investigated within-breed variation in traits associated with seasonal breeding (McKinney, 1984; Hanrahan and Quirke, 1986; Notter, 1992). Thus, the objectives of this study were to estimate variance components, heritabilities (h^2) and repeatabilities of ewe spring fertility and litter size as well as the genetic and phenotypic correlations among them.

Materials and Methods

Management

Data for this study came from a pedigreed sheep population undergoing selection for ability to lamb in fall. The population was a three-breed composite containing 50% Dorset (D), 25% Rambouillet (R) and 25% Finnsheep (F) breeding. Development of this population was initiated in 1983. The specific selection criterion is the ability to conceive in May and June, because these months are associated with the lowest fertility levels in temperate breeds of sheep. Procedures used to form this flock were discussed by Fossceco and Notter (1995). By fall 1987, all animals in the flock were progeny of three-way-cross (D x FR) males and females. All matings to form this flock were made in the fall to avoid undocumented selection against seasonality during flock formation. Following the spring, 1987 lambing, 180 ewes were transferred to a fall lambing flock. These ewes had been bred in fall of 1986 for spring 1987, lambing and were not re-exposed to rams until spring of 1988. These animals were considered as the base population for selection. Data for this study came from the 1988 through 1994 fall lambings.

Two control flocks were established to evaluate selection response. An environmental control (EC) flock was maintained in spring breeding contemporary to the selected (S) flock. No replacements were retained from this flock. Also a genetic control (GC) flock was maintained in fall breeding. Replacements for both the EC and GC flocks came from spring-born GC lambs. Thus, EC animals were both unselected and evaluated contemporaneously to selected animals. Each year 125 ewes and 10 rams, and 55 ewes and 5 rams were mated in S and EC, respectively. Up to one third of ewes and one half of the rams were replaced each year, and a similar ewe age distribution was maintained in both flocks. Forty-five ewes and 5 rams were mated

each year in the GC flock. Rams and ewes were replaced only due to death or unsoundness in this flock to minimize rates of genetic change and inbreeding.

Ewe lamb selection for fertility was based on fall lambing performance of both the dam and the lamb herself. All ewe lambs born in the S flock were exposed for breeding, with up to 42 eventually retained as replacements. If less than 42 ewe lambs were pregnant, open ewe lambs were chosen based on breeding performance of their dams. Ram lamb selection was based on the breeding performance of dams, augmented with results of a breeding soundness examination and a libido test.

Ewes in S and EC were exposed to rams beginning May 1 in single-sire pens at a ram:ewe ratio of 1 to 13 for S and of 1 to 11 for EC. Breeding of S and EC ewes continued for about 60 days (until June 30). All S and EC ewes were re-exposed to rams for 30 days beginning August 1 to permit mating of ewes that failed to conceive at May-June exposure. Ewes bred in August lambed in January were returned to the spring-bred flock the following May. Dzabirski and Notter (1989) reported that Dorset ewes lambing in October or January did not differ in subsequent fertility in April. Ewes in GC were bred for 42 d beginning October 1 in single sire pastures at a ram:ewe ratio of 1:9. Ewes in all flocks were weighed and scored for body condition at breeding and lambed in an enclosed barn. Following lambing, ewes and their lambs were then moved to an open-fronted barn on an elevated expanded metal floor. Fall lambs were weaned in late December or early January, and spring lambs were weaned in mid May. All were raised on expanded metal floors until 120 d of age.

Traits. Fertility from May-June matings was recorded for both S and EC flocks. A fertility score of 1 was assigned if the ewe lambed and score of 0 was assigned if the ewe failed to lamb. Across years, a total of 1,102 exposures involving 420 ewes were made for fall lambings (Table 1). Litter size was defined as the

number of lambs born (dead or alive) per ewe lambing . Mean litter size was 1.75, 1.77 and 2.15 for fall, winter and spring lambing, respectively.

Statistical Analysis

Mixed Linear Model. The general linear animal model that was used can be represented in matrix notation as:

$$\mathbf{y} = \mathbf{xb} + \mathbf{z_a a} + \mathbf{z_c c} + \mathbf{z_s s} + \boldsymbol{\varepsilon}$$

where

$\mathbf{y}$ = the vector of records,

$\mathbf{b}$ = the vector of fixed effects in the model with association matrix $\mathbf{x}$,

$\mathbf{a}$ = the vector of random additive genetic effects with association matrix $\mathbf{z_a}$,

$\mathbf{c}$ = the vector of random permanent environmental effects with association matrix $\mathbf{z_c}$,

$\mathbf{s}$ = the vector of random service sire (breeding pasture) effects with association matrix $\mathbf{z_s}$ and

ε = the vector of residual (temporary environmental) effects.

Preliminary least squares analyses were conducted for the different traits using the GLM procedures of SAS (1989) to identify nongenetic factors influencing spring fertility and litter size. Factors considered included year (7 years), ewe age and season (litter size only). At first lambing, ewes were categorized as either true yearlings (age class 11, the 12-month-old ewes in the S and GC flocks) or long yearlings (age class 12, the 19-month-old ewes transferred from GC to EC). Post-yearling ewes were categorized as either at their second lambing or their third and greater potential lambing to give a total of four ewe age classes (Table 2). No age distinction between ewe lambs entering the flocks at 12 or 19 months was made after first lambing. For litter size, the factors were the same, except that when litter sizes

from all seasons were considered, the effects of season (3 levels) were included (Table 3). In addition, the effects of service sire within year (85 sire-year) were alternatively included as either fixed and random effects on fertility.

The variance-covariance structure for the random effects in the model was:

$$V = \begin{bmatrix} a \\ c \\ s \\ e \end{bmatrix} = \begin{bmatrix} A\sigma_a^2 & 0 & 0 & 0 \\ & I_c\sigma_c^2 & 0 & 0 \\ & & I_s\sigma_s^2 & 0 \\ & & & I_n\sigma_e^2 \end{bmatrix},$$

where A is the numerator relationship matrix, I_c is an identity matrix with order equal to the number of ewes, I_s is an identity matrix with order equal to the number of service sires, and I_n is an identity matrix with order equal to the number of records. Under this model, estimates of heritability ($\mathbf{h^2}$) and repeatability (**t**) are given, respectively, by

$$h^2 = \frac{\sigma_a^2}{\sigma_P^2} \qquad \text{and} \qquad t = \frac{\sigma_a^2 + \sigma_{pe}^2}{\sigma_P^2},$$

where $\sigma_P^2 = \sigma_a^2 + \sigma_{pe}^2 + \sigma_s^2 + \sigma_e^2$ or $\sigma_a^2 + \sigma_{pe}^2 + \sigma_e^2$, depending upon whether service sire effects are considered random or fixed, respectively.

REML (co)variance component estimates. Variance components were initially estimated using a single trait animal model with derivative-free restricted maximum-likelihood (DFREML) procedures (Graser et al., 1987). The computer programs of Boldman et al. (1993) were used.

Due to very low fertility of yearling ewes, data were reanalyzed using only data on ewes 2 years old and older. The analysis of litter size was also conducted on two data sets. One was restricted to fall lambings where as the other used all lambing records (fall, winter and spring). Covariance components for spring fertility and litter size were estimated using only fall lambing records.

Results and Discussion

Fertility

Results of variance component analyses for fertility are presented in Table 4. Relative variance due to direct genetic effect (h^2) ranged from .07 to .11 with an average of .09. In Both sets of data, estimates of heritability decreased when service sire effects were assumed random (Table 4). Variance due to permanent environmental effects (c^2) ranged from 6 to 12% and averaged 10% of the total variance. Variance due to service sire effects (s^2) averaged 9% of the total variance.

The mean heritability estimate in this study (.09) was higher than most previously reported estimates (Purser, 1965; Shelton and Menzies, 1970; Clarke and Hohenboken, 1983; Atkins, 1986; Bodin et al., 1988, Gabina, 1989; Bunge et al., 1990). However, heritabilities for fertility of .06 to .07 were reported by Fogerty et al. (1985) in sheep of similar breeding. In addition, a heritability estimate 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 this study.

Repeatability estimates for spring fertility are presented in Table 4. The average number of records was 2.6 for records on all ewes and 2.3 for records on only adult ewes. The general trend in this study was the for relative effects of permanent environment (c^2) on fertility to also increase as heritability estimates

increased. Repeatability estimates for the second data set in which yearling ewes were excluded were higher than those from the entire data set.

Estimates of repeatability of fertility found in the present study are among the highest found in the literature. Clarke and Hohenboken (1983) reported a repeatability estimate of .15 in a crossbred sheep flock. Bunge et al. (1990) obtained a repeatability of .03 for fertility in Rambouillet sheep. Repeatability for fertility of .17 was reported by Davis and Kinghorn (1986) in Merino sheep. Notter (1981) computed repeatabilities of conception rate ranging from .14 to .23 in a study with Finnsheep crossed under an accelerated lambing system.

Litter size

Parameters estimates for litter size are presented in Table 5. The heritability estimate derived using only fall lambing data was higher than that using data from all seasons (.10 vs. .05). Variance due to permanent environmental effects ($\mathbf{c^2}$) were lower in fall lambing data.

Literature estimates of heritability for litter size range from 0 to .35, but most estimates are .1 or less (Turner, 1969; Bradford, 1985). Estimates for this trait from the present study are within the range cited. Reports of $\mathbf{c^2}$ estimates for litter size in sheep are few. Our estimates of c^2 for litter size are similar to that observed by Waldron and Thomas (1992).

Repeatability estimates for litter size are presented in Table 5. The average numbers of records were 3.4 and 4.9 for fall lambings and for all lambings, respectively. Repeatability estimates were .11 and .14 for fall lambings and for all lambings, respectively. Repeatability estimates from the literature range from .08 to .24 (Purser, 1965; Shelton and Menzies, 1970, Fogarty et al., 1985; Abdulkhaliq et al.,

1989). Estimates of repeatability found in the present study are within the range of those reported in the literature.

Genetic Correlation

Genetic and phenotypic correlations between spring fertility and fall litter size using different models are presented in Table 6. Estimates of the genetic correlation for this study were .56. Few estimates of genetic correlations between litter size and fertility were found the literature. Fogarty et al. (1985) reported a genetic correlation between fertility and litter size born of -.34 $\pm$ .28 and a phenotypic correlation of .03 + .02 for ewes mated in the normal breeding season. The higher genetic correlation in our study indicates that selection for multiple births in out of season breeding should result in genetic improvement in spring fertility.

Implications

Heritability estimates for fertility in the normal fall breeding season are numerous and generally low. However, estimates for spring fertility are scarce. In our study, heritability estimates are somewhat higher than otheres found in the literature, indicating that selection to improve fertility may be more effective in out-of-season breeding than in the normal breeding season. The moderately higher estimates of repeatability for spring fertility indicate considerable contribution of permanent environmental effects, especially when yearling data were excluded. Also, the relatively high genetic correlation between spring fertility and litter size suggests use of litter size as an indirect selection criterion to improve spring fertility.

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Table 3.1. Summary statistics for spring fertility and fall and overall litter size.

	Fertility	Fall litter size[a]	Litter size[bc]
Categories	0,1	1,2,3	1,2,3
Mean ± SD	.40 ± .49	1.75 ± .61	1.86 ± .70
C.V. ,(%)	120	34	37
No. of records	1102	447	1018
Pedigree file	2596	2596	2596
No. of service sires across years	52	52	-[d]
No. ewe/sire	21.2	8.6	-[d]
No. of ewes across years	420	230	378
No. records/ewe	2.62	1.94	2.68

[a] Frequencies were 18.85%, 66.25% and 14.9 % for 1, 2 and 3, respectively

[b] Frequencies were 17%, 57.5% and 25.5% for 1, 2 and 3 respectively.

[c] Litter size data from all lambings (fall, winter clean-up and spring).

[d] Unknown service sire in winter lambings (clean-up)

Table 3.2. Number of records (n) and means for fertility by year and ewe age class.

Age class	Year													
	1989		1990		1991		1992		1993		1994		All	
	n	Mean	n	Mean	n	Mean	n	Mean	n	Mean	n	Mean	n	Mean
11[a]	-	-	15	.13	53	.07	21	.09	41	.12	38	.15	168	.11
12[b]	122	.09	8	.50	20	.25	10	.20	18	.50	14	.28	192	.18
2	53	.15	103	.51	20	.55	71	.39	24	.33	51	.72	322	.45
≥3	6	.33	47	.68	96	.60	89	.52	95	.46	87	.76	420	.59
All	181	.11	173	.52	189	.41	191	.41	178	.37	190	.59	1102	.41

[a] <12 months old from S flock;
[b] 19 months old from EC flock.

Table 3.3. Number of records (n) and means for litter size by season and age class of the ewe.

	Age class									
	11[a]		12[b]		2		3		All	
Season	n	Mean	n	Mean	n	Mean	n	Mean	n	Mean
Fall	18	1.27	34	1.50	145	1.73	250	1.82	447	1.75
Winter	68	1.42	69	1.55	79	1.86	109	2.08	325	1.77
Spring	55	1.45	-	-	61	2.06	130	2.52	246	2.17
All	141	1.41	103	1.53	285	1.83	489	2.06	1018	1.89

[a] <12 months old from S flock;
[b] 19 months old from EC flock.

Table 3.4. Estimates of genetic, environmental, and phenotypic parameters for fertility

	Fertility			
	Random service sire		Fixed service sire	
Parameters	All ewes	Adult ewes	All ewes	Adult ewes
σ^2_a	.012	.020	.014	.023
σ^2_{pe}	.014	.025	.014	.026
σ^2_s	.014	.023	-	-
σ^2_e	.156	.163	.154	.162
σ	.190	.232	.182	.211
h^2	.07	.09	.08	.11
c^2	.06	.11	.08	.12
s^2	.08	.10	-	-
t	.13	.19	.15	.23

Table 3.5. Estimates of genetic, environmental, and phenotypic parameters for litter size

	Litter size	
	Fall lambing	All lambings
σ^2_a	.033	.018
σ^2_{pe}	.050	.040
σ^2_e	.306	.343
σ^2	.345	.400
h^2	.10	.05
c^2	.02	.10
t	.11	.14

Table 3.6. Genetic correlations (above the diagonal) and heritability estimates (on the diagonal) between spring fertility and fall litter size with different models..

	Analysis A[a]		Analysis B[b]		Analysis C[c]		Analysis D[d]	
FERT	**.09**	.56*	**.09**	.81**	**.13**	.49*	**.12**	.49*
LS	-	**.06**	-	**.06**	-	**.09**	-	**.08**

[a] Models included additive, permanent environmental and service sire effects for fertility, with additive as well as permanent environmental effects for litter size

[b] Same as A, except that covariance between permanent environmental effects was excluded.

[c] Same as A, but yearling ewes were not included

[d] Same as B, but yearling ewes were excluded

* Observed correlation differs from 0 (P <.10)

** Observed correlation differs from 0 (P <.05)

Chapter 4

Genetic Variation and Covariation for Growth, Scrotal Circumference and Reproduction in Crossbred Sheep

Summary

Genetic parameters for growth, scrotal circumference and reproduction in a composite sheep population containing 50% Dorset, 25% Rambouillet and 25% Finnsheep inheritance were estimated by restricted maximum likelihood using various animal models. Heritability estimates for direct additive genetic effects for live weights at birth (BWT), weaning at 60 days (WWT), 90 days (90WT) and 120 days (120WT) were .17, .05, .08 and .19, respectively. Significant maternal and litter effects were found only in BWT and WWT (.13 and .27, respectively, for BWT and .19 and .11, respectively, for WWT, as a proportion of phenotypic variance). Estimates of permanent environmental effects in the dam, as a proportion of phenotypic variance, were .12, .05, .15 and .16 for BWT, WWT, 90WT and 120WT, respectively. Heritability estimates for scrotal circumference at weaning (WSC), 90 days (90SC) and 120 days (120SC) were .15, .25 and .02, respectively. Genetic correlations among body weights at all ages ranged from .77 to unity. The genetic correlations of litter size with BWT, 90WT and 90SC were .17, .33

and .36, respectively. Genetic correlations of spring fertility (SFERT) with BWT, 90WT and 90SC were .22, -.31 and .29, respectively.

Key Words: *Sheep, Genetic Parameters, Growth, Reproduction, Scrotal circumference.*

Introduction

The efficiency of lamb production depends primarily upon three functions: female production, reproduction and growth of lambs (Dickerson, 1970). Thus, two important goals for increasing the profitability of sheep are to increase the rate of reproduction and to improve growth performance of the lambs. The first objective can be achieved by increasing prolificacy and fertility of ewes, whereas the second requires improvement of growth potential and survival rate of the lambs.

Selection involving traits such as fertility and prolificacy is difficult because the traits are lowly heritable, expressed in categorical fashion and sex-limited. It would thus be helpful to identify continuous traits in both rams and ewes that are genetically correlated with female reproductive traits. A number of publications have suggested the use of testicular size as a trait in the male that can be used as a selection criterion to genetically improve female reproductive performance (Land, 1973; Land and Carr, 1975; Notter et al., 1981; Notter et al., 1985; Purvis et al., 1988; Matos and Thomas, 1992). Although few studies have attempted to relate measures of testis growth to seasonal breeding, a study by Fossceco and Notter (1995) has suggested that indirect selection based on male testis size may be a useful supplement to direct selection based on measures of female fertility in spring.

Accurate estimates of genetic parameters of growth and reproductive traits are essential to evaluate and compare alternative breeding plans as well as to predict breeding values. Therefore, the objectives of this study were to estimate genetic and phenotypic

(co)variances among growth, scrotal circumference and reproductive traits in a composite sheep population containing 50% Dorset, 25% Rambouillet and 25% Finnsheep breeding.

Materials and Methods

Animal Management

A detailed description of the experimental design and the management of the flock was given in the previous chapter and only information pertinent to this portion of the study are given here. The data were collected over 7 yr, beginning in 1988. Lambs were born in a 2-month period beginning in late September for fall lambing, and during March and April for spring lambing.

At parturition , lambing date, number of lambs born, sexes of lambs, and lamb birth weight were recorded. Each ewe and her offspring were then placed in an individual lambing pen for about 2 d and then moved to larger rearing pens with other ewes until weaning. Fall lambs were weaned and weighed in one or two groups in late December and early January at an average of 65.8 $\pm$5.5 d of age and stayed in the same barn until 120 d of age. Spring lambs were weaned and weighed in mid-May at an average of 65.1 $\pm$ 6.4 d of age. Lambs were subsequently weighed at about 90 d ($\bar{x}$= 96.6 $\pm$8.4) and 120 d ($\bar{x}$ =128.2 $\pm$ 8.1) of age. Scrotal circumference was measured on male lambs at each postnatal weighing. All available lambs from the select (S) , genetic control (GC) and environmental control (EC) flocks were included (Tables 1 and 2).

To simplify the model for (co) variance component estimation , data were preadjusted for some environmental effects. Postnatal weights and testicular measurements were adjusted for additive effects of age of ewe and type of birth and rearing. Birth weights were adjusted for ewe age and birth type (single, twin or $\geq$ triplet). The five birth-rearing classes considered for weights and scrotal circumferences were

single birth and rearing (11), twin birth and single rearing (21), twin birth and rearing (22), triplet birth and twin rearing (32) and triplet birth and rearing (33). However, the 21 class was combined with the 11 class for 90 d and 120 d testicular measurements, due to the reduced subclass numbers when data were restricted to male lambs.

To determine which environmental effects were important, linear models were fitted using the general linear model (GLM) procedure in the Statistical Analysis System (SAS, 1989):

$$\mathbf{y} = \mathbf{x}_1\mathbf{b}_1 + \mathbf{x}_2\mathbf{b}_2 + \varepsilon,$$

where,

$\mathbf{y}$ = vector of observations,

$\mathbf{b}_1$ = vector of fixed effects to be absorbed,

$\mathbf{b}_2$ = vector of fixed effects to be estimated,

$\mathbf{x}_1$ and $\mathbf{x}_2$ = incidence matrices, and

ε = vector of a residual errors distributed $(0, I\sigma^2 e)$.

Models were fitted separately to estimate the effects of type of birth-rearing and the age of ewe due to some confounding between these effects. Thus, if constants for type of birth-rearing (LTR) were to be estimated, $\mathbf{b}_1$ included the absorbed effects of the overall mean (μ), lamb birth year(YR), flock(FL), sire and age of ewe(EA), leaving effects of type of birth-rearing, sex and regression on lamb age in $\mathbf{b}_2$. Similarly, if ewe age constants were considered, $\mathbf{b}_1$ included the absorbed effects of μ,YR, FL, sire and LTR. The GLM procedure of SAS assumed the absorbed effects to be nested and thus, the classes were absorbed sequentially as they entered the model. Parameters estimates used to calculate adjustment factors were derived from the solution vector of the GLM procedure (SAS, 1989). The twin birth and rearing subclass (22) was chosen as a reference subclass for type of birth and rearing, and performance of lambs from 2-year-old ewes was adjusted to a 3-year-old ewe basis (Tables 3 and 4). Performance of lambs

from yearling ewes was not adjusted; instead lambs from yearling ewes were placed in different contemporary groups from lambs from older ewes in the (co) variance component estimation analyses.

Each observation was adjusted by subtracting the estimated mean reference group effect from the estimated effect of the group from which an observation came from; the resulting adjustment factor was then added to observations to obtain adjusted measurements (Tables 3 and 4). This procedure was followed for each fixed effect for which a trait was adjusted.

Variance components. Estimates of single trait variance components were obtained under an animal model using derivative-free restricted maximum-likelihood (DFREML) procedures (Graser et al., 1987). The general representation for the "complete" animal model used was as follows:

$$\mathbf{y} = \mathbf{xb} + \mathbf{z_a a} + \mathbf{z_m m} + \mathbf{z_p pe} + \mathbf{z_l l} + \boldsymbol{\varepsilon}$$

where

$\mathbf{y}$ = the vector of adjusted records,

$\mathbf{b}$ = the fixed effects in the model with association matrix $\mathbf{x}$,

$\mathbf{a}$ = The vector of additive genetic effects with association matrix $\mathbf{z_a}$,

$\mathbf{m}$ = The vector of maternal genetic effects with association matrix $\mathbf{z_m}$,

$\mathbf{pe}$ = the vector of permanent maternal environmental effects with association matrix $\mathbf{z_{pe}}$,

$\mathbf{l}$ = the vector of litter environmental effects with association matrix $\mathbf{z_l}$ and

$\boldsymbol{\varepsilon}$ = the vector of residual (temporary environmental) effects.

The (co) variance structure for the analysis can then be described as follows:

$$V\begin{bmatrix} a \\ m \\ pe \\ l \\ e \end{bmatrix} = \begin{bmatrix} A\sigma_a^2 & A\sigma_{am} & 0 & 0 & 0 \\ & A\sigma_m^2 & 0 & 0 & 0 \\ & & I_{pe}\sigma_{pe}^2 & 0 & 0 \\ & & & I_l\sigma_l^2 & 0 \\ & & & & I_n\sigma_e^2 \end{bmatrix}$$

where σ_a^2 is the additive genetic variance, σ_m^2 is the maternal genetic variance, σ_{am} is the direct-maternal genetic covariance, σ_{pe}^2 is the maternal permanent environmental variance, σ_l^2 is the litter variance and σ_e^2 is the error variance. In addition, A is the numerator relationship matrix between animals, I_{pe} is an identity matrix with order equal to the number of ewes, I_l is an identity matrix with order equal to the number of litters and I_n is an identity matrix with order equal to the number of records.

Fixed effects of contemporary groups were fitted. Contemporary groups were defined as combinations of year of birth (7 years), ewe age at breeding (12 mo, 18 mo, or $\geq$ 2 yr), date of weighing and lamb sex. The 12 and 18 mo ewe age classes discriminate between replacement ewes drawn from within the S and GC flocks and those transferred to EC from GC (see the previous chapter). Sex of lamb was considered as a separate fixed effect rather than as a contemporary group definition for birth weight and weaning weights because lambs of the two sexes were always maintained together through weaning. In addition the regression of lamb age on weight was fitted for all traits except birth weight (Table 5).

Including maternal genetic effects and the genetic covariance between direct and maternal effects as well as permanent environmental and litter effects defined six parameters for each trait . However, all sources of variation were not expected to be important for all traits, so a series of reduced models were fitted to evaluate the

significance of the various parameters. Model 1 was a simple animal model with additive genetic effects as the only random effect. Genetic variance from this model is overestimated in the presence of any sort of maternal and/or litter effects. Model 2 allowed for a permanent environmental effect due to the dam, fitted as an additional random effect uncorrelated with all other effects in the model. The permanent environmental effect with variance $I\sigma^2_{pe}$ was expected to include some of the maternal genetic and litter effects . Model 3 attributed all maternal effects to the additive genotype of the dam, fitting the maternal genetic effect as a second random effect with variance $A\sigma^2_{m}$., but assumed that direct and maternal genetic effects were uncorrelated. This model does not discriminate among maternal genetic, permanent environmental and litter effects but, like model 2, allowed approximate assessment of total maternal variance. Models 4 and 5 included both permanent environmental and additive maternal effects, ignoring and fitting, respectively, a genetic correlation between direct and maternal effects. Model 6 included permanent environmental and additive maternal effects as well as litter effects, but without a genetic correlation between direct and maternal effects. Parameters estimated for each model are defined in Table 6.

The (co) variance structure for the additive genetic and additive maternal effects can then be described in the six models as follows:

model 1: $\mathbf{Z_a a}$ $\quad Var(\mathbf{a}) = A\sigma^2_a$

model 2: $\mathbf{Z_a a} + \mathbf{Z_m p}$

model 3: $\mathbf{Z_a a} + \mathbf{Z_m m}$ $\quad Var\begin{bmatrix} a \\ m \end{bmatrix} = \begin{bmatrix} A\sigma^2_a & 0 \\ 0 & A\sigma^2_a \end{bmatrix}$

model 4: $\mathbf{Z_a a} + \mathbf{Z_m m} + \mathbf{Z_m p}$ $\quad Var\begin{bmatrix} a \\ m \end{bmatrix} =$ as above

model 4: $\mathbf{Z_a a} + \mathbf{Z_m m} + \mathbf{Z_m p}$ $$Var\begin{bmatrix} a \\ m \end{bmatrix} = \begin{bmatrix} A\sigma_a^2 & A\sigma_{am} \\ sym & A\sigma_a^2 \end{bmatrix}$$

model 6: $\mathbf{Z_a a} + \mathbf{Z_m m} + \mathbf{Z_m p} + \mathbf{Z_l l}$ $$Var\begin{bmatrix} a \\ m \end{bmatrix} = \begin{bmatrix} A\sigma_a^2 & 0 \\ 0 & A\sigma_a^2 \end{bmatrix}$$

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 (Tables 1 and 2). All calculations were carried out using the MTDFREML programs (Boldman et al., 1993). Depending on the model , the log-likelihood function was maximized 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 effects as a proportion of phenotypic variance (d), the permanent environmental variance due to the dam as a proportion of the phenotypic variance (pe^2), and litter variance as a proportion of the phenotypic variance (l^2). The error variance was estimated directly from the residual sum of squares.

The overall importance of each parameter for each trait was assessed by comparing the ratios of likelihoods of sequentially reduced models (Rao, 1973). The ratio -2 [$\log \Lambda_i$ - $\log \Lambda_j$] is asymptotically distributed as chi-square with degrees of freedom equal to the difference in the number of parameters in models i and j , where Λ is the value of the maximized likelihood function for the model following achievement of the convergence criterion . Show (1987) and Meyer et al. (1990) considered the use of a likelihood ratio test in conjunction with REML estimation of genetic parameters.

Additive covariances and genetic correlations were estimated considering only two traits at a time and estimating up to 11 (co)variance components per bivariate analysis. Fixed effects fitted were those used in previous single trait analyses. All bivariate analyses fitted a random effect for the additive genetic merit of each animal and each trait and

included all available pedigree information. Whether or not the model of analysis included additional random effects representing maternal, permanent environmental or litter effects depended on the pair of traits considered. Three different types of covariance analyses were distinguished.

The first type of analysis dealt with growth traits. Both temporary (σ_{e12}) and maternal permanent environmental (σ_{c12}) covariances were accounted for. The second type of analysis (analysis 2) considered a male reproductive trait (scrotal circumference) together with a female reproductive trait (litter size or spring fertility) with traits measured on different subsets of animals and with both σ_{e12} and σ_{c12} assumed to be zero. Analysis 3 dealt with reproductive (spring fertility, litter size, and scrotal circumference in male) and weight traits (birth weight and 90 d weight) and σ_{e12} was accounted for. To obtain good starting values, the likelihood was first maximized with respect to the 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 (co)variances (Meyer, 1994). In addition, there has been some evidence for convergence of multivariate animal model REML procedures to local maxima. Thus, 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}. The total heritability (h_t^2), defined by Willham, (1972) as $h_t^2 = (\sigma_a^2 + 0.5\sigma_m^2 + 1.5\sigma_{am})$ was also determined.

Results and Discussion.

Birth weight

Estimates of variance components and genetic parameters for birth weight (BWT) from each model are presented in Table 7. Model 1 ignored total maternal effects and

yielded a substantially higher heritability estimate (.52) than other models. Fitting a permanent environmental effect (model 2) increased value of log L (Table 8) markedly over that of model 1. Thus, some overall maternal effect was important and contributed 29% of the total variation in BWT. Correspondingly, the estimate of σ^2_a was reduced.

Fitting an additive maternal effect instead of a permanent environmental effect (model 3) resulted in a larger increase in log L (compared with model 1) than did model 2. Thus, model 3 provided a better fit to the data than did model 2. With an estimate of the m^2 of .35, the estimate of direct h^2 was reduced to .18 in model 3. Model 4 indicated that both permanent environmental and additive maternal effects were significant (model 4 vs models 2 and 3). Permanent environmental effects of the dam seemed to be more important than additive maternal effects (.18 vs .12).

The estimates of the genetic covariance between direct and maternal effects for BWT was -.02 with a corresponding estimate of r_{am} of -.17. Inclusion of this covariance resulted in a small but not significant increase in log L compared with model 4 in which σ_{am} was ignored. Thus, including the correlation between direct and maternal genetic effects did not add meaningful information. Litter effects (model 6) accounted for 27% of phenotypic variation, even after adjustment for average effects of litter size, and resulted in a significant increase in log L values when compared with that of model 4. The estimates of σ^2_{pe} and σ^2_e were correspondingly reduced.

Estimates of direct heritability are well within the range of values reported in the literature. Waldron et al. (1990) reported h^2 estimates for BWT in crossbred lambs (Suffolk, Dorset and Rambouillet) of .13. Fossceco and Notter (1995), working with the foundation lambs of this study, obtained an estimate of h^2 for BWT of .15. Maria et al. (1993) obtained a heritability estimate of .04 for BWT in Romanov sheep. The estimate of h^2 in this study is similar to that obtained by Tosh and Kemp (1994) for Polled Dorset sheep. However, they reported an estimate of .39 for Hampshire sheep. The estimates of maternal heritability in this study are similar to those reported by Tosh and Kemp (1994)

for Romanov sheep and smaller than those observed by Maria et al. (1993). The estimate of relative variance due to permanent environmental effects (pe^2) in the dam is similar to those reported by Fossceco and Notter (1995) and Maria et al. (1993). Tosh and Kemp (1994) reported an estimate of .32. However, the estimates obtained by those authors contained mostly litter effects. Reports of l^2 estimates for BWT in sheep are few. In general, our estimates of l^2 are similar to that reported by Fossceco and Notter (1995). While most studies in beef cattle and sheep found the relationship between direct and additive maternal effects to be negative (Eikje, 1975; Gould and Whiteman, 1975; Burfening and Kress, 1993; Maria et al., 1993; Tosh and Kemp, 1994) , a few studies found it to be positive (Hanrahan,1976). Results from this analysis suggest that there is little association between direct and maternal effects on BWT in this population.

Weaning Weight

Results for WWT are summarized in Table 9. As clearly demonstrated by likelihood values (Table 8), weaning weight was strongly influenced by net maternal effects (models 2 and 3). Ignoring either maternal genetic (model 3) or permanent environmental maternal effects (model 2) resulted in significant increase in log L values over those of model 1 (Table 8). With an estimate of m^2 of .18, the estimate of direct heritability was reduced to .05 in model 3. Model 4 indicated that the total maternal effect was difficult to partition into its components. The estimate of the genetic covariance between direct and maternal effects (model 5) was essentially zero and changed likelihood little compared to model 4 in which σ_{am} was ignored. Allowing for litter effects (model 6) resulted in a significant increase in log L value over that of model 4; estimates of σ^2_{pe} and σ^2_e were both reduced.

Fossceco and Notter (1995), considering the foundation animals of this study, reported estimates of .20, 0 and .14 for h^2, m^2 and pe^2, respectively, for an analysis under model 4. Their analysis was performed using only one random lamb per ewe per year, and

there had been no selection for spring fertility. Maria et al. (1993) reported estimates of .34, .25 and 0 for h^2, m^2, and pe^2, respectively in Romanov sheep. Also, estimates of .23, 0 and .17 were reported by Fossceco and Notter (1995) for h^2, pe^2 and l^2, respectively, using a model with additive, maternal and litter effects. Estimates of direct heritability for WWT reported in the literature ranged from .05 to .35 (e.g., Bennett et al., 1991; Davis and Kinghorn, 1986). Maria et al. (1993) obtained large negative estimates of σ_{am} for WWT in Romanov sheep. Results from this study suggest that since the negative relationship between preweaning growth and maternal ability has been suggested to be mainly environmental in origin and associated with plane of nutrition (Johnson and Morant, 1984; Burfening and Kress, 1993), the homogenous treatment of ewes and their daughters in this study may have masked the negative relationships.

90-d Weight

Results for 90-d weight (90WT) are presented in Table 10. Fitting either a maternal permanent environmental or additive maternal effect (models 2, and 3, respectively) increased the likelihood significantly over that for a simple animal model (model 1). Results from model 3 indicated that the environmental influence of the dam was more important than the additive maternal influence for this weight. Allowing for permanent environmental effects in model 4 reduced the maternal effect to .05. Again, the estimate of σ_{am} was positive but did not increase the likelihood significantly. Results from model 6 indicated that the variance due to the litter effects (l^2) was reduced to 1% (compared to 27% and 11% for BWT and WWT, respectively).

Estimate of h^2, m^2 and pe^2 of this study are in full agreement with those reported by Maria et al. (1993) for Romanov lambs. Our estimates differed from the results of Fossceco and Notter (1995), who reported estimates of .22, 0, .02 for h^2, m^2 and l^2, respectively, using the foundation lambs of these populations.

120-d Weight

While some carry-over effects of the maternal influence at weaning on 90WT was anticipated, these effects were expected to become less important for 120-d weight (120WT). While the maternal genetic variance was reduced to 0% (compared to 10% for WWT), the estimate of direct heritability increased to 19% (vs 5% for WWT) (Table 11). The estimate of σ_{am} was negative, but did not increase the likelihood significantly. Again the estimate of l^2 was not significant. Fossceco and Notter (1995) reported an estimate of h^2a of .25, using spring-born lambs with animals' additive genetic effect as the only random effect.

Scrotal circumference measurements

Estimates of variance components and genetic parameters for scrotal circumference measurements (SC) are presented in Table 12. Owing to the small size of individual data sets, estimated heritabilities varied widely, but there was no indication of significant maternal effects on SC at any age (Table 8). The additive heritability estimates were .15 for WSC, .25 for 90SC. and .01 for 120SC. Although there was considerable variation among measurements in heritability estimates, phenotypic coefficients of variation were similar for the three measurements (Table 2). Heritability estimates in this study are lower than most of those published by other authors for testicular traits in sheep. Fossceco and Notter (1995) reported heritability estimates for WSC, 90SC and 120SC of .22, .52 and .09, respectively. However their estimates were based on spring born lambs and the model of analysis included only animals' direct effect. Lee and Land (1985) reported a realized heritability of .40 for testis diameter from a divergent selection experiment in Finnish Landrace x Dorset sheep. Matos et al. (1992) estimated heritabilities for scrotal circumference growth ranging from .17 to .60 in Rambouillet ram lambs aged 3

to 6 mo. Fogarty et al. (1980) obtained a heritability estimate of .14 ± .08 at 140 d for scrotal circumference.

Correlations among traits

Estimates of genetic and phenotypic correlations between traits are given in Tables 13 and 14. Genetic correlations among weights at all ages (table 13) were high. Correlations between adjacent weights were highest. Thus, selection for any one of these weights should result in an increase in all other weights. Heritability estimates were very similar to those from corresponding single trait analyses. The genetic correlation of ewe spring fertility and 90SC (table 14) was positive (.29), indicating that selection of ram lambs with larger SC should result in ewe offspring that were more fertile in spring. In addition, a positive nonsignificant genetic correlation estimate between spring fertility and BWT was found (.22; table 14). However, 90WT had a nonsignificant negative genetic correlation with spring fertility of -.31, suggesting that selection of individuals based on weight may have a negative impact on spring ewe fertility. The genetic correlations of litter size with BWT, 90WT and 90SC were positive (.17, .33 and .36, respectively), but not significantly different from zero. These results suggest that larger animals and daughters of animals with larger SC were somewhat more likely to produce more lambs per lambing.

General Discussion

Parameters estimates from the "best" fitted model for each trait are summarized in Table 15. Except for BWT, none of the traits required fitting of all five of the potentially important variance components (additive, additive maternal, permanent maternal environmental, litter and temporary environmental). However, when the models are viewed together, a reasonably consistent picture of the relative importance of the different sources of variation emerges. The estimate of additive heritability of .17 for birth weight

was similar to the average estimate of .15 reported in the literature. For postnatal weights, additive heritabilities were lower but within the range of estimates in the literature.

Maternal additive genetic effects on weights were clearly important only for BWT and WWT. The maternal additive genetic effects (m^2) of .13 for BWT and .18 for WWT agreed well with the average values in the literature (Burfening and Kress, 1992; Maria et al., 1993; Tosh and Kemp, 1994; Fossceco and Notter, 1995). Genetic correlations between direct and maternal additive genetic effects (r_{am}) were small and not significant. This result is in contrast to the consistently moderate to high negative estimates of r_{am} reported in the literature (Ch'ang and Rae, 1972; Burfening and Kress, 1993; Maria et al., 1993; Tosh and Kemp, 1994). In the current study, management was such that environmental correlations, which can cause negative estimates of genetic correlations (Mangus and Brinks, 1971), were probably small and resulted in non-significant estimates of r_{am}. The estimates from the current study suggest that selection for live weight of the lamb without consideration of maternal effects may not change the maternal ability of the ewe. Such a conclusion would, however, be specific to this environment, and would not necessarily be repeated under a different management system.

Partition of maternal genetic and permanent environmental effects is often difficult due to confounding of these effects. However, the mating schemes used in this study did provide for substantial numbers of half-sib ewe families to be used to identify genetic maternal effects through resemblances among related ewes. However, a reasonably convincing partition was achieved only for BWT. High and modest litter components for BWT and WWT, respectively, were observed. Resulting a cross-year (half-sib) and within-year (full-sib) repeatabilities of ewe performance would be about .29 and .60, respectively, for BWT and .16 and .28, respectively, for WWT.

Since maternal effects were consistently nonsignificant for scrotal circumference measurements, model 1 was considered the best model (Table 15). Heritability estimates

were smaller than those observed by Fossceco and Notter (1995), whose estimates of h^2 were .21 (WSC), .52 (90SC) and .09 (120SC). These discrepancies may be due to seasonal depression in testis size that occurs from late winter to early spring for lambs born in the fall (Land and Sales, 1977). Matos and Thomas (1992) reported that heritability estimates for various measures of testis size ranged from 0 to .75 with an average of about .33. Heritability of 120SC was very low, especially given the relatively high heritability for body weight at this age (.19). Fogarty et al. (1980) reported a heritability of SC for whiteface crosses to be .13 $\pm$ .08 at 140 d. The growth pattern of SC in the current study agrees well with that reported by Fossceco and Notter (1995) and Notter et al. (1985), who illustrated that rapid testis growth begins around 60 d of age, terminates after 120 d of age and reaches its maximum at about 90 d of age.

Genetic correlations of litter size with BWT, 90WT and 90SC were positive but not significantly different from zero. These results suggest that larger animals were somewhat more likely to produce more lambs per lambing. Brien (1986) reviewed the relationship between growth and reproduction and concluded that a positive relationship existed between mating weight and number of lambs born per ewe lambing. Spring ewe fertility was genetically negatively correlated (-.31) with 90WT, suggesting that ewe lambs that were larger at 90 d may have been later maturing and less likely to conceive at both 7 mo and at later ages. The positive genetic correlation between spring ewe fertility and 90SC indicates that scrotal circumference might be used as an indirect selection criterion to improve spring ewe fertility. Results of Walkley and Smith (1980) indicated that a greater genetic gain in selection for a ewe reproductive measure could be achieved if direct selection for the ewe reproductive trait was complemented with indirect selection based on male trait with an approximate heritability of .35 and genetic correlation with the female reproductive trait of $\geq$ .30.

Implications

Among weight traits, weaning weight had the lowest direct heritability, which is due to the maternal component that may have masked it. Thus, the portion of the selection differential in weaning weight that would be realized is expected to be low. Permanent environmental effects seem to have influenced postweaning weights more than preweaning weights; part of these effects are additive maternal 'carry-over' effects of those affecting BWT and WWT. Litter variance, due to environmental effects common to littermates, accounts for a major portion of variation in BWT. Genetic correlations among weight traits were high, indicating that selection for any of the traits should result in genetic improvement in the other traits. Except for the negative correlation between spring fertility and 90WT, no unfavorable genetic correlations were identified in this study. Hence, joint selection for fertility and growth should improve genetic potential in both.

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Table 4.1. Summary statistics for growth traits.

	BWT	WWT	90WT	120WT
Mean ± SD, kg	3.8 ± .9	22.5 ± 4.4	31.7 ± 6.0	39.4 + 7.4
C. V., %	22.8	19.8	18.9	17.9
No. of records	1878	979	853	662
Ram lambs				
N	930	461	404	333
Mean, kg	3.91	24.0	34.2	43.9
Ewe lambs				
N	948	518	449	329
Mean, kg	3.63	21.1	29.4	34.2
Animals in pedigree file	2596	2596	2596	2596
No. of dams	402	280	270	228
No. of litters	1044	596	524	414
No. of sires	63	55	54	52
Contemporary groups	31	48	58	51

BWT = Birth weight.
WWT = Weaning weight at about 60 d of age.
90WT = Weight at about 90 d of age.
120WT = Weight at about 120 d of age.

Table 4.2. Summary statistics for scrotal circumference measurements.

	WSC	90SC	120SC
mean ± SD, cm	14.5 ± 1.9	21.4 ± 2.8	26.1 ± 2.7
C. V., %	13.5	13.3	10.3
No. of records	308	318	284
Animals in pedigree file	2596	2596	2596
No. of dams	175	174	173
No. of sires	47	48	47
Contemporary groups	25	21	21

WSC = Scrotal circumference at about 60 d of age.
90SC = Scrotal circumference at about 90 d of age.
120SC = Scrotal circumference 120 d of age.

Table 4.3. Adjustment factors for birth weight, kg.

No. born	BWT adjustment	Class	Ewe age
1	-.81	2	.53
2	0.00	≥ 3	0.0
3	.72		

Table 4.4. Adjustment factors for body weights and scrotal circumferences

variable	class	Body weights, kg			Scrotal circumference, cm		
		WWT	90WT	120WT	WSC	90SC	120SC
Birth-	11	-3.33	-3.85	-3.93	-1.01	-.95	ns
rearing-	21	-1.80	-2.01	-2.21	-	-	-
type	22	0.00	0.00	0.00	0.00	0.00	ns
	32	1.35	1.40	1.98	.52	1.20	ns
	33	2.52	2.80	2.85	1.92	3.10	ns
ewe age	2	1.80	1.66	1.49	.70	1.25	ns
	≥3	0.00	0.00	0.00	0.0	0.0	ns

ns= no significant effect.

Table 4.5. Linear regression coefficients of lamb performance traits on age

Trait	Regression coefficient (/d)
Weaning weight, kg	.478
90-d weight, kg	.608
120-d weight, kg	.610
Weaning scrotal circumference, cm	.145
90-d scrotal circumference, cm	.276
120-d scrotal circumference, cm	.126

Table 4.6. Abbreviations and corresponding definitions.

Abbreviation	Definition
σ^2_a	Direct additive genetic variance
σ^2_m	Maternal additive genetic variance
σ_{am}	Covariance between direct and maternal genetic effects
σ^2_{pe}	Permanent environmental variance
σ^2_l	Litter effect variance
σ^2_e	Error variance
σ^2	Phenotypic variance
h^2_a	Direct heritability, σ^2_a / σ^2
m^2	σ^2_m / σ^2
d	σ_{am} / σ^2
r_{am}	Correlation between direct and maternal additive genetic effects
pe^2	σ^2_{pe} / σ^2
l^2	$\sigma^2_l / \sigma^2 c$
h^2_t	$(\sigma^2_a + .5\ \sigma^2_m + 1.5\sigma_{am} / \sigma^2)$

Table 4.7. (Co) variance component and genetic parameter estimates for birth weight*.

	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6
σ^2_a	.36	.15	.13	.13	.14	.12
σ^2_m			.26	.08	.10	.12
σ_{am}					-.02	
σ^2_{pe}		.19		.13	.13	.08
σ^2_l						.19
σ^2_e	.33	.34	.35	.34	.33	.21
σ^2	.69	.68	.72	.70	.69	.70
h^2_a	.52	.21	.18	.19	.21	.17
m^2			.35	.12	.15	.13
d					-.03	
r_{am}					-.17	
pe^2		.29		.18	.18	.12
l^2						.27
$h^{2\,b}_t$				.25	.23	

* Definitions of parameters are listed in Table 4.6.

Table 4.8. Values of -2[log Λ_i- log Λ_j], the differences between the likelihood functions of two different animal models), using chi-square distribution with numbers of degrees of freedom =1.

	Model 1 - Model 2	Model 1 - Model 3	Model 2- Model 4	Model 3 - Model 4	Model 4- Model 5	Model 4- Model 6
BWT	120.1**	127.00**	5.2*	12.10**	.6	104.15**
WWT	23.52**	23.80**	2.8	2.5	.0	4.5*
90WT	23.00**	18.50**	.50	4.9*	.0	.94
120WT	12.70**	3.82*	.0	8.9*	.0	.82
WSC	0	0	-	-		
90SC	0	0	-	-		
120SC	0	0	-	-		

** $P < .001$

* $P < .05$

Table 4.9. (Co) variance component and genetic parameter estimates for weaning weight (WWT)*.

	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6
σ^2_a	3.08	1.05	.65	.69	.69	.57
σ^2_m			2.41	1.26	1.25	1.32
σ_{am}					.01	
σ^2_{pe}		2.24		1.17	1.17	.68
σ^2_l						1.48
σ^2_e	9.95	9.56	10.00	9.80	9.79	8.83
σ^2	12.98	12.87	13.07	12.92	12.91	12.92
h^2_a	.23	.08	.05	.05	.05	.04
m^2			.18	.10	.10	.10
d^*					.00	
r_{am}					.01	
pe^2		.17		.09	.09	.05
l^2						.11
h^2_t				.10	.10	.09

* Definitions of parameters are listed in Table 6.

Table 4.10. (Co) variance component and genetic parameter estimates for 90-d weight*.

	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6
σ^2_a	6.87	2.29	1.88	2.00	1.71	1.81
σ^2_m			4.67	1.02	.46	1.07
σ_{am}					.55	
σ^2_{pe}		4.13		3.32	3.42	2.85
σ^2_l						.19
σ^2_e	15.17	15.07	15.50	15.21	15.40	14.50
σ^2	22.05	22.15	22.21	22.56	21.50	21.50
h^2_a	.31	.11	.08	.09	.08	.08
m^2			.21	.05	.02	.05
d^*					.02	
r_{am}					.62	
pe^2		.19		.15	.16	.13
l_2						.01
h^2_t				.11	.12	

* Definitions of parameters are listed in Table 6.

Table 4.11. (Co) variance component and genetic parameters estimates for 120-d weight*.

	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6
σ^2_a	6.78	4.73	4.88	4.75	4.74	.12
σ^2_m			2.56	0	0	4.50
σ_{am}					-.01	0
σ^2_{pe}		3.82		3.81	3.82	3.29
σ^2_l						1.45
σ^2_e	17.33	15.92	17.17	15.91	15.92	24.42
σ^2	24.33	24.46	24.61	24.48	24.47	15.16
h^2_a	.28	.19	.20	.19	.19	.18
m^2			.10	0	0	0
d					.00	
r_{am}					-.01	
pe^2		.16		.16	.16	.13
l^2						.06
h^2_t				.19	.19	.18

* Definitions of parameters are listed in Table 6.

Table 4.12. Variance components estimates for scrotal circumference measurements*.

Model	Item	Scrortal circumferences (cm)		
		WSC	SC1	SC2
1	σ^2_a	.32	1.59	.07
	σ^2_e	1.82	4.76	5.65
	σ^2	2.14	6.36	5.72
	h^2	.15	.25	.01
2	σ^2a	.27	1.58	.00
	σ^2m	.15	.00	.17
	σ^2e	1.72	4.76	5.56
	σ^2	2.16	6.36	5.73
	h^2	.13	.25	0
	m2	.07	0	.03
3	σ^2a	.32	1.27	.00
	σ^2pe	.01	.74	.75
	σ^2e	1.81	4.36	4.95
	σ^2	2.14	6.38	5.70
	h^2	.15	.20	.00
	p2	.00	.12	.13
4	σ^2a	.26	1.51	.44
	σ^2m	.15	.00	.00
	σ^2pe	.00	.58	.37
	σ^2e	1.73	4.38	4.61
	σ^2	2.16	6.48	5.73
	h^2	.12	.23	.02
	m^2	.07	.00	.00
	p^2	.00	.09	.06

* Definitions of parameters are listed in Table 4.6.

Table 4.13. Genetic correlations (above diagonal), and phenotypic correlations (below diagonal) among birth weight (BWT), weaning weight (WW), 90-day weight (90WT) and 120-day weight (120WT). Heritability estimates are on the diagonal[a].

	BWT	WWT	90WT	120WT
BWT	.25	.79*	.77*	.78*
WWT	.28	.07	1.0**	.86**
90WT	.33	.86	.08	.94**
120WT	.32	.62	.87	.19

[a] Heritability is the average of all bivariate estimates

** observed correlation differs from 0 (P <.01).

* observed correlation differs from 0 (P <.05).

Table 4.14. Genetic correlations (above diagonal), and phenotypic correlations (below diagonal) among litter size (LS), spring fertility (SFERT), 90-day scrotal circumferences (90SC), 90-day weight (90WT) and birth weight (BWT). Heritability estimates are on the diagonal*.

	LS	SFERT	90SC	90WT	BWT
LS	.05	.56	.36	.33	.17
SFERT	.10	.09	.29	-.31	.22
90SC	-	-	.26	.60	.37
90WT	.11	-.04	.67	.14	.77
BWT	.07	.25	.26	.33	.18

* Heritability is the average of all bivaraite estimates

Table 4.15. Parameter estimates, obtained with "best" fitted model, for each trait

Trait	BWT	WWT	WT1	WT2	WSC	SC1	SC2
$\sigma^2_a + 1/2\ \sigma^2_m$	.18	1.23	2.51	4.75	-	_	_
σ^2	.70	12.92	15.21	24.48	2.14	6.36	5.72
h^2_d	.17	.04	.09	.19	.15	.25	.02
m^2	.13	.10	.05	0	_	_	_
pe^2	.12	.05	.15	.16	_	_	_
l^2	.27	.11	-	-	_	_	_
'Best" model	6	6	4	4	1	1	1

Chapter 5

Selection for Fall Lambing in Crossbred Sheep
I. Genetic and Environmental Changes in Female Reproductive Performance

Summary

Mixed model methodology was applied to estimate genetic and environmental trends for spring fertility and fall litter size in a composite sheep population containing 50% Dorset, 25% Rambouillet and 25% Finnsheep inheritance. Animal models and REML estimates of variance components were used to predict breeding values. Annual rates of genetic change were estimated as the regression of the mean predicted breeding value on year. Permanent environmental trends were calculated by averaging predictions of permanent environmental effects for all ewes mated in each year. Likewise, service sire trends were calculated averages of service sire predictions in each year. Genetic trends were 1.32 $\pm$ .11% in S compared with .57 $\pm$ .19% in EC for spring fertility and .0065 $\pm$ .0015 lambs/yr in S compared with .0024 $\pm$ .0022 lambs/yr in EC for fall litter size. Estimates of permanent environment trends for spring fertility were similar in S and EC flocks (.21$\pm$ .07% and .22$\pm$ .13%, respectively).

There was no permanent environmental trends for fall litter size in either flock. Service sire trends in spring fertility were positive for the EC flock (.64±.29%) and negative for the S flock (-.32±.15%).

Key words: *Spring Fertility, Fall Litter Size, Genetic Trends, Mixed Model Methodology*

Introduction

Mixed model methodology with animal models is used to measure selection response in farm animals (Blair and Pollak, 1984; Van Vleck et al., 1986; Parnell et al., 1986; Estany et al., 1989; Southwood and Kennedy, 1991; Cantet et al., 1993). The use of mixed models allows the separation of genetic and environmental effects and takes into account the relationships among animals (Henderson, 1975; Sorensen and Kennedy, 1986; Kennedy, 1988). In addition, this method accounts for the effects of selection as well as nonrandom mating if all the information related to selection is included in the analysis (Kennedy, 1988).

The objective of this study was to estimate genetic and environmental trends for spring fertility and fall litter size in a composite sheep population containing 50% Dorset, 25% Rambouillet and 25% Finnsheep breeding and under selection for ability to lamb in the fall.

Materials and Methods

Data

Data for this study came from a pedigreed sheep population undergoing selection for ability to lamb in the fall. Data were collected over the period 1989-1994. The specific selection criterion was the ability to conceive in May and June,

because these months are associated with lowest fertility levels in temperate breeds of sheep. Another trait of interest was fall litter size, defined as the number of lambs born per ewe lambing. Additional details of mating, lambing and related management, as well as models of analyses were presented in previous chapters.

Breeding values were estimated using the derivative-free restricted maximum likelihood approach of Boldman et al. (1993) with an animal model. In addition to the error term, the model included additive direct and permanent environmental effects of ewes as uncorrelated random effects. Also, service sires were included as an uncorrelated random effects on fertility only. Fixed effects included year (6 years), ewe age (4 levels) and season (3 levels; litter size only). Summary information for spring fertility and fall litter size is presented in Table 1. Estimates of genetic trends for S and EC were obtained by averaging corresponding breeding values for all lambs born (LB), all ewes exposed to mating (EM) and for all mated pairs (MA; the average of ewe and service sire) in each year, and regressing these averages on year of mating (Blair and Pollak, 1984; Southwood and Kennedy, 1991). Permanent environmental trends were calculated by taking averages of predictions of permanent environmental effects (c) for all ewes mated in a given year (Cantet et al., 1993). Likewise service sire effects were calculated by taking averages of service sire predictions (s) for all sires used in a given year. Inbreeding coefficients were obtained for all lambs in all flocks , using the inbreeding coefficient procedure (INBREED) in SAS (1994).

Results and Discussion

Inbreeding coefficients. Average inbreeding coefficients by year of birth for all lambs in selected and control flocks are presented in Table 2. There was no change in

the average inbreeding coefficients across years, however, the maximum inbreeding coefficient increased from about .06 in the foundation animals to .265 in 1994. Thus, all flocks had a relatively low level of inbreeding with the selected flock averaging only about 2% higher than the control flocks in the final years.

Phenotypic trend. Least-square estimates for year effects from SAS, and means for yearly breeding values, permanent environmental effects, service sire effects and year constants (which represent the environmental trends) from the REML analysis are shown in Table 3. Least-square estimates for year effects which represent total phenotypic trends ($\dot{\dot{P}}$) were obtained using general linear model procedures (GLM) in SAS with a model that included only year and ewe age effects. The components of phenotypic trend from the REML analysis were also summed to give an estimate of overall phenotypic effects ($\hat{P}$) adjusted for ewe age effects. Least-squares estimates of $\dot{\dot{P}}$ and REML estimates of $\hat{P}$ were similar, which indicates that mixed model methodology had succeeded in separating the total phenotypic trend into its various genetic and environmental components (Blair and Pollak, 1984) and that there was no confounding between fixed and random components (Thompson, 1986). The success of this procedure in this study was in part dependent on genetic connectedness across years. A ewe and her full and paternal half-sib relatives giving records in 1 year became dams and grand dams in other years to create the genetic linkages across years in this population. These linkages were used for building the additive relationship matrix through the pedigree information.

Genetic and environmental trends.

Spring fertility. The genetic trends based upon average breeding values of LB, all EM and all MA, expressed in percentage , are depicted for the S flock in

Figure 1. The differences between EM trend and MA trend represents the contribution of the mean breeding value of the service sires. The variation in mean breeding value based upon lambs born reflects year differences in mean fertility and , therefore, the number of lambs included in each average. In years when fertility is low, such as 1989, the lambs born are descended from a more highly selected group of parents and mean breeding values are correspondingly higher.

Graphs of permanent environmental and service sire effects along with genetic trends based on ewes mated are presented for the S flock in Figure 2. Positive permanent environmental effects were observed for S. However, the annual rate of increase was similar in S and EC flocks (.21± .07% and .22± .13%, respectively; Table 4). The service sire effects were variable from year to year (Figure 2), and their annual trend was negative (-.32±.15%) for S flock and positive (.64±.29%) for EC flock (Table 4). The difference in service sire trend between flocks was due primarily to the large differences in service sire effect means in 1993 (-4.0% for S vs 9.2% for EC). Estimates of genetic trends in S and EC based on ewes mated are given in Figure 3. The genetic origin of these two flocks was the same. The response observed in EC flock might be due to natural selection.

Genetic trends, calculated by regression of the ewes' average breeding values on year of mating (1989 to 1994), showed an increase in breeding values for spring fertility in both S and EC (Table 4). Rate of increase based upon breeding values of all ewes mated was 1.34 ± .11% in line S compared with .57 ± .19% in EC. A significant difference ($P < .05$) between S and EC was observed.

Fall litter size. The genetic trends by LB, EM and MA in line S for fall litter size are shown in Figure 4. The genetic trends for fall litter size was positive in the selected line only (Figure 5), whereas average permanent environmental effects

remained close to zero (Figure 6). The regression of ewes' average breeding values on year of mating was .0065 ± .0013 lambs/yr in line S compared to .0024 ± .0022 lambs/yr in EC (Table 4). Genetic trends for litter size found in this study were larger than the values of .0028 lambs/yr reported by Bhuiyan and Curran (1993) for Romney Marsh sheep selected for prolificacy and litter size using mixed model techniques. There are no other published estimates of genetic and environmental trends obtained with an animal model for litter size in sheep. In general, the genetic gains found in the present study are within the range of those reported in the literature (Turner, 1978; Hanrahan, 1982; Bradford and Quirke, 1986; Owen et al., 1986). However, the specific selection objective in the above studies was to increase number of lambs born, whereas in our study the specific selection criterion was the ability of ewes to conceive in May and June.

Implications

This study indicates that selection for spring fertility was effective and resulted in positive genetic gains in both spring fertility and litter size. Rate of increase was higher for fertility than litter size, which is due to direct selection pressure on fertility. In addition, the high correlated genetic response in litter size confirms the relatively high genetic correlation between fertility and litter size reported in the previous chapters. The present study also indicates that mixed model technique can be used for estimating genetic and environmental trends in reproductive traits in sheep.

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Table 5.1. Summary information of spring fertility and fall litter size.

	Spring fertility	Fall litter size
Animals in pedigree file	2596	2596
Total no. of records	1102	447
No. of S records	774	311
No. of EC records	328	136
No. of ewes	420	230
No. of service sires	52	52

Table 5.2. Average inbreeding coefficients, standard deviation and maximum inbreeding coefficient for all lambs born by year of birth and flock.

	Flock					
	Selected flock			Control flocks		
Year	$\bar{x}$	SD	Maximum	$\bar{x}$	SD	Maximum
Base animal	.0350	.0142	.0782	.0350	.0142	.0782
1989	.0325	.0368	.1320	.0448	.0632	.2580
1990	.0297	.0351	.1620	.0219	.0175	.0610
1991	.0294	.0360	.1600	.0326	.0314	.1400
1992	.0323	.0510	.2482	.0363	.0468	.2470
1993	.0434	.0569	.2570	.0250	.0348	.1345
1994	.0420	.0460	.2610	.0265	.0421	.2610

Table 5.3. Least-squares year effects ($\dot{\dot{P}}$), and REML average yearly breeding values ($\hat{BV}$), genetic, and environmental trends and yearly phenotype means ($\hat{P}$) for spring fertility in selected and environmental flocks combined.

			Environmental trend			
Year	$\dot{\dot{P}}$	$\hat{BV}$	PE[a]	SS[b]	Y[c]	$\hat{P}$
1989	.096	.011	-.0001	.0016	.085	.097
1990	.439	.024	.001	.00005	.403	.430
1991	.378	.032	.001	.0037	.345	.382
1992	.314	.046	.004	.0062	.253	.309
1993	.314	.051	.009	-.004	.242	.299
1994	.531	.061	.009	.0013	.450	.522

[a] Permanent environmental effects.

[b] Service sire effects.

[c] Mixed model estimates of year effects.

Table 5.4. Annual genetic and environmental trends (Δ) and their standard errors (s.e.) for S and EC flocks.

	Flock			
	S		EC	
Trait	Δ	s.e.	Δ	s.e.
Spring fertility				
1. Genetic trends				
Animal	.0091*	.0014	.0024	.0020
Ewe	.0134*	.0011	.0057	.0019
Mating	.0132*	.0007	.0051	.0015
2. PE trends	.0021	.0007	.0022	.0013
3. SS trends	-.0032	.0015	.0064	.0029
Fall litter size				
1. Genetic trends				
Animal	.0087+	.0014	.0025	.0021
Ewe	.0065	.0013	.0024	.0022
Mating	.0089*	.0011	.0020	.0015
2. PE trends	.00	.00	.00	.00

+ Trends in S and EC differ (P < .10)

* Trends in S and EC differ (P < .05)

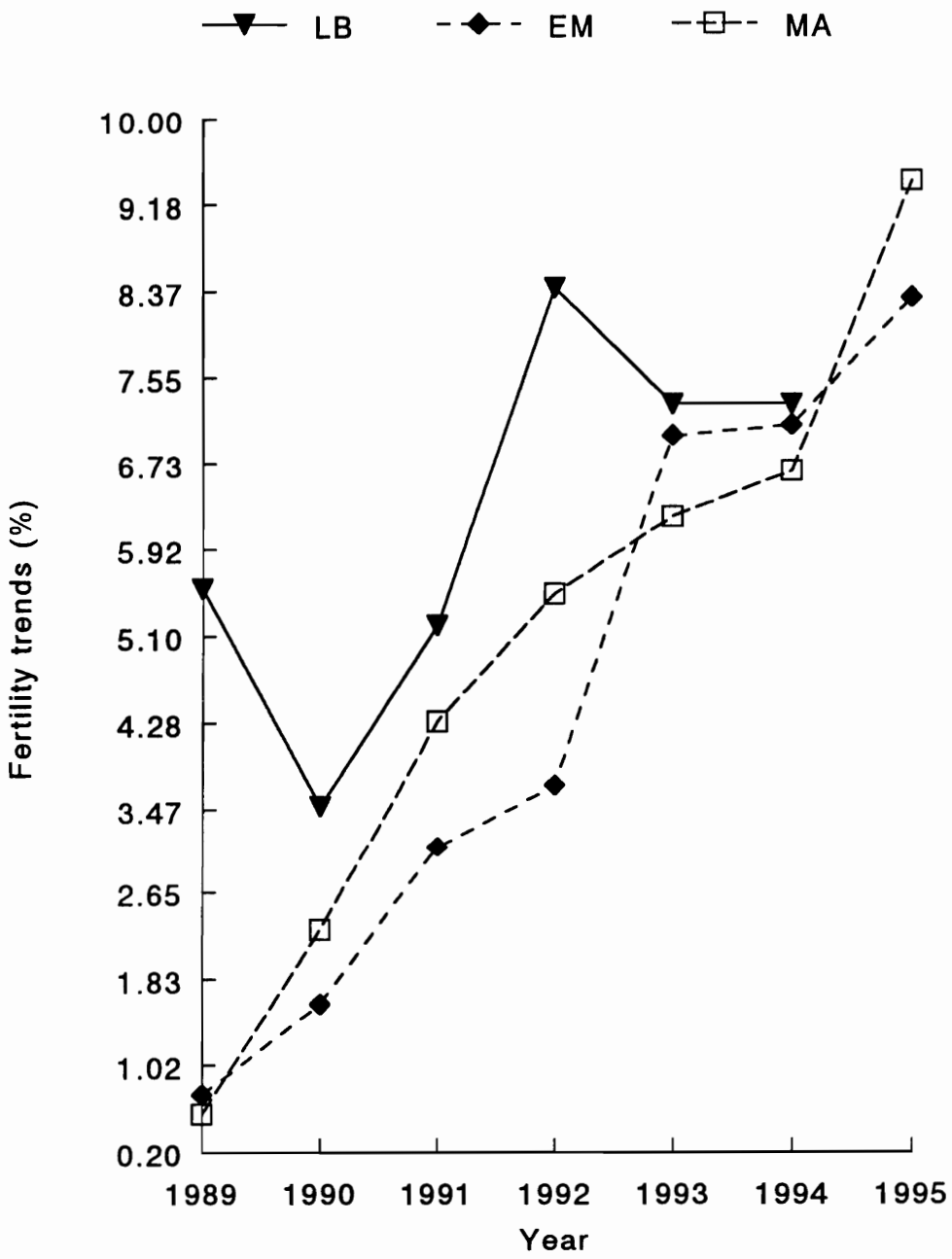

Figure 5.1. Estimates of genetic trends in line S for spring fertility by averaging breeding values of lambs born (LB), ewes mated (EM), and mating averages (MA).

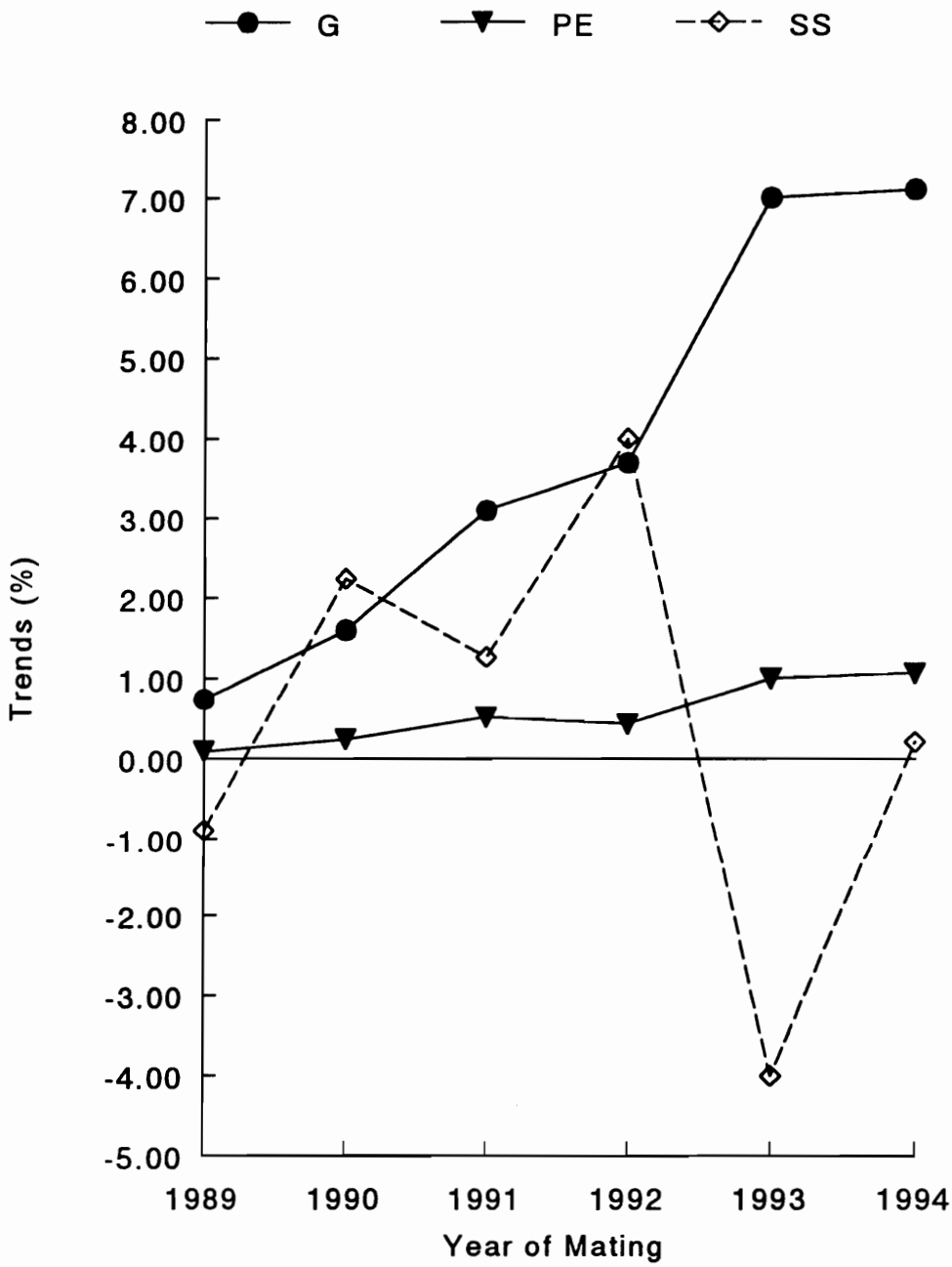

Figure 5.2. Estimates of genetic(G; based on EM), permanent environmental (PE) and service sire (SS) trends for spring fertility in selected flock.

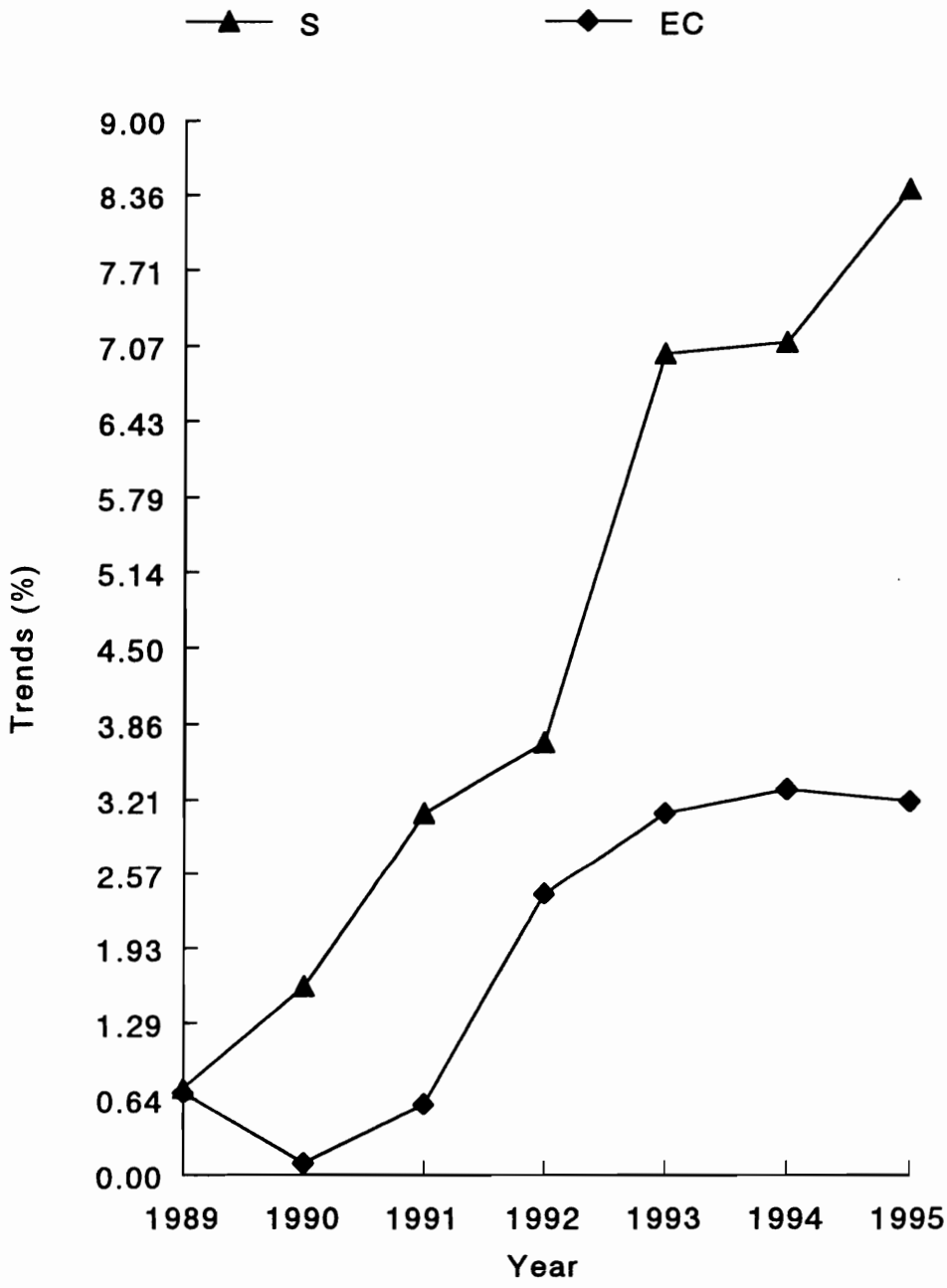

Figure 5.3. Estimates of genetic trends based on EM for spring fertility in selected (S) and environmental control (EC) flocks.

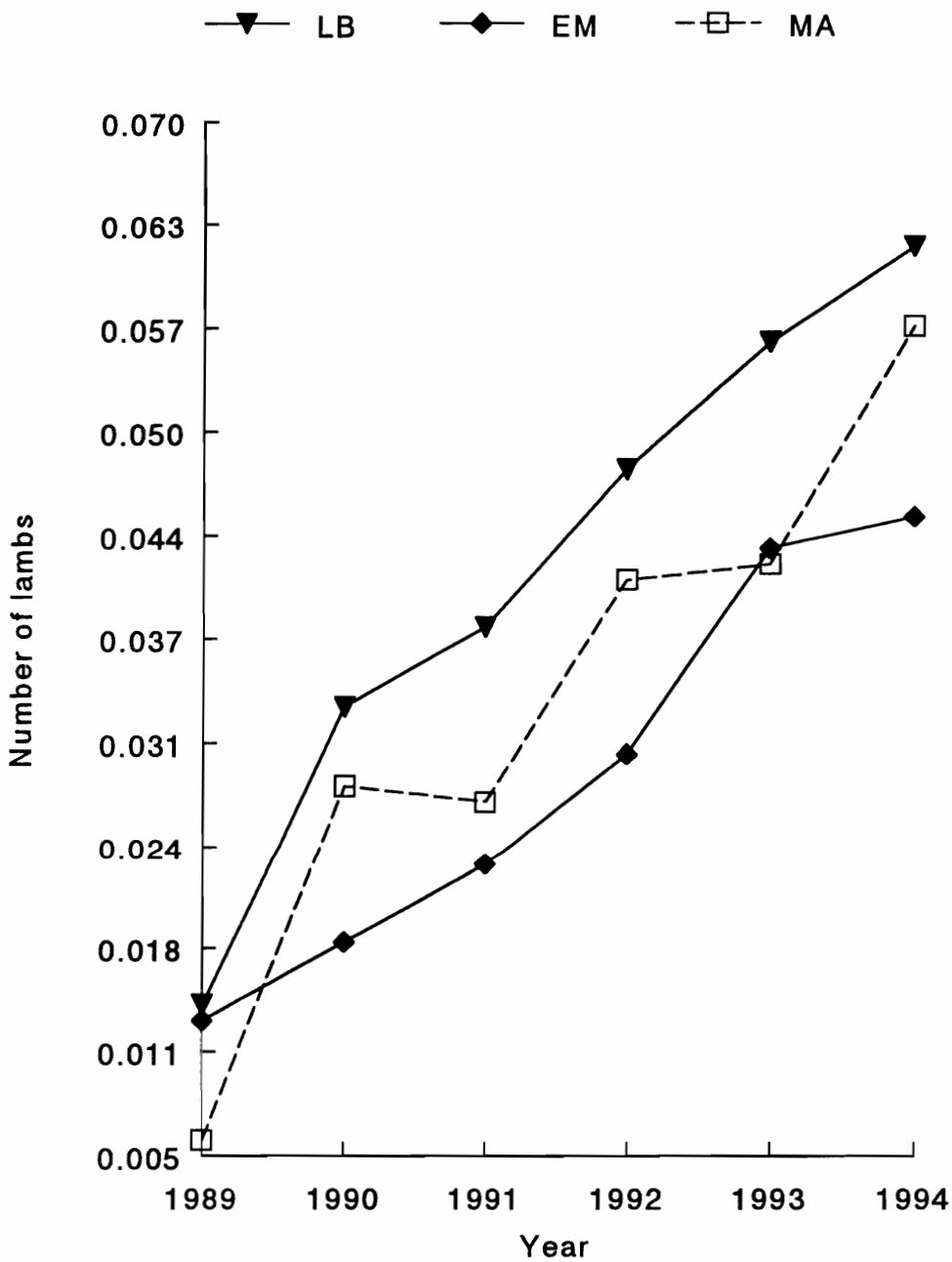

Figure 5.4. Estimates of genetic trends in line S for fall litter size by averaging breeding values of lambs born (LB), ewes mated (EM), and mating averages (MA).

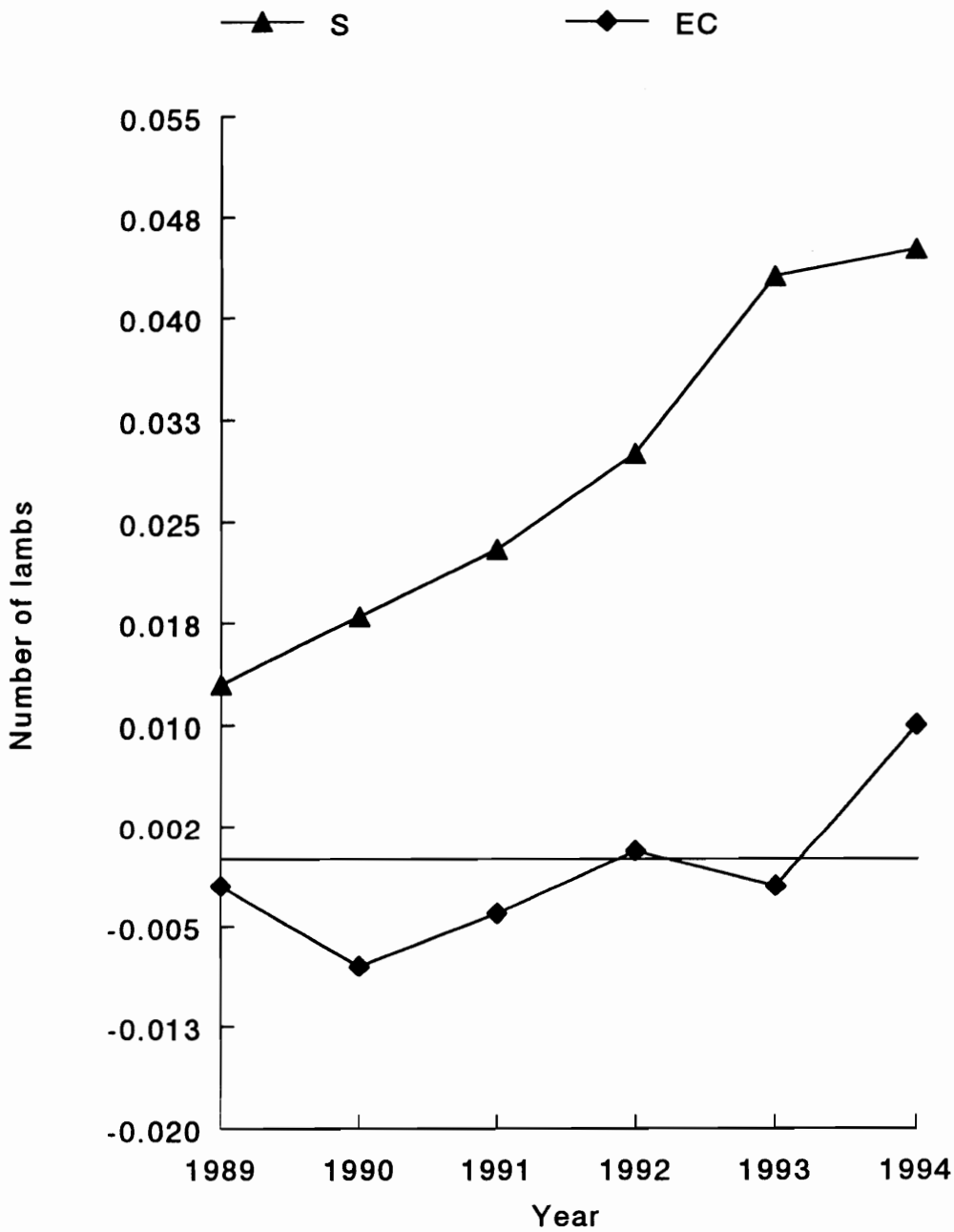

Figure 5.5. Estimates of genetic trends based on EM for fall litter size in selected (S) and environmental control (EC) flocks.

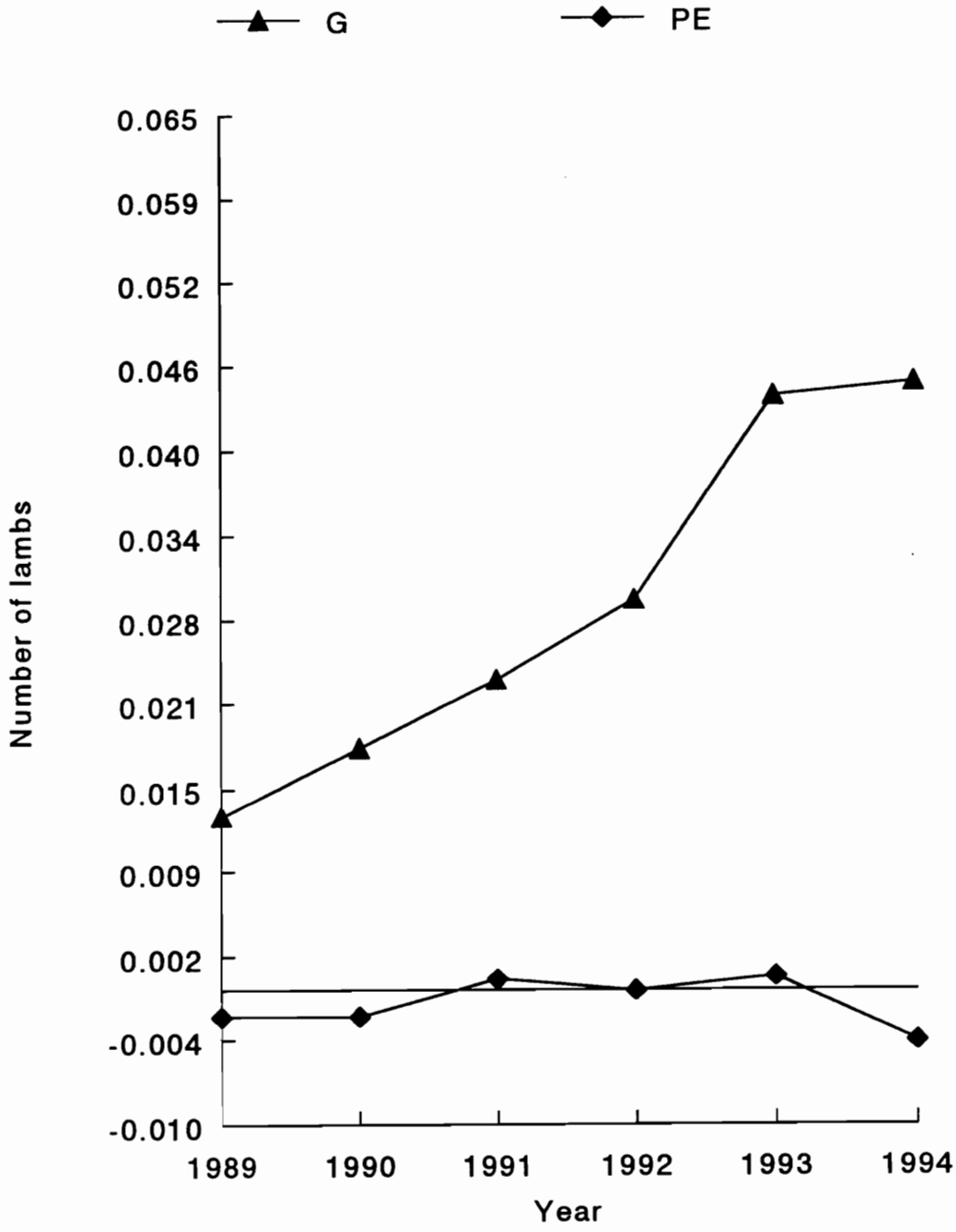

Figure 5.6. Estimates of genetic(G; based on EM) and permanent environmental (PE) trends for fall litter size in Selected flock.

Chapter 6

Selection for Fall Lambing in Crossbred sheep
II. Genetic changes in Growth Traits and 90-d Scrotal Circumference

Summary

Mixed model methodology was applied to estimate genetic changes in crossbred sheep under selection for spring fertility. Selection was successful for spring fertility and fall litter size, with more improvement made in spring fertility. Correlated response were also analyzed using mixed model methodology for birth, weaning and 90-d weight, and 90-d scrotal circumference. Selection for spring fertility did not cause correlated changes in birth weight. Both direct and maternal additive genetic trends for weaning weight were positive and significant ($P<.05$) in both the S and EC flocks. The increase in additive maternal breeding value ($.023\pm .006$ kg/yr for S and $.023\pm.011$ kg/yr for EC) was greater than that for direct breeding value. The estimated genetic trend for 90-d weight was positive and similar in both flocks at .03 to .04 kg/yr. Estimates of genetic trend for 90-d scrotal circumference were variable in both flocks, depending on the type of information used.

Key words: Selection, correlated response, crossbred sheep, spring fertility, mixed model methodology).

Introduction

Improving the genetic potential for out-of-season breeding through selection within existing breeds has a great potential to improve the efficiency of lamb production.

In chapter 5 of this thesis, the effects of selection for spring fertility on fertility and litter size in a crossbred population containing 50% Dorset, 25% Rambouillet and 25% Finnsheep inheritance were reported. Rates of change were positive and higher for spring fertility than fall litter size, which was due to direct selection pressure on fertility. In this chapter, we report information on the correlated changes in birth weight, weaning weight, 90-d weight and 90-d scrotal circumference, resulting from the selection for spring fertility.

Materials and Methods

Correlated traits investigated were birth weight, weaning weight, 90-d weight and 90-d scrotal circumference measurement. Data were adjusted for environmental effects of ewe age, birth type and sex of lamb, and statistical analyses were carried out as described in the previous chapters. Numbers of animals with records for selected (S) and environmental control (EC) flocks are presented in Table 1.

Results and Discussion

Regression coefficients of mean annual breeding values for weights and scrotal circumference on year mating based upon average breeding values of all lambs born or upon all ewes mated are given in Table 2 for S and EC flocks. The flocks did not differ significantly in rate of change in any of the traits analyzed. Selection for spring fertility did not cause any correlated change in birth weight (Table 2).

The direct and maternal additive genetic trends for weaning weight, based upon ewes mated (EM), are depicted in Figures 1 and 2, respectively. Selection for fall lambing caused a correlated increase in both direct and maternal effects in both flocks (Table 2). The regressions of average direct breeding values on year were .011$\pm$ .002 and .015$\pm$ .004 kg/yr in S and EC flocks, respectively. The corresponding regressions of additive maternal effects on year were .023$\pm$.006 and .023$\pm$.011 kg/yr for S and EC flocks, respectively.

In the case of 90-d weight, positive correlated changes were found in both flocks (Figure 3). Genetic trends, calculated by regression of ewes average breeding values on year of mating (1989 to 1994) showed a similar increase for 90-d weight in both S and EC. Rate of increase was .030 $\pm$ .004 and .041 $\pm$ .013 kg/yr in S and EC, respectively. The higher response observed for 90-d weight may be due to selection for testis size (Lee and Land, 1985).

The genetic trends based upon regressions on breeding values for lambs born (LB) and EM are depicted for scrotal circumference in Figure 4 and 5, respectively, for both flocks. Owing to the small number of individuals with records in both flocks (152 for S and 25 for EC; Table 1), estimated genetic trends varied widely for LB and EM. In addition, genetic trends based on EM included all ewes mated in which most

of their male relatives had not been subjected to selection for larger testis size, thus correlated change was variable in the S flock.

Implications

In general, selection for spring fertility did not cause significant correlated changes in traits analyzed. Thus, no genetic antagonism resulted from the selection for fall lambing.

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Table 6.1. Number of fall lambing records for birth, weaning and 90-d weights and 90-d scrotal circumference for S and EC flocks.

	S	EC
Birth weight	483	190
Weaning weight	427	150
90-d weight	396	113
90-d scrotal circumference	151	25

Table 6.2. Annual genetic trends (ΔG) and their standard errors (s.e.) for S and EC flocks.

	Flock			
	S		EC	
Trait	ΔG	s.e.	ΔG	s.e.
Birth weight	-.002	.0011	.006	.003
Weaning weight				
Direct effects	.011	.002	.015	.003
Maternal effects	.023	.006	.023	.011
90-d weight	.030	.004	.041	.013
90-d scrotal circumference				
1. Animal[a]	.032	.0035	-.008	.050
2. Ewe[b]	-.005	.0018	.012	.005

[a] Lambs born.

[b] Ewes mated.

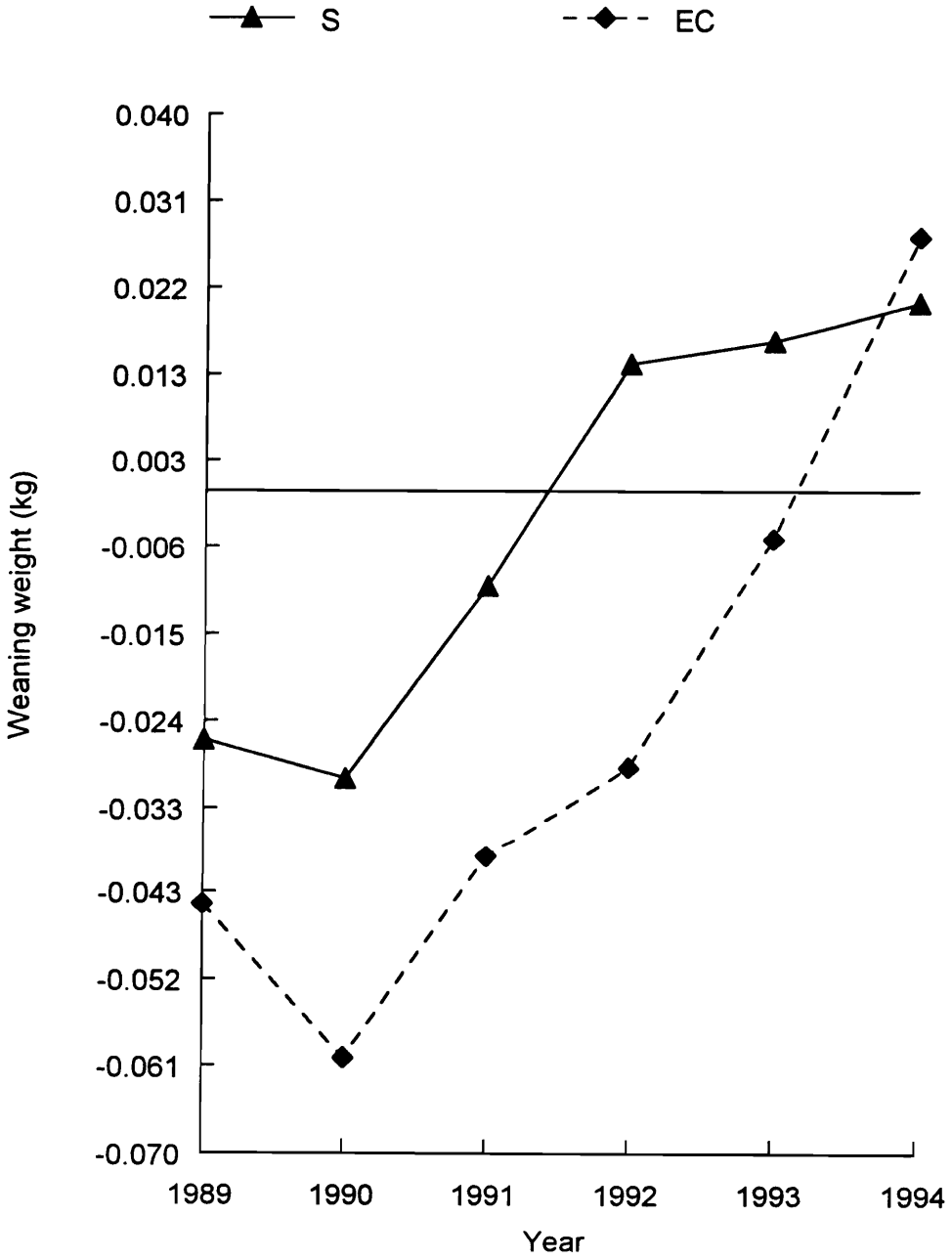

Figure 6.1. Estimates of genetic trends by averaging breeding values of ewes mated (EM) for weaning weight in S and EC flocks.

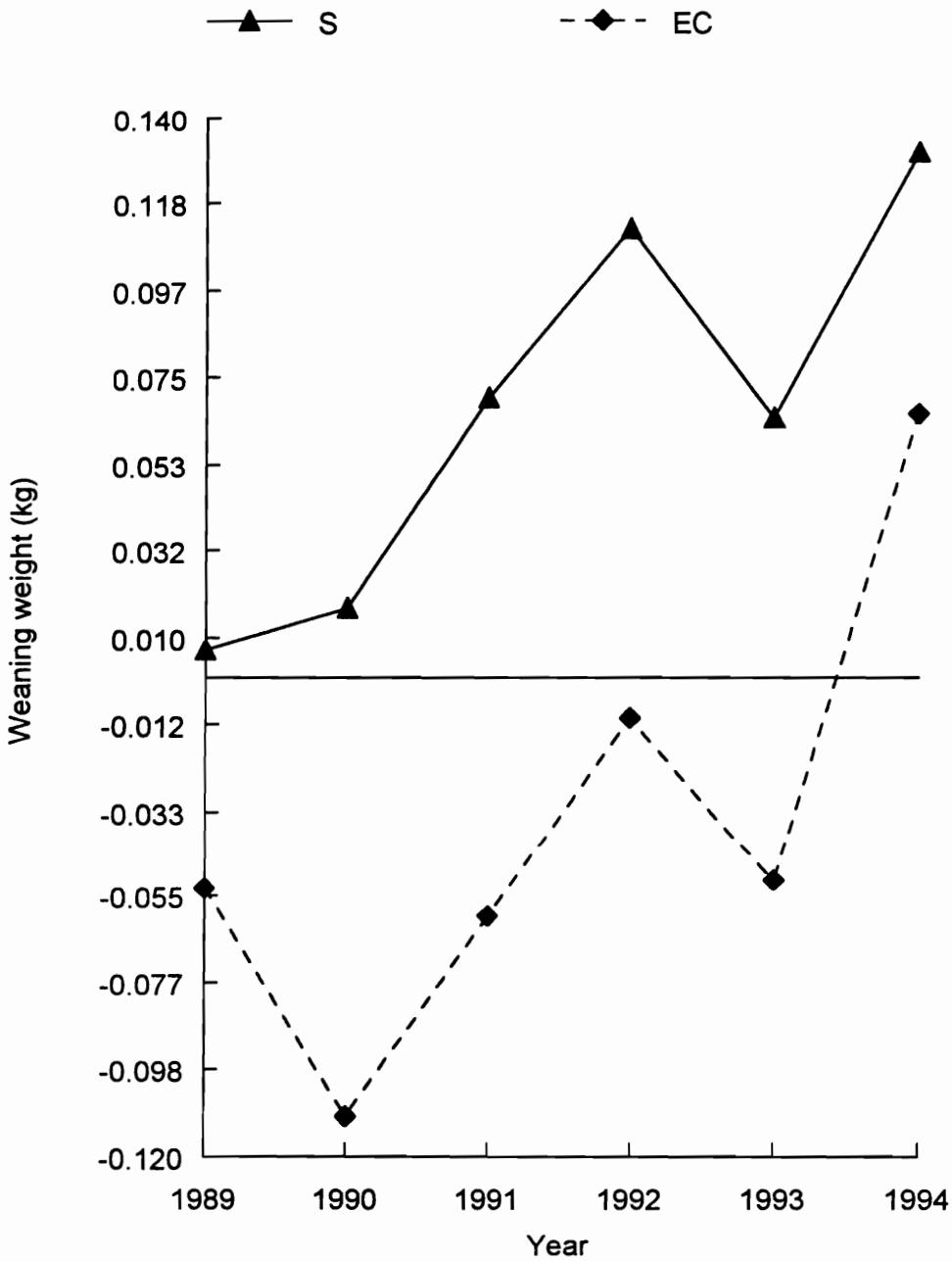

Figure 6.2. Estimates of genetic trends by averaging breeding values of EM for maternal weaning weight in S and EC flocks.

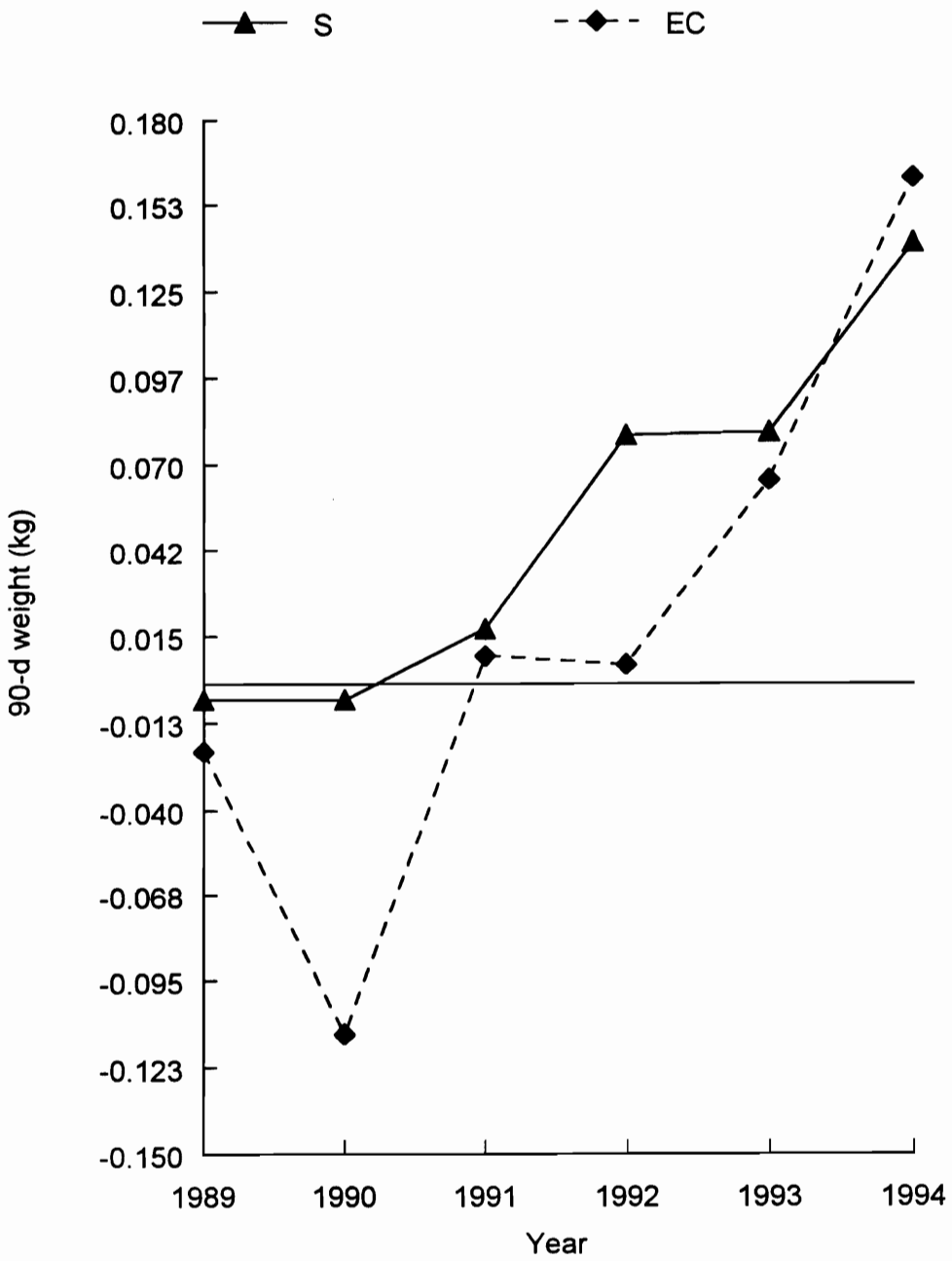

Figure 6.3. Estimates of genetic trends by averaging breeding values of EM for 90-d weight in S and EC flocks.

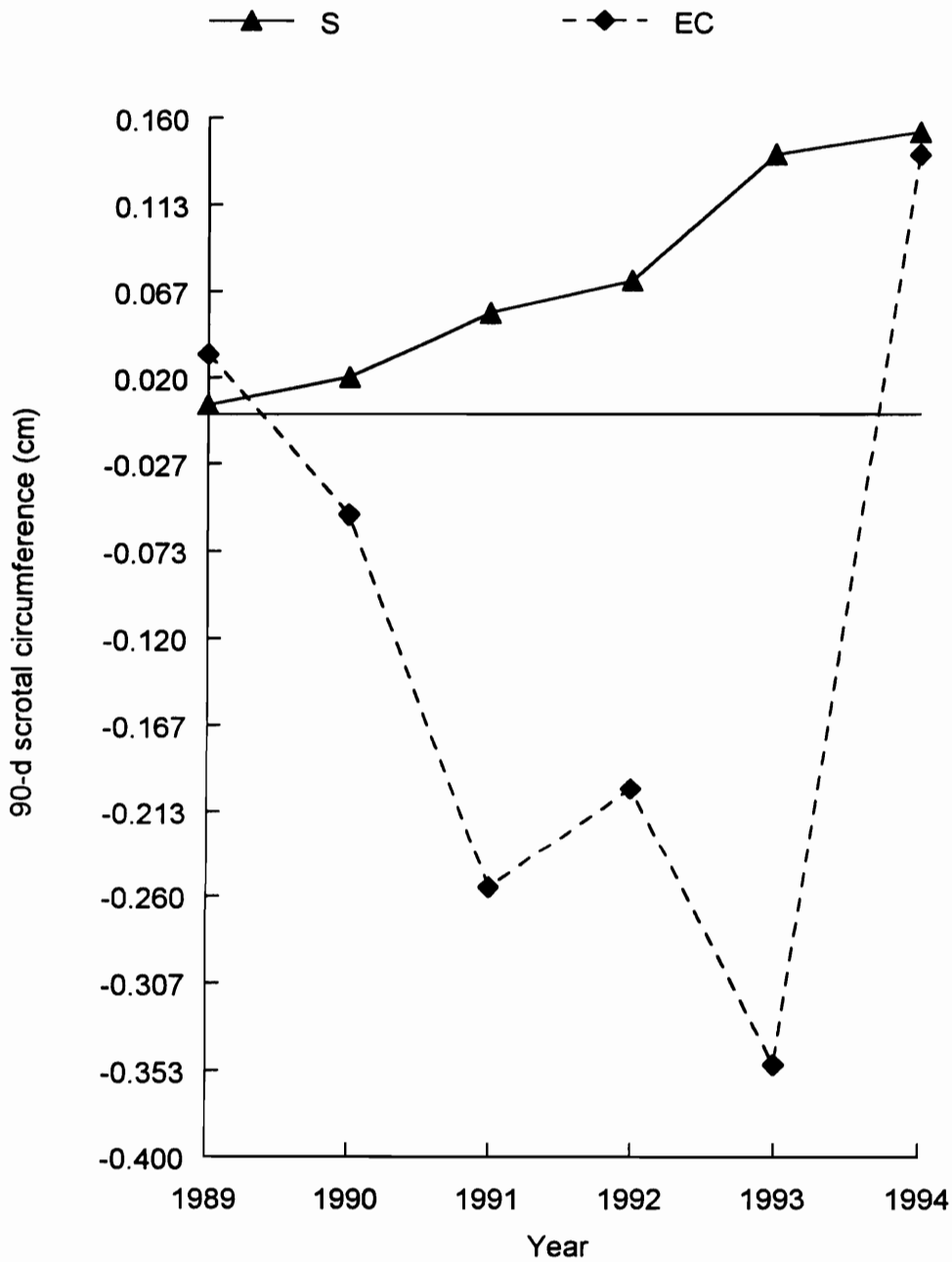

Figure 6.4. Estimates of genetic trends by averaging breeding values of lambs born (LB) for 90-d scrotal circumference in S and EC flocks.

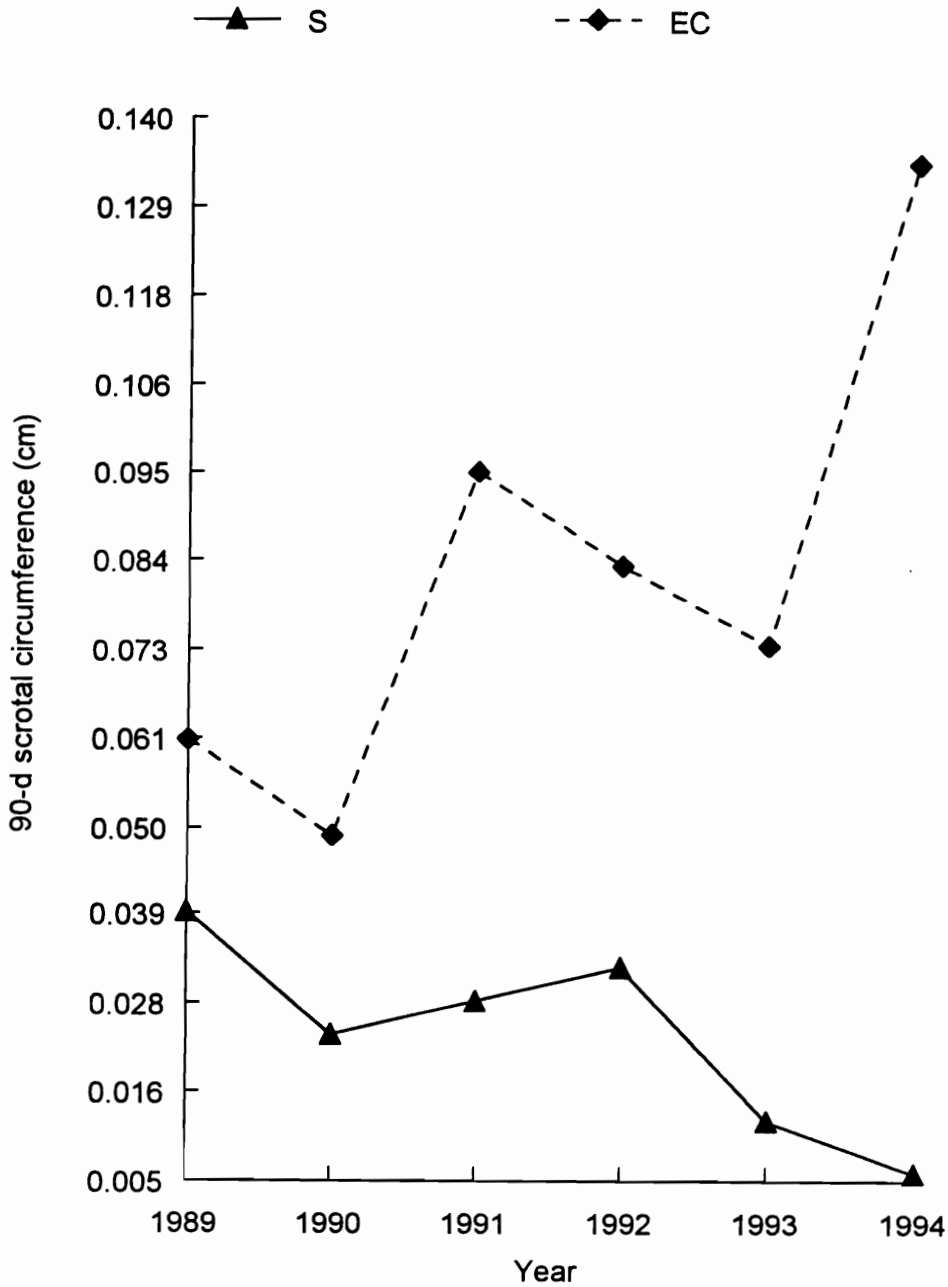

Figure 6.5. Estimates of genetic trends by averaging breeding values of EM for 90-d scrotal circumference in S and EC flocks.

Chapter 7

General Conclusions

Procedures to estimate genetic parameters and breeding values for spring fertility in out-of-season breeding programs are relatively more complex than those required for other traits. This result occurs because of the all-or-none expression of fertility and because a successful mating is a manifestation of a successful male and female interaction that can not be attributed to one parent alone. The binary expression of fertility means that ewes in a flock can be categorized for reproduction into only two categories (those that lamb and those that do not lamb). Thus, it is difficult to discriminate among ewes within these two classes. Linear approaches to estimation of genetic parameters and breeding values for fertility and litter size do not consider the discrete nature of the data. As alternatives, non-linear models such as the threshold and Poisson models have been proposed to handle analyses of discontinuous data in animal breeding (i. g., Harville and Mee, 1984; Meijering and Gianola, 1985; Foulley and Gianola, 1987; Misztal et al., 1989). Matos (1993) found that heritability estimates for reproductive performance in Rambouillet and Finnsheep populations were greater when derived using non-linear approaches than when obtained with a linear approach. It can therefore be concluded that application of a non-linear

approach may exploit more variation in spring fertility than that estimated by a linear approach.

Since both female reproduction and testis growth are mediated through the same hormonal pathways (i.g., Land and Carr 1975), and hence, gene complexes, it was expected that the genetic correlation between fertility and 90-d scrotal circumference might be higher in out-of-season breeding than in the normal breeding season. However, for the small number of observations available in this study, the genetic correlation was somewhat less than expected from previous experiments. Use of larger data sets may , however, modify this conclusion.

One could logically ask the question " why breed out of season?" The major reason is to produce products wanted by the consumer. The consumer wants a year around supply of lamb. It is well documented that the majority of the lambs in the US are born in a 2-3 month period in the spring and are ready for market in the fall and early winter (SID, 1990). Thus, the current seasonally short supply periods provide some economic stimulus to out of season breeding. Another reason for breeding out of season is to optimize the use of farm resources. However, there also some constraints to economically viable out of season production. The first constraint is feed resources. Naturally, the normal fall breeding season and spring lambing generally synchronizes the peak nutrient needs of the sheep with the peak of natural feed supplies. Deviations from this breeding and lambing cycle may result in the need for expensive purchased feed inputs. The second constraint is farm facilities. Lambing in fall may require fewer facilities than winter or early spring lambing.

From the results found in this thesis, it can be concluded that genetic improvement of out of season breeding performance is very promising. However, breeders and producers need to take all inputs and outputs into account before incorporating out of season breeding into their system.

Since spring fertility reached 85% for adult ewes in the final year, the question that posts is "where to go from here?" It has been noticed that several ewes and their daughters lambed in fall at every opportunity . It is important to determine whether these ewes cycled continuously during the year and they were induced to cycle by the ram effect. This can be determined by drawing a random sample of these ewes and monitoring changes of their hormonal profile year around. This experiment would aid in determining the genetic mechanisms that control cycling behavior of these ewes. Along with this experiment, genetic and biochemical approaches should be applied to localize and identify gene(s) corresponding to out of season breeding ability.

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Vita

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