A MIXED MODEL APPROACH FOR SELECTING MERINO EWES

by

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CHAPTER 1

1. INTRODUCTION

1.1 General

The South African Merino is a specialist wool producing sheep breed and selection efforts in the past have been largely directed at increasing the quantity and quality of its wool. However, there is an old English adage (quoted by Youatt, 1837) which reads: "Ewes yearly by twinning rich masters do make; the lambs of such twinners for breeders go take." This emphasises the general importance of reproductive performance and also indicates a real possibility that it can be improved by selection. As far as the Merino is concerned, the position is perhaps best summed up by Laubscher (1965) who states that producers must realise that the weaned lamb is as much a component of production as the wool fleece.

Low reproduction is cited by many researchers (summarised by De Klerk, Düvel and Terblanche, 1983) as one of the most important bottle-necks in the South African wool industry. According to the above-mentioned authors, the average lambing percentage in South African Merino flocks was only 71,0% in 1982, while the average figure quoted for Spain, the historical home of the Merino, is 110,0% (Hernandez, 1986). It therefore stands to reason that the genetic improvement of reproductive performance should receive at least as much attention as the future improvement of wool production.

Much research has been conducted into ways and means of genetically increasing reproductive performance in sheep. Several of the components of reproduction have been investigated and at present it seems as if selection for higher prolificacy is the most promising (Turner, 1977). The validity of the general recommendation (Turner, 1977) that replacements be selected from multiple-born

animals has also been verified in South Africa (Cloete,1986). Indirect me-thods such as selection for ovulation rate, early oestrus, short interlambing period, testis circumference and even haemoglobin type have been researched worldwide with inconsistent results.

An alternative to the conventional method of selecting ewe replacements on one or more single components of reproduction is to make use of the concept of measuring the total lifetime productive capabilities of every ewe. In a study on lifetime ewe efficiency, Saoud and Hohenboken (1984b) conclude that selec-ting twin or single born ewes as the sole criterion, would not be expected to improve the overall productive merit of the flock. In a subsequent article, Saoud and Hohenboken (1984c) suggest that a scheme allowing selection of some single-born ewes would be more appropriate. A definite shortcoming in Saoud and Hohenboken's (1984) definition of ewe production was however that "...wool income was not included because accurate wool production records from indivi-dual ewes were not available."

According to the arguments of Winters (1940) and De Lange(1979), measurement of ewe productivity should be based on the following general principles:
Ewe replacements for a ram breeding nucleus should be selected only after proof exists of the reproductive merit of the ewes under commercial condi-tions. Furthermore, when the lamb or lambs that a ewe produces is regarded as a component of production (Laubscher, 1965), the rearing ability of the ewe (mothering ability and milk production) as expressed by the weaning mass of her lambs, becomes as important as parturition. When using total mass of lamb weaned by the ewe as selection criterion, it is extremely difficult to sepa-rate fertility and rearing ability since a record of zero mass of lamb at weaning could be due to either lower fertility or poorer mothering ability and milk production (or incidental deaths).

In the case of woolled sheep, inclusion of wool production becomes an additional complicating factor. Winters (1940) used maiden fleece mass of the ewe. Repeatability estimates for fleece mass are generally high (Turner and Young, 1969) but for obvious reasons data from dry sheep are normally used when these estimates are made. Use of the fleece mass of the ewe after lambing and rearing of the lamb would account for individual differences in the ability to produce both products (wool and lamb) simultaneously.

1.2 Current scheme for measuring ewe productivivity

A scheme for measuring ewe productivity, based on the principles above, was developed and implemented during 1983 by the National Performance and Progeny Testing Scheme for Woolled Sheep. This was devised mainly to provide a selection criterion for ewes in open nucleus breeding schemes where ewe replacements for a ram breeding nucleus are selected not only from the nucleus itself but also from large numbers of commercial ewes. This is done either by a group of farmers forming a group breeding scheme or by individuals with large commercial flocks. Preliminary selection is based on maiden performance in greasy fleece mass and body mass.

The information supplied by this scheme to its members, is as follows:

Ewe number

Number of times mated

Number of times lambed

Number of lambs born

Number of lambs weaned

Total production to date

(i) kg wool

(ii) kg lamb

Number of lambs with weaning mass ratio of less than 70 produced by each

ewe

Ewe production record (EPR)

The items on reproduction above is derived in the normal way and needs no further discussion. The last two items (number of lambs with weaning mass ratio of less than 70 and ewe production record) are both based on the following calculations:

Percentage deviations within management groups are calculated separately after lamb masses have been corrected for age, sex and differences in standard deviation among groups. In the case of multiple births, weaning masses of the multiples are summed before calculating percentage deviations in order to derive percentage deviation in total mass of lamb weaned by a ewe. The fact that no correction is made for birth status is in agreement with the method for calculating ewe productivity used by Saoud and Hohenboken (1984) who corrected individual lamb masses for sex but not for type of rearing.

Record is kept of the number of lambs with a percentage deviation in weaning mass of less than 70 by calculating a second percentage deviation from the management group average after the same adjustments as mentioned above were made. In this case, however, no summation of multiple born lambs is performed since the purpose of this measurement is to identify ewes incapable of raising multiple lambs satisfactorily.

The ewe production record (EPR) is calculated as the combination of each ewe's lamb and wool producing ability. The obvious method of combining corrected mass of lamb(s) weaned and greasy fleece mass would be summation after weighting each according to its relative economic importance.

As general guideline to the members of the Scheme for measuring ewe productivity, the relative economic importance of lamb liveweight to wool production is supplied by using the following method:

Firstly, time trends of the price for both mutton and wool are constructed. Figure 1.1 provides the mean annual realised price for mutton and greasy wool over the past ten years.

FIGURE 1.1   MEAN ANNAUL REALISED PRICE FOR MUTTON (IN CONTROLLED AREAS) AND GREASY WOOL

Source: S.A. Wool Board, S.A. Meat Board and Abstract of Agricultural Statistics (Government Printer, Pretoria).

By fitting linear regression equations to the above graphs, the relative predicted price ratios for live mass of lamb (based on a carcass yield of 48%) and greasy wool were calculated as 1:2.88 for 1988. In the ten year period depicted, mutton prices rose by 18% and wool prices by 17% annually. It seems therefore, that the relative prices of the two products remain fairly stable

and the ratio between them can safely be rounded off to 1:3. This ratio which is also used in the present study is, interestingly enough, not far deviant from the ratio of 1:3.4 suggested by Winters (1940). The ratio will, of course, be dependent on local market conditions and one ratio can therefore not be recommended for universal use by all members of the Ewe Productivity Scheme. An estimate of ewe productivity, termed ewe production record (EPR), is obtained by combining the percentage deviation in wool production with that of total mass of lamb weaned on the basis of the price ratio.

Use of EPR proved to be an efficient management tool to measure returns from the ewe flock. France, Neal, Probert, and Pollatt (1983) even used ewe productivity in the case of agricultural modelling to optimise income per unit of area of land. The prime objective in both cases (above), can therefore not be regarded as being in conflict with genetic aims.

Results obtained thus far in group breeding schemes, indicate large differences in estimated total income from comparable ewes over the same number of lambing seasons. In one group breeding scheme, for instance, the estimated income of the top half of the ewes was nearly double that of the bottom half over four lambing seasons. This variation was still prevalent in spite of the strict selection procedure, namely of selecting only 40% of the available ewes from the nucleus and roughly only five percent of the available ewes from contributing flocks on maiden performance. Variation, the prerequisite for genetic improvement, was therefore still present, and as this variation represents total income, further investigation is warranted.

In a preliminary investigation (Delport, 1984, unpublished) on 175 ewes born in the Carnarvon experimental flock, a correlation of 0.54 ± 0.12 was found between first EPR and remaining lifetime EPR (after five mating seasons). Combination of the first and second EPR, yielded a correlation of 0.70 ± 0.09

with lifetime EPR. As the number of ewes lambed was only roughly 60%, the EPR's were highly influenced by zero values for total mass of lamb weaned. Since the repeatability of lambing performance has generally been found to be low, these estimates are probably lower than would be found in a more favourable situation with a lambing percentage of roughly 90%. It does seem, therefore, that in practice two subsequent records of EPR would suffice as an indication of lifetime production.

1.3 Shortcomings of the current scheme

The main problem with the widespread measure of ewe productivity in non-woolled sheep breeds as a mere calculation of the total mass of lamb weaned is that it is a combination of two categorical traits (fertility and fecundity) and a continuous trait (maternal ability defined as rearing ability and milk production). Most recording schemes treat the number of lambs born or reared as a continuous trait even though it may take only two or three values and thus does not fulfil the requirements of continuity (Rae, 1984).

Another problem is that in specialised wool producing breeds such as the Merino, it is sometimes assumed that wool production is negatively related to lamb production (Cloete 1986). Erasmus, De Lange and Delport (1984) however found that large differences in both these traits exist in two Merino flocks measured over two years after heavy culling on maiden fleece mass. It was also found that the regression of total mass of lamb weaned on post-weaning fleece mass was not significantly deviant from zero. Laas (1982) found that with Döhne Merinos, weaning mass of lamb(s) had a negligible effect on the wool production of the ewe(s). It therefore seems justifiable to investigate the ewe's ability to produce both wool and lamb (mutton) which could be used as a selection criterion to increase total productivity.

Apart from the two fundamental problems discussed above, the following short-comings in the technical execution of the Ewe Productivity Scheme can be listed:

* Phenotypic deviations as an indication of "breeding values" for total mass of lamb weaned are calculated for ewes by making use of information on relatively small number of progeny of the ewe only. Therefore full use is not being made of advantages provided by using selection index theory to incorporate information on other relatives as well.

* The fact that both the phenotypic and genetic (co)variance structures are ignored, imposes serious bias on the effectiveness of any selection practised (Quaas and Pollak, 1980).

* The concept of EPR is implemented by making use of within year, flock and management group ratios. The obvious consequence is therefore that comparison over years and on an across flock basis to identify superior females is rendered impossible.

1.4 Objectives

The objective of the present study is to develop and investigate possible methods of estimating breeding values for ewe productivity by multiple trait mixed model methodology in Merino sheep.

Since mass of lamb(s) weaned by a ewe is a function of two categorical traits, *viz.* fertility and fecundity and one continuous trait *viz.* maternal ability (mothering ability and milk production), the logical way of handling ewe productivity would be to apply a multiple trait model with fertility, fecundity, maternal ability and fleece mass as different traits. The application of such a complex model is at present not practically feasible. Apart from computational limitations, determination of (co)variance structure poses a serious

problem. In this regard, Landis and Koch (1977), quoted by Rae and Anderson (1982), mention that variance and covariance estimation from categorical data has progressed only as far as the one-way classification model and that calculating covariances between discrete and continuous random variables requires further investigation. In view of the above limitations, it was decided to use total mass of lamb weaned, the end product of the ewe's total reproductive cycle, together with fleece mass, in a multiple trait mixed model analysis.

Application of Henderson's mixed model methodology to the concept of ewe productivity offers an avenue to exploit relationships. Firstly, breeding values can be estimated utilising information from all female relatives for the possible prediction of young ewes' breeding values even before they have reared progeny, and secondly, breeding value solutions for sires regarding their ability to produce daughters with higher total productivity could possibly be obtained.

Another problem is the possible negative relationship between lamb and wool production which may be regarded as a biological reality (if it exists). Effective selection is the only possible solution to this problem.

Multiple-trait analysis is computationally extremely demanding (Quaas and Pollak, 1980). The use of canonical transformation of data when all traits are measured on all animals, may render multiple-trait analysis a practical possibility (Arnason, 1984). With canonical transformation the multiple-trait model is reduced to n single trait models, where n equals the number of traits. Although this procedure does not provide for sequential culling (Arnason, 1984) it is ideally suited for analising experimental data which comply to the prerequisite of having observations on all animals for all traits. The application of this technique on a broad basis in the woolled sheep may therefore be limited. It is however, hopefully envisaged that the

computer programmes developed for this study and the knowledge obtained in their application will find more widespread use in solving other, possibly even unrelated, problems.

When investigating a new procedure of evaluating animals, it may be tempting to compare an existing scheme with the one under development. Henderson (1975b), however, clearly states that "applying different methods to the same set of data has limited value except possibly to conclude that methods differ much or little when applied to that particular set of data (p. 760)". From this reasoning by Henderson it is clear that a comparison between the current scheme and a mixed model approach would serve little purpose (the theoretical advantages being obvious). It was therefore decided to concentrate on the development of a mixed model procedure to facilitate the effective application of ewe productivity as a selection criterion. The effect of selection for maiden ewe performance on later ewe productivity will also be considered.

2. DATA DESCRIPTION

2.1 Prerequisites to which the data must comply

According to the theoretical definition of ewe productivity presented in Chapter 1, both total mass of lamb weaned and wool production need to be measured for the determination of a "ewe productivity index" (EPI) which can, in contrast to EPR (an index based on ratios) be defined as (breeding value of total mass of lamb weaned) + 3(breeding value of post-weaning fleece mass of ewe) summed over the ewe's first two lambing opportunities. The consequences of the implementation of this definition in terms of prerequisites, may theoretically be analysed as follows:

Total mass of lamb weaned should represent the outcome of one reproductive cycle from the, time of conception to weaning (Winters, 1940). Following this approach all the components of a complete reproductive cycle must be taken into account when deciding on the manner by which measurements must be taken. The components to be considered are the following:

(i) Fertility, defined as the ability of the ewe to produce one or more lambs. Although a composite trait itself, the practical implication of accommodating this component is essentially that it introduces the problems of a binomial distribution into the measure of mass of lamb weaned. This implies that ewes which did not rear a lamb, or lambs, should be denoted a total of zero mass of lambs weaned. Zero values are therefore not regarded as missing values.

(ii) Fecundity, or the ability of the ewe to produce multiple lambs, has a two-fold influence on EPI. Firstly it introduces the additional effect of a threshold trait into the measurement of mass of lamb weaned. Secondly the complication of summation of the individual masses of ram and ewe lambs arises. Sex of the lamb(s) must there-

fore be known in order to make the necessary prior adjustments.

(iii) Genetic growth potential of the lamb itself. On account of the fact that EPI serves to select ewes, the growth potential of their lambs can introduce a bias, since the ram to which a ewe is mated also contributes to this component. Parentage should therefore be known in order to make an adjustment in the weaning mass of each lamb for the breeding value of the sire.

(iv) Mothering ability of the ewe. During the early stages of the lamb's life, its growth is more dependent on its mother's milk production and nursing ability than on its own growth potential. It is clear that mass of lamb weaned should therefore be measured early in the lamb's life to be the most accurate indication of the ewe's milk production and rearing ability. According to Owen (1971), 42 days of age is generally considered to be the best stage to measure weaning mass as indication of milk production in woolled sheep. Measurements should therefore be taken as close as possible to this age. Naturally a short lambing season will lead to smaller and more accurate adjustments for age differences.

Unlike mutton breeds, the measure of ewe productivity must obviously include wool production when dealing with woolled sheep. In order to obtain a measure of the total monetary return from one complete productive/reproductive cycle, it is necessary to measure wool production over exactly the same period as the reproductive cycle.

Since the repeatability of most of the components of reproduction are generally regarded to be low (Dzakuma, Whiteman and McNew, 1982 and Cloete, 1986), it is accepted that two measurements of mass of lamb weaned are a more accurate indication of lifetime reproductivity. Taking more measurements, although an even better criterion of lifetime reproductivity, seems to be impractical,

since the average remaining productive lifetime of the ewe would then be extremely short. Two measurements of each trait (total mass of lamb weaned and the fleece mass produced during the complete reproductive cycle) were therefore used for the present investigation.

Additionally, it is required that as far as possible, not only both parents of the ewe be known, but also the year in which observations were made. The motivation being to use as much information as possible on relatives as well as known environmental influences to assess breeding values accurately.

2.2 Source of data

Data from the selection experiment at Klerefontein, Carnarvon, analysed by Olivier (1980) and Erasmus (1988) were used. This is presently the only data-set available which complies with the requirements stated above (2.1). Several other sets of data were considered, but found to have either incomplete pedigrees or no measurements on ewes from the first and subsequent lambings.

As the Klerefontein Research Station is located in a semi-desert environment with a low and erratic rainfall and extreme temperatures (Olivier, 1980; Erasmus, 1988), abnormally low reproductive and productive performance can be expected, with important accompanying implications on the data structure.

The sheep used in the present study were run together, but were allocated to three flocks according to the selection procedure followed at 18 months of age. The "objective" flock was selected for high clean fleece mass determined objectively, the "subjective" flock was selected visually for overall excellence, while in the "control" flock replacements were counted off at random.

2.3 Data structure

The data available from the Klerefontein selection experiment comprised 2248 ewes with at least one lambing record. Of these only 1907 had two complete lambing and fleece records. The fact that figures for the subjective flock are subsequently not presented for 1982, is due to the premature discontinuation of the flock, probably as a result of the feeding expenses in the midst of an extreme drought.

The effect of this harsh environment on the weaning percentages, is presented in Figure 2.1 (compiled from data supplied by Olivier (unpublished)). The processed figures are presented in Appendix A.
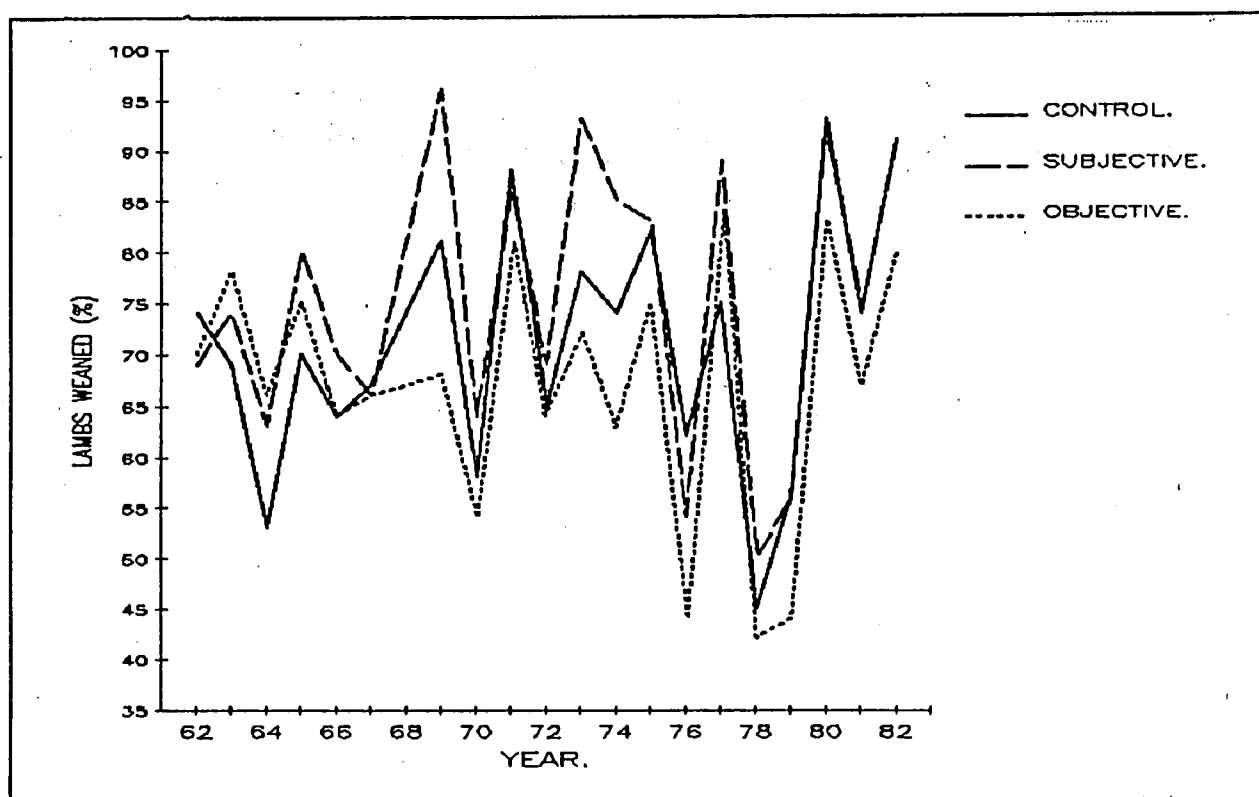

FIGURE 2.1   PERCENTAGE OF LAMBS WEANED PER EWE MATED

Annual weaning percentages for the control flock varied from 45% to 93% compared to the 42% to 84% of the objective flock and the 50% to 96% of the sub-

jectively selected flock. According to the result of Erasmus (1988), the substantial genetic gain in body mass of the subjective flock compared to the other flocks may have accounted for the relatively higher reproductive performance of that flock (Figure 2.1). This finding is in agreement with all available literature reviews on this matter (Turner, 1969; Turner, 1972; Turner, 1977; Cloete, 1986).

The low weaning percentage (Figure 2.1) will not only influence the total mass of lamb weaned, but also the form of its distribution (to be discussed later in this section).

The structure of the data will likewise be affected by the frequency of multiple births which is provided in Table 2.1.

TABLE 2.1 FREQUENCY OF MULTIPLE BIRTHS

LAMBING RECORD OF EWE						
	1st		2nd		TOTAL	
Flock	n	%	n	%	n	%
Objective	42	6.47	30	4.62	72	5.39
Subjective	25	4.18	68	11.44	93	7.59
Control	19	2.87	50	7.57	69	5.53

Results presented in Table 2.1 indicate a significantly higher twinning rate ($P<0.05$) for the subjectively selected flock. It must however be noted that the superiority of the subjectively selected flock occurred only in the second record and not in the first. The essential conclusion is therefore that the harshness of the environment is of overriding importance with respect to young ewes (their first lambing record being made at two years of age).

·The low frequency of twins also led to the problem that seven subclasses contained less than five observations. Since deviations from the subclass means for fixed effects (section 3.2) were less than three standard deviation units, the data comprising these subclasses were retained for all analyses.

The measurements taken on this set of experimental data had the following shortcomings pertinent to the present study:

(i) Lambs were weaned at 120 days of age and no prior lamb masses were recorded because of the unfavourable conditions. The lamb mass at 120 days of age is no longer a sole function of the dam's capabilities since some lambs may have stopped sucking completely. The two measurements after the first and second lambing opportunities are subsequently termed ML1 and ML2.

(ii) The ewes were not shorn immediately after weaning their lambs but half-way into the following gestation period. It is, however, unlikely that this early part of the subsequent gestation could have had a marked effect on the fleece produced. Consecutive measurements during the later half of January every year however led to the same bias for every complete reproductive cycle throughout the total experimental period of 20 years. Abbreviations for these two measurements of greasy fleece mass are FM1 and FM2 respectively.

2.4 Means and distribution

Overall means and standard deviations for the four traits constituting EPI are given in Table 2.2. The data is presented separately for the three flocks, since reproductive differences (Figure 2.1 and Table 2.1) occurred among these flocks.

TABLE 2.2 MEANS AND STANDARD DEVIATIONS (KG) FOR THE TWO COMPONENTS OF EWE PRODUCTIVITY (EPI)

SELECTION FLOCK	TRAIT								
	ML1	sd	ML2	sd	FM1	sd	FM2	sd	n
Objective	7.37	10.20	13.08	11.66	5.01	1.04	5.80	1.07	649
Subjective	9.34	10.69	14.72	11.77	4.76	1.02	5.44	1.00	595
Control	9.28	10.39	14.47	11.46	4.72	0.49	5.40	1.09	663
OVERALL MEAN	8.65	10.46	14.07	11.64	4.83	1.02	5.55	1.08	1907

Both the averages and standard deviations for the two ML traits are very similar (Table 2.2). The average values (Table 2.2) might seem low compared to weaning masses reported in literature, but it should be borne in mind that mass of lamb weaned, to a large extent a composite trait, also reflects reproductive ability (ewes producing nil lambs). The low averages with extremely high standard deviations therefore indicate non-normal distributed traits. This is probably due to the extremely harsh environment.

It is interesting to note that very little difference in distribution of fleece mass occurred, except for the first record measured in the control flock. The coefficient of variation of 10.38% (the lowest figure for FM in Table 2.2) for this measurement in the control flock is well below the average accepted figure of approximately 13% for fleece mass (Heydenrych, 1975). The coefficients of variation of fleece mass for all other measurements of FM traits are approximately 20% which are substantially higher than the figures presented by Heydenrych (1975). This apparent discrepancy may be due to the fact that Heydenrych's (1975) data were adjusted for year effects. Another possibility is the possible better buffering of ewes against the effects of pregnancy and lactation under the better environmental conditions (camp size as well as nutritional, managerial,climatic conditions) encountered at Rivier-

sonderend (Heydenrych, 1975).

The frequency distributions of these four traits are depicted in Figures 2.2
and 2.3.
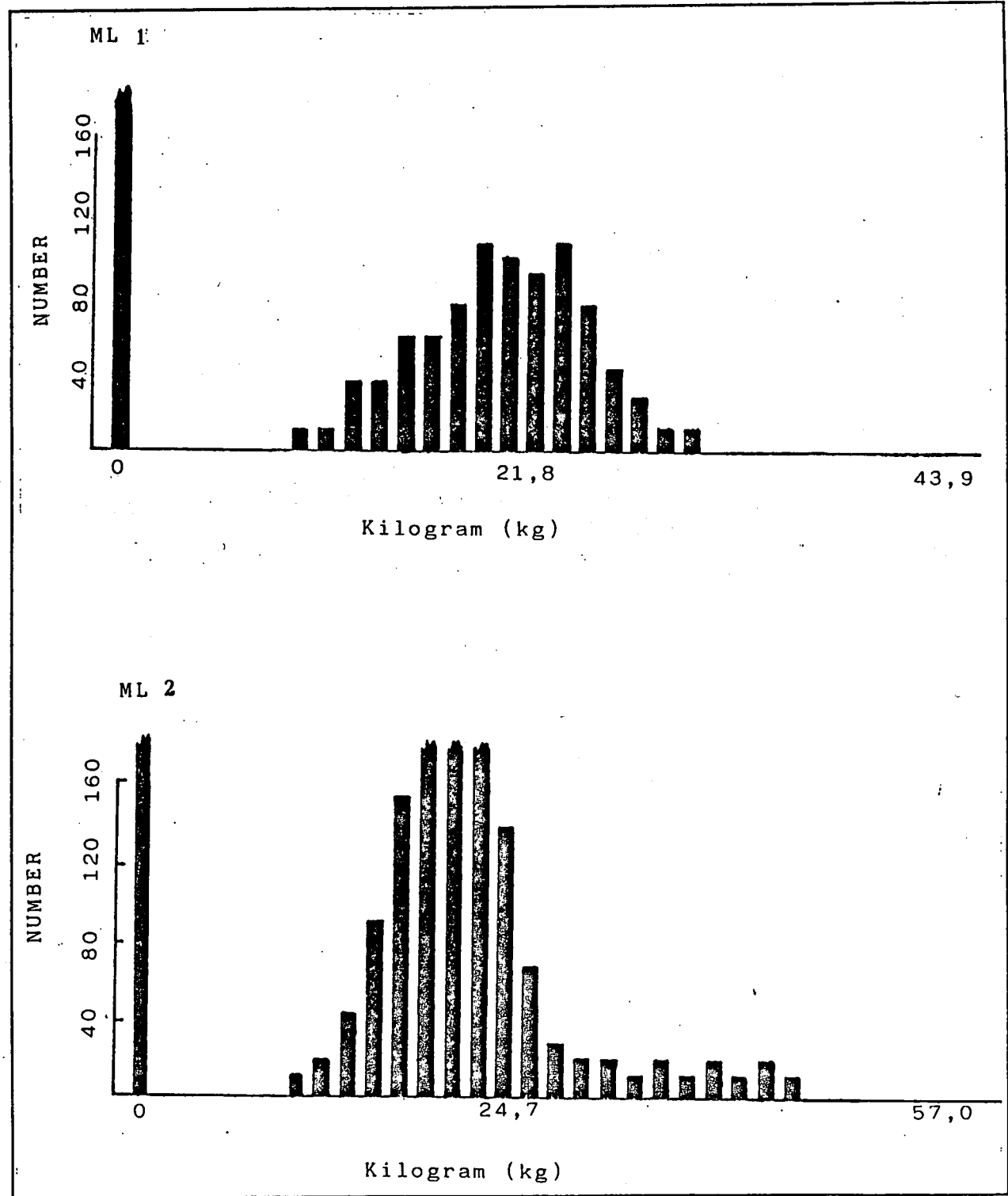
FIGURE 2.2   DISTRIBUTION OF ML1 AND ML2

With respect to the ML traits, the high frequency of barren ewes (especially two-year-old ewes) followed by a positive skew distribution of ewes which lambed, is clearly indicated in Figure 2.2.
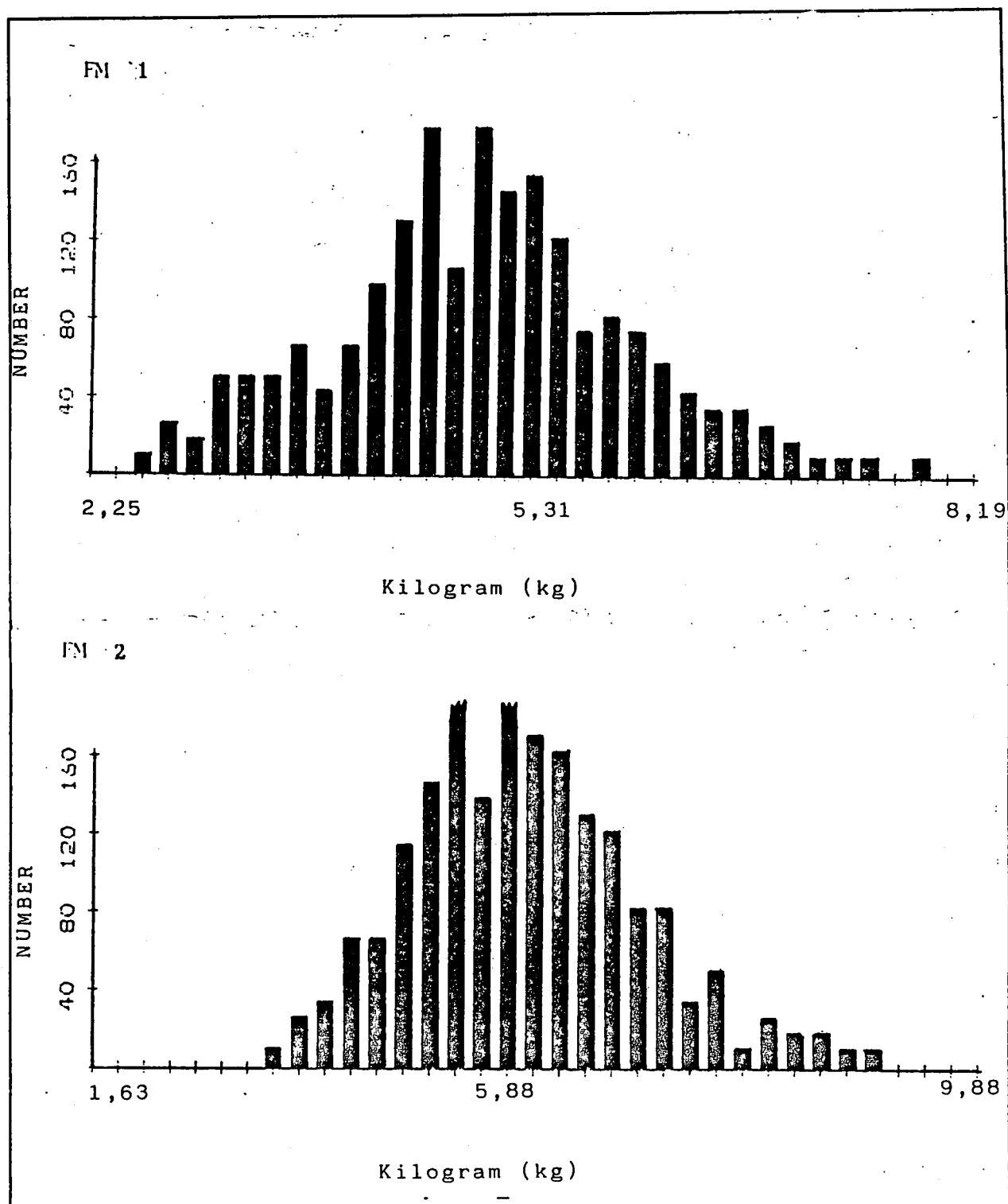

FIGURE 2.3   DISTRIBUTION OF FM1 AND FM2

In comparison the distribution of the FM traits are not significantly deviant ($P<0.05$) from the normal distribution according to the tests done for skewness and kurtosis.

3. THEORETICAL CONSIDERATIONS

3.1 Multiple-trait analysis

From a biological viewpoint it is reasonable to regard ML1 and ML2, as well as FM1 and FM2, as only two traits with two repeated measurements. In such a case "real producing abilities", in the vocabulary of Van Vleck (1979), rather than breeding values would be determined. Henderson (1984) states that the assumptions for the simple repeatability model "are not entirely realistic", one of the main problems being that this model does not separate genetic covariance and environmental covariance between records. It was decided to regard ML1 and ML2 as well as FM1 and FM2 as separate traits in order to make use of differential (co)variances between records. This is in accordance with the American Dairy Industry which resorted to investigating multiple-trait models for repeated measurements of milk production (Powell and Norman, 1981; Cassell and McDaniel, 1983; Blake, 1984; Weller, 1986). Initial results from the estimation of a (co)variance structure for these milk production models indicate genetic correlations of higher than 0.70 between first and second lactation records (Rothschild, Henderson and Quaas, 1979; Tong, Kennedy and Moxley, 1979; Lin and Lee, 1986). The authors cited above, however, seem not to agree fully on the principle as to whether the two repeated measurements represent the same trait genetically. Since different sets of genes could be responsible for the expression of a trait measured at different stages, it seems justified to employ multiple-trait procedures when investigating a new selection criterion involving repeated measurements since it makes provision for the genetic (co)variance between repeated measurements.

The reason for examining two successive records of ML is an effort to improve the accuracy of EPI as selection criterion. Regarding the reproductive

components of EPI, Fogarty (1984) mentions that the heritability of various reproductive traits is low, but that it is generally doubled if mean performance over two or more joinings is used. Van der Westhuysen (1973) came to the conclusion that, under South African conditions, a more detailed evaluation of the ewe's reproductive abilities can be done after her second reproductive year. In the present study these arguments are even more valid, considering that only 42.1% of all maiden ewes lambed (Chapter 2).

No information could be found on the consequence of using two post-weaning FM records. It was decided to include two FM records in order to investigate the effect of the use of the covariance between both FM and ML traits on the accuracy of breeding value predictions for the ML traits.

3.2 Models used to adjust the data

The observations on the ML and FM traits are influenced by different fixed effects. To arrive at a single value describing both components of ewe productivity *viz.* total mass of lamb weaned and post weaning fleece mass, two models must be specified to adjust the ML traits.

The observation on mass of lamb weaned must take into account the following fixed effects:

Two fixed effects, namely sex and age of the lamb, exert their influence only on the total mass of lamb weaned record. It is not possible to include sex in a model when total mass of lamb weaned is taken as the y-value, because multiple born lambs could be of different sexes. The effect of sex will therefore have to be removed beforehand. This was done by adjusting for sex within years to make provision for possible sex x year interactions. Adjustments for age of lamb were made by calculating the average daily gain of each lamb based on a fixed birth mass of

4.2 kg and regressing each record to an age of 120 days. This was done on the basis of the findings of Gregory, Roberts and James (1976) who investigated different methods of adjustments of weaning mass for age and found little difference in their efficiency.

Olivier (1980) who analysed the same data, found that birth year of the ewe had a significant effect on both weaning mass and greasy fleece mass. This fixed effect must therefore be included in the model.
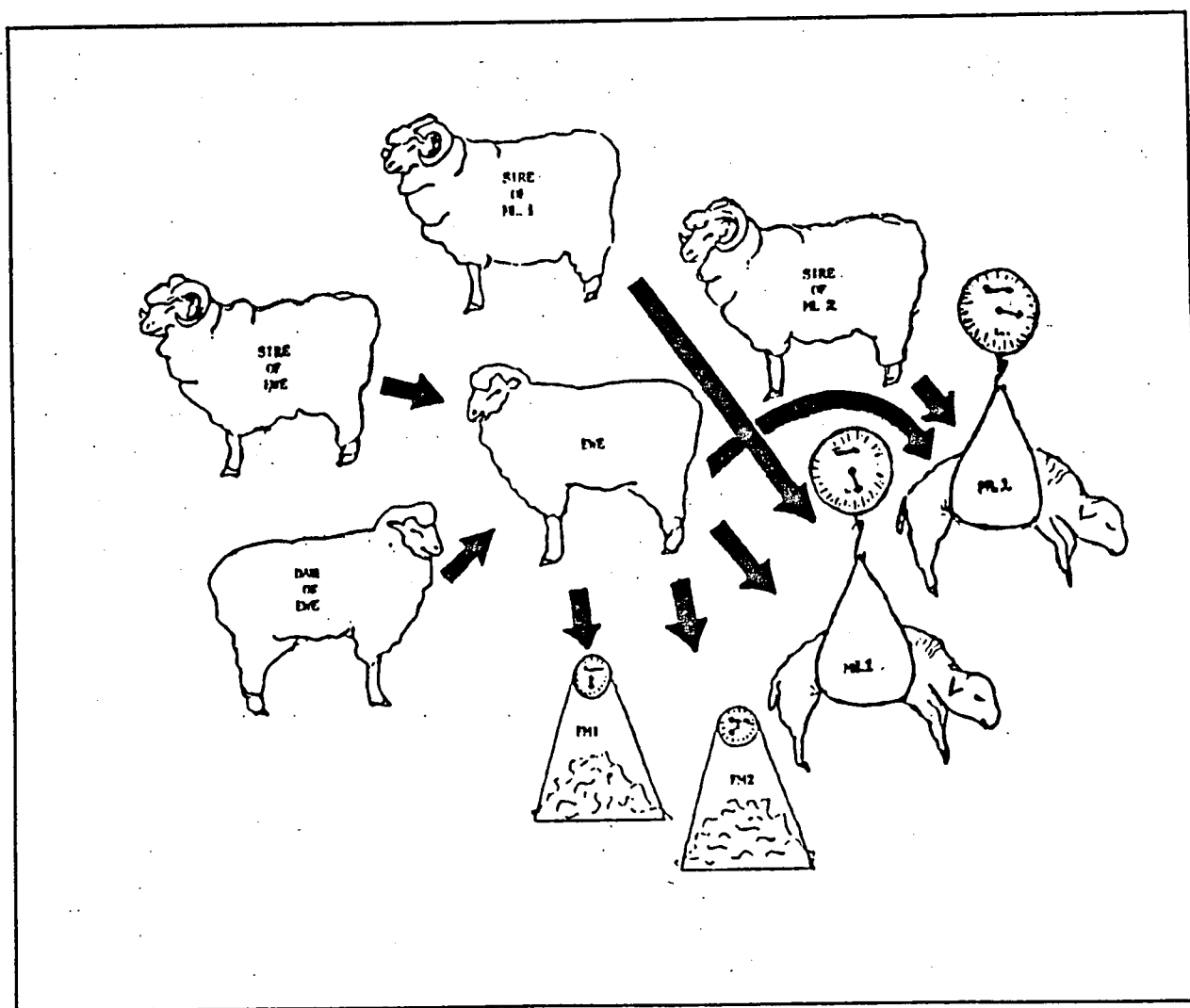

FIGURE 3.1   SCHEMATIC REPRESENTATION OF GENETIC INFLUENCES ON EWE PRODUC-
               TIVITY

A random effect, namely the breeding value for weaning mass of the ram to which the ewe was mated should also be removed before the model for ewe pro-

ductivity is specified. The motivation for making this adjustment is depicted in Figure 3.1 on page 23.

According to Figure 3.1 the ML traits of the ewe are, barring fixed effects, a function of the following:

(i) The gene sample for growth potential contributed by the sire of each individual lamb.

(ii) The gene sample for growth potential contributed by the "ewe" (dam) of each individual lamb.

(iii) The inherent ability of the ewe (dam) of each progeny to rear lamb(s) succesfully and the ewe's milk production.

When the ML traits are regarded as a selection criterion for the ewes, the genetic effect (random) of each lamb's sire should be removed since ewes may be mated to sires of different genetic merit. In the case of ewe productivity being defined as a measure of mothering ability and milk production only, the genetic contribution of the ewe to the lamb's growth potential should also be removed. It is, however, obvious that there is little sense in separating the effects pointed out in (ii) and (iii) for the purpose of estimating ewe productivity, as it is their combined effect which is important in evaluating the total production of a ewe. It is also not clear how such a separation can be accomplished in practice (Van Vleck, 1979, p. 27-30).

A method of removing the genetic effect of the ram to which the ewe was mated was provided by Wilson (1984). This method involves the estimation of breeding values for each individual for weaning mass. The breeding value of the appropriate sire is used to adjust the y-value of each lamb. The animal model used to make this adjustment is as follows:

$$y_{ijk} = \mu + A_i + B_j + U_k + e_{ijk} \qquad \ldots\ldots\ldots[1]$$

where y_{ijk} = the 120-day weaning mass (adjusted for age) of the k-th individual in the i-th birth year and j-th handicap class (sex, age of dam and birth status),

μ = the population mean,

A_i = the fixed effect of the i-th birth year of the individual,

B_j = the j-th handicap class comprising the combined effect of birth status, sex and age of dam (maiden or mature),

U_k = the random genetic effect of the k-th lamb,

e_{ijk} = random error.

This breeding value prediction for weaning mass obtained for the sire to which each ewe was mated was then used to adjust each weaning mass record of the ewes' lambs as follows:

$$(y_{ijk})_{adjusted} = y_{ijk} - U_k/2$$

where y_{ijk} = the weaning mass of the k-th individual in the i-th birth year and j-th handicap class,

U_k = the predicted breeding value (for weaning mass) of the k-th individual (where the k-th individual is the sire of the lamb on which y_{ijk} is observed) computed from the animal model [1] above.

When making this adjustment, it is, of course, assumed that the ram to which a ewe was mated, has no effect on the number of lambs dropped or weaned. In practice, however, it may happen that zero weaning mass records are due to infertile or sub-fertile rams.

3.3 Model for predicting breeding values

The adjustments above having been made, the following animal model can now be

- 25 -

fitted for total mass of lamb weaned (ML1 and ML2):

$$y_{ij} = \mu + A_i + U_j + e_{ij}$$

where y_{ij} =   the total mass of lamb weaned from the j-th ewe which lambed in the i-th year,

         μ =   the population mean,

         A_i =   the fixed effect of the i-th year of lambing,

         U_j =   the summation of the random genetic effect of the j-th ewe for lamb growth and the random effect of the j-th ewe for rearing ability and milk production,

         e_{ij} =   random error.

When specifying a model describing fleece mass in the context of ewe productivity, the fixed effects, normally associated with fleece mass measured at 18 months of age, *viz.* sex, age of dam and birth status, need no longer be included. The data set contains only ewes and therefore sex is excluded while birth status and age of dam no longer have a significant effect on the production of mature ewes (Turner and Young, 1969). Birth year of the ewe should however still be included to account for the effects of different production years.

The only random effect to be specified is that of the ewe for greasy fleece mass.

The linear animal model describing both fleece mass traits (FM1 and FM2) can now be written simply as:

$$y_{ij} = \mu + A_i + U_j + e_{ij}$$

where y_{ij} =   the observation on the j-th ewe lambing in the i-th year,

         μ =   the population mean,

A_i = the fixed effect of the i-th year of lambing,

U_j = the random effect of the j-th ewe,

e_{ij} = random error.

The two models specified for ML1 and ML2, as well as for FM1 and FM2 are now identical since they include the same fixed effect (year of lambing) and the same random effect (breeding value of the ewe). This situation therefore complies with the requirements necessary for executing a four-trait animal model analysis using canonical transformation. Three different variations of such a four trait animal model analysis were performed using three different (co)variance structures. Additionally each trait was analysed separately using four single trait analyses. This was done to compare different strategies of computing ewe productivity.

3.4 Combining the three flocks into one analysis

Fixed effects are specified to make provision for different environmental effects such as management, sex, age of dam, etc. in a mixed model. Following the advice of Sorensen and Kennedy (1986), selection experiments should be analysed treating the different selection flocks as a single entity. Putting the model specified above (3.3) into practice, confronts one with the question as to whether the management regimes were the same for all three flocks since the flocks were separated at lambing and there could be reason to believe that differences in environmental effects may have been present.

In order to investigate the possibility of differential treatment of the three selection flocks, the flocks were analysed both separately and as a single entity by using single-trait analyses of ML1, ML2, FM1 and FM2. The single-trait analyses were performed by using the variances determined for Approach 3 (Chapter 4).

Table 3.1 depicts differences in the estimates of year effects for FM1 and FM2 when doing separate analyses compared to the estimates determined by the combined analysis of the three selection flocks. The analyses of ML1 and ML2 were omitted from Table 3.1 on account of the abnormal variances of these traits but used in a further investigation of the effect of separate versus combined analyses on the accuracy of breeding value prediction as reported later.

TABLE 3.1 MAXIMUM DIFFERENCE IN YEAR EFFECTS OF FLEECE MASS BETWEEN SEPARATE AND COMBINED ANALYSES

TRAIT	FM1			FM2		
FLOCK	Control	Subj	Obj	Control	Subj	Obj
Absolute	0.431	0.159	0.419	0.391	0.392	0.418
Percentage	8.84	3.26	8.59	7.14	7.16	7.64

The maximum difference in any fleece trait in the data set (comprising 20 years) was only 8.84% (for FM1 in the control flock). It can therefore be safely argued that, as far as fleece traits are concerned, the flocks received identical treatment.

Following the general argument for any least squares analysis that small numbers of records per subclass are associated with increased error variance of estimated fixed effects, the result presented in Table 3.1 becomes even more meaningful, the reason being that each separate flock forms only one third of the total analysis and smaller subclass numbers may therefore have contributed towards larger differences in some individual years concerning flocks that were analysed separately.

The maximum difference which occurred in weaning traits (ML1 and ML2),

although not presented in Table 3.1, was 39.15%. This obviously indicates apparent differential treatment. It must, however, be kept in mind that a part-whole relationship exists between these traits and reproduction. Increased variance (Table 2.2) and differential reproduction (Figure 2.1) mentioned in Chapter 2 could therefore be responsible for this high percentage difference. These traits should therefore be ignored for the purpose of deciding on a combined analysis for the three selection flocks.

The effect of doing separate analyses on each flock on breeding value prediction was subsequently investigated. In a symposium on biases in genetic evaluation, Van Vleck (1987) stated that the definition of fixed effects may influence prediction error variance (PEV), of breeding values. PEV again measures the accuracy of evaluation and is therefore also related to genetic gain obtained by selection. Accuracy in this application is usually defined as the correlation between the estimated breeding value of an individual and its true breeding value.

The obvious method of deciding on the best method of analysis would therefore be to choose the method which leads to the smallest PEV. It was however, impossible to follow this approach since a method for the calculation of accurate PEV values for the computational strategy used for the present investigation (the animal model as adapted from Schaeffer and Kennedy, 1986) is currently unavailable.

Approximate methods based on the use of the inverse of only the diagonal elements of the coefficient matrix of the sire model, lead to reasonable results (Wilson, 1984). In an animal model this method is ineffective because of the large relative importance of off-diagonal elements (Chesnais and Song, 1988).

It was decided to compare the genetic trends to detect possible differences

due to different subclass sizes in the four traits concerned as the next best alternative to the two methods described above. The trends presented in Figure 3.2 indicate vast differences in breeding value solutions, due to different sizes of subclasses (separate vs. combined analyses).
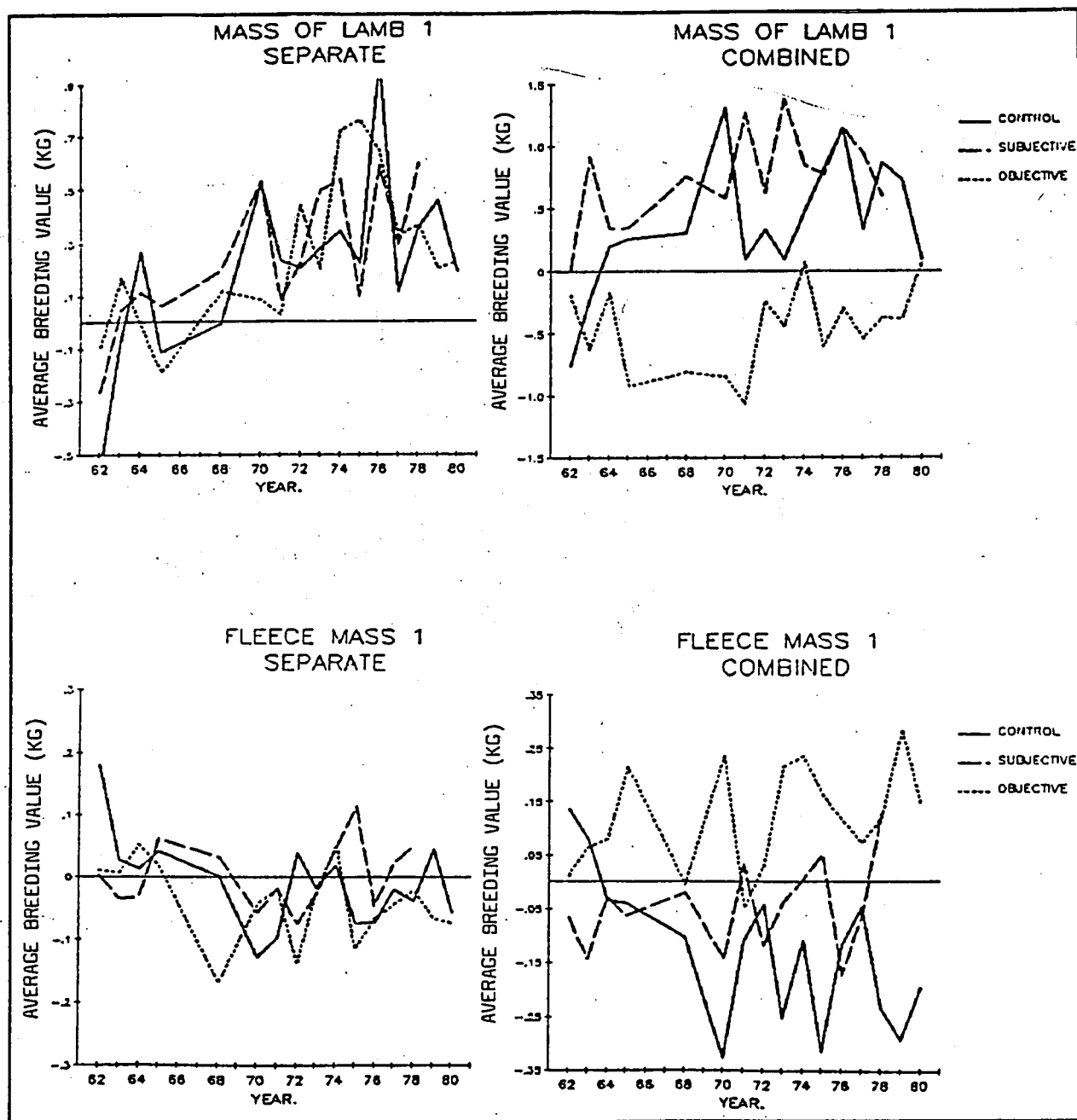
FIGURE 3.2   GENETIC TRENDS (AVERAGE BREEDING VALUES) IN TWO COMPONENTS OF EPI FOR THREE SELECTION FLOCKS

Figure 3.2 not only indicates different trends between the theoretically more

accurate combined analysis and the separate analyses. It can also be deduced from the analysis by Erasmus (1988) that the trends depicted for the combined analysis, coincide more closely to the genetic response which can be expected from the selection policy executed on the three flocks. Results for ML2 and FM2 are not presented, since they essentially lead to the same conclusion as derived with ML1 and FM1.

CHAPTER 4

4. METHODS

4.1 Development of computational procedures

Henderson's interest in the theoretical development of mixed model procedures
dates back to 1948 when he endeavoured to derive selection criteria from badly
unbalanced data in the presence of confusing environmental effects (Henderson,
1984). However, it is only during the 1980's that the increased computational
power of high technology computers and development of efficient mixed model
algorithms made practical implementation of this methodology a reality.

The first important breakthrough in the practical implementation of mixed
model methods of breeding value prediction of individual animals was the
development of a reduced but equivalent model to the full animal model, namely
the Reduced Animal Model (RAM), by Quaas and Pollak during 1980. An equiva-
lent model is one that generates the same first and second moments of the
observations. The computational strategy for RAM can briefly be outlined as
follows:

> The computing strategy used in RAM implies that mixed model equations are
> constructed for parents only. The equations pertaining to non-parents
> are absorbed into those applicable for contemporary groups and parents.
> Usually the coefficient matrix is still too large for inversion and
> iterative procedures are used for solving the equations. Utilising the
> fact that the breeding value for a non-parent is merely a function of the
> breeding value of its parents and the prediction of its own Mendelian
> sampling effect, back-solving is used to obtain solutions for
> non-parents.

The development of RAM was also heavily dependent on the discovery by

Henderson (1975a) that it is easier to compute the inverse of Wright's (1922) numerator relationship matrix than the relationships themselves. This rendered the use of information on all relatives' performance for breeding value calculation a practical possibility.

The development of RAM brought the solving of the equations within the range of the computational power of mainframe computers.

More recently a "simple" algorithm for the sire model was developed by Schaeffer and Kennedy (1986). Use of this algorithm on an animal model adaptation in this development (subsequently reffered to as the Simple Method), eliminates explicitly setting up the mixed model equations as required in the conventional model. The efficiency of this method compared to RAM will be pointed out in Appendix C. Naturally, the development of multiple-trait procedures followed soon after the development of RAM. Developing the theory of multiple-trait evaluation using relatives' records, Henderson and Quaas (1976) stated that "This does not imply, however, that such methods should always be used. One needs to balance accuracy of prediction against computational labour". This implies that this procedure still requires a large amount of computational labour. The algorithm of Schaeffer and Kennedy (1986) may, however, change this viewpoint in the near future.

Another simplification of multiple-trait analysis, namely the use of canonical transformations was used in the multiple trait analyses for the present study since it drastically reduces the computational labour needed for implementing this technique (Arnason, 1984).

The fact that multiple-trait analysis leads to decreased prediction error variance (Henderson and Quaas, 1976) balanced against the use of less efficient methods for including repeated measurements, was a further consideration

for using this technique in the present study.

4.2 Simple Method

In contrast to RAM (outlined above), the same solutions may be obtained by the Simple Method (Schaeffer and Kennedy, 1986) without constructing equations.

The method described by Schaeffer and Kennedy (1986) for the sire model (making provision for maternal grand-sire relationships), was converted to an animal model algorithm to suit the intended use in the present study. This 'not so simple' algorithm for the animal model briefly involves the following steps:

(i) The first round of calculation assumes zero solutions for all fixed and random effects. As a first step all arrays needed in computer memory are cleared.

(ii) Set up a storage array containing the first set of fixed effects (if there are more than one set of fixed effects)

(iii) Store deviations of observations from solutions for first fixed effect and animal solutions in an array containing the second fixed effect (normally referred to as Herd-Year-Seasons in Mixed Model terminology) since an animal can only be present in one Herd-Year-Season.

(iv) Keep track of the incidence of each level of the first fixed effect within a level of the second fixed effect.

(v) Accumulate deviations of observations from solutions for the first fixed effect into a work vector for animal solutions.

(vi) Calculate the solution for the first level of the second fixed effect. Before proceeding to the next level this solution is used to adjust the animal solutions contained in the work vector. In the same way a work vector for solutions of the first fixed effect is

adjusted. Proceed to the next level of the second fixed effect.

(vii) A coded pedigree file is used to adjust the first animal's solution for all possible relationships following Henderson's (1975a) rules.

(viii) Adjust the work vector for the first fixed effect for new animal solution, before proceeding to the next animal.

(ix) Calculate a new solution for the first fixed effect.

(x) Proceed to the next round of iteration and repeat until convergence occurs.

The following are some of the features of the Simple Method:

(i) The matrix constructed for the first fixed effect can readily accommodate more fixed effects as well as interactions between different fixed effects.

(ii) No back-solving is required and solutions for animals are provided directly.

(iii) The Simple Method converges more rapidly than RAM and requires less computing time, largely due to fewer read operations with each round of iteration.

The above algorithm was used to write more efficient computing programs than RAM (Appendix C) for the purpose of this study. The programs developed, already proved to be useful for the analysis of other research projects of similar nature.

A possible disadvantage of using the Simple Method when analysing extremely large data set, may be that the construction of a matrix for fixed effects and simultaneous solution of all animals' breeding values, leads to the use of more computer memory than in the case of RAM (Appendix C).

4.3 Multiple-trait procedures

Canonical transformation was used to execute the multiple-trait analyses used in the present study. The concept of canonical transformation was developed by Hotelling (1936) and has been used extensively in animal breeding situations (Lee, 1979; Lin and Lee, 1986). It involves transformation of all correlated traits, using estimates of a matrix of environmental and genetic (co)variances (R_0 and G_0 respectively), into uncorrelated canonical traits. A single-trait animal model analysis can then be carried out on the canonical traits and the solutions back-transformed to the original scale. It has the advantage that a multiple trait animal model can be analysed as n single-trait models, where n is the number of traits. This procedure is subject to the requirement of observations on all the traits on all animals.

The model for the i-th canonical trait, in matrix notation, is as follows:

$$\underline{y}_i^* = X\underline{b}_i^* + Z\underline{u}_i^* + \underline{e}_i^*$$

Furthermore:

$$E = \begin{bmatrix} \underline{u}_i^* \\ \underline{e}_i^* \end{bmatrix} = \begin{bmatrix} 0 \\ 0 \end{bmatrix}$$

and

$$Var = \begin{bmatrix} \underline{u}_i^* \\ \underline{e}_i^* \end{bmatrix} = \begin{bmatrix} A_{\lambda_i} & 0 \\ 0 & I \end{bmatrix}$$

where $\underline{y}_i^*$ =   a data vector of the i-th canonical trait,

$\underline{b}_i^*$ =   a vector of fixed effects,

$\underline{u}_i^*$ =   a vector of random effects (breeding values),

X,Z   =   incidence matrices associated with $\underline{b}_i^*$ and $\underline{u}_i^*$ respectively,

A = Wright's numerator relationship matrix among animals

and

λ_i = the i-th eigen value of [R G] where G and R are the additive animal and residual variance- (co)variance matrices respectively.

A brief algebraic explanation of how canonical transformations and back-transformations were performed, is presented in Appendix B.

5. OBTAINING (CO)VARIANCES

5.1 Possible options for obtaining (co)variances

Estimates of (co)variances are necessary when using a mixed model to predict breeding values simultaneously for more than one trait. Gianola, Foulley and Fernando (1986) have the following to say about the parameters needed for mixed model breeding value prediction: "If the objective of the analysis is to make selection decisions, these parameters should be regarded as 'nuisances'". They are however necessary and had to be obtained for the present study.

There are three options open for obtaining estimates of R_0 and G_0 (matrices of environmental and genetic variances and covariances respectively):

(i) Prior estimates can be obtained from the literature or,

(ii) it can be calculated beforehand from the available data using traditional techniques,

or,

(iii) estimates can be obtained by Rao's (1971) Minimum Variance Quadratic Unbiased Estimator (MIVQUE) or Patterson and Thompson's (1971) Restricted Maximum Likelihood (REML) while solving the mixed model equations (Sorensen and Kennedy, 1986).

Using prior estimates from the literature when it is possible to determine more accurate estimates from the available data, is generally regarded to be unfeasible. Obtaining estimates from the literature in this case had the further implication that not all required estimates were available (on account of the manner in which the relevant traits were defined). No covariance estimates between mass of lamb weaned and post-weaning fleece mass, for instance,

are available. In any event, as Erasmus (1988) has pointed out, literature estimates sometimes even vary in sign which makes the selection of appropriate values an extremely difficult, if not impossible, task. Secondly estimates of genetic correlations in Merino sheep are also normally characterized by large standard errors (Erasmus, 1988).

Obtaining estimates of R_0 and G_0 from the available data is a feasible proposition when the design of the data set is appropriate to the execution of the available computational methods. The following shortcomings in the data were, however, evident:

(i) The experimental design was not optimum for calculating (co)variance components. The number of progeny per sire as well as the total degrees of freedom were far from adequate. Whereas Falconer (1960) recommends a family size of 30 for this type of analysis, the mean family size in the present study was only fractionally higher than four.

(ii) The design of the experiment was typically that of a selection experiment and not ideally suited to (co)variance estimation by traditional methods. When selection is present, these methods are almost guaranteed to lead to bias (Henderson, 1984).

(iii) There are different fixed effects influencing the fleece mass and mass of lamb weaned records. Prior adjustments of the records for these fixed effects possibly also introduced an amount of bias and increased the sampling variance.

Apart from these data-specific problems it must also be borne in mind that although Henderson's Method 3 is generally regarded as being superior to other current methods, it does not overcome the important limitation of ignoring all but half-sib relationships. Calculating (co)variances only from the data available for the present study can therefore not be expected to lead to

satisfactory results.

The third option (using MIVQUE or REML), however, requires a generalised inverse of the coefficient matrix and was computationally not feasible on account of, firstly, the large size of the data set (1907 records) and secondly the limited computing ability of the available computer.

5.2 Methods

In view of the discussion above, it was decided to make use of estimates from the data as well as a combination of these estimates with the little information available in the literature in four different approaches. A half-sib analysis of variance using Henderson's Method 3 (Henderson, 1953) utilising the library computer programme LSML-76 (Harvey, 1977) was used for estimation.

APPROACH 1: With this approach exactly the same data structure as described in Chapter 2 for breeding value determination was used for estimation. Therefore zero values for either ML1 or ML2 were included as having nil production values.

The following arguments led to specification of a model used for calculating R_0 and G_0 for Approach 1:

> At first it was attempted to apply a prior correction for the year in which an ML observation was made since Olivier (1980) indicated a significant effect of year on weaning mass. Lewer, Rae, and Wickham (1983), however, found, in agreement with the present study, that "year effect controlled only a small proportion of the variation" when dealing with total mass of lamb weaned as a trait of the ewe. It was ascribed to the large chance element as to whether a ewe reared 0, 1 or 2 lambs a year. Birth year of the ewe had to be included as a fixed effect on account of

its significant ($P<0.05$) influence (Olivier, 1980).

Following the same argument as in section 3.2, only birth year of the ewe was included as fixed effect for both FM traits.

The sire model used to calculate R_0 and G_0 was the following:

$$y_{ijk} = \mu + A_i + U_j + e_{ijk}$$

where y_{ijk} = the observation (ML1, ML2, FM1, FM2) on the k-th ewe born in the i-th year,

μ = the population mean,

A_i = the fixed effect of the i-th birth year,

U_j = the random effect of the j-th sire,

e_{ijk} = random error.

To illustrate the effect of including ewes which did not lamb in the measurement of the ML-traits on the distribution pattern of the data, the number and percentage of ewes with zero ML-values (either ML1 or ML2 or both) used for calculating R_0 and G_0 is presented in Table 5.1.

TABLE 5.1 NUMBER AND PERCENTAGE OF EWES WITH ZERO ML1 AND ML2 RECORDS

	NUMBER	PERCENTAGE
ML1 = 0 but not ML2	403	35.4
ML1 = 0 and ML2 = 0	256	22.5
ML2 = 0 but not ML1	153	13.4
Total ML1 = 0	659	57.9
Total ML2 = 0	409	35.9
Total no. of ewes	1139	-

Table 5.1 clearly indicates the extremely high frequency of zero mass of lamb

weaned. The consequence of using this non-normally distributed trait on (co)variance determination by Henderson's method 3 is not clear due to the effect of zero-observations (More O'Ferral, 1976). Nevertheless, this author obtained reasonable results using this technique. It therefore seems reasonable to test this approach despite the extremely large deviation from normality of the data set.

The number of observations (1139) was considerably lower than for the data set used for breeding value prediction (1907), the reasons being the following:

(i) Several sires in the data set (87) had only one ewe progeny with a complete ewe productivity record. These records were discarded for they served to reduce the average number of progeny per sire.

(ii) Some sires (22) had ewe progeny in two consecutive years while the rest were mated in one year only. The result therefore led to intermingling of a nested and cross classified experimental design. The data of all rams with records in more than one year were therefore discarded. The reason for discarding all this data, is that this data represented ewes used for the formation of the Afrino breed in 1968. As the exact change in the original experimental design was not known, data from these sires were discarded.

(iii) In order to make direct comparisons between Approach 1 and Approach 2 (discussed later), which used a completely different data set, it was decided to use records of exactly the same sires. This resulted in the loss of 38 records. This loss can be regarded as unimportant because only 15 sires, with an average of only 2.53 records per sire, were involved.

APPROACH 2: A data set comprising the first two ML records of an ewe, consisting of the weaning mass of only single born lamb records, was constructed. Naturally, the corresponding two measurements of the FM traits were included.

These two records (consisting of an ML and FM trait each) were not necessarily made in two succeeding years, the reason being to make use of all possible information and, even more importantly, to evade the possibility of including ML records with zero values. Only single born lambs were used in order to remove the effect of fecundity completely. With this approach mass of lamb weaned could therefore be biologically defined as a measure of the rearing ability of the ewe. It must, however, be noted that zero mass of lamb weaned by a ewe, could be due to poor mothering ability. These records were excluded from the data set used for this approach.

In order to specify the model used for calculating R_0 and G_0 for Approach 2, the following important aspects were taken into consideration:

* As the two records (of ML and FM respectively) used were from a random two year-period and were not coupled to the birth year of the ewe, prior adjustments had to be made for the year in which the records of the FM traits were made.

* Similarly, birth year was consequently not used as a fixed effect for the ML traits but was replaced with age of the ewe, and her previous reproduction record as fixed effects, as an analysis of variance (Olivier , 1980) indicated significant effects of these two environmental effects. Mass of lamb weaned measured in this manner is similar to weaning mass analysed by Olivier (1980). The same *a priori* adjustments discussed in section 3.2 for ML1 and ML2 are applicable in this case. The principle of adjusting for the females' previous round of reproduction, was recently demonstrated again by Neville Jr.,Richardson, Williams and Utley (1987).

The LSML-76 program could not apply different fixed effects on each of the two ML traits in one mixed model, therefore prior least square adjustments for the two effects (above) were applied. No fixed effects remained and the following

random effects sire model was fitted:

$$y_{ij} = \mu + U_i + e_{ij}$$

where y_{ij} =   the observation on the j-th individual,

μ =   the population mean,

U_i =   the random effect of the i-th sire,

e_{ij} =   random error.

APPROACH 3:   As both Approaches 1 and 2 yielded the odd estimate which could be questionable, an arbitrary R_0 and G_0 was constructed by calculating the average value of the elements obtained from Approach 1 and 2 plus data from the literature which seemed the most realistic in terms of present knowledge. Although Approach 3 is not strictly speaking a "method", the resulting values used are given in section 5.3.

APPROACH 4:   Only variances are used, thus implying no covariances among the four traits for the purpose of breeding value determination.   Although, also not strictly an experimental procedure, it is mentioned for the sake of completeness.   With this approach the variances obtained by following Approach 3 were used for breeding value prediction.

Using these four different approaches afforded the opportunity of evaluating the effect of different (co)variance structures on the outcome of breeding value prediction using multiple-trait mixed model analyses.   By including a single-trait analysis, the effect of totally ignoring the correlation between traits could be evaluated.

5.3 Results and discussion

The heritabilities (h^2), genetic- (r_g) and environmental correlations (r_e)

obtained for Approach 1 and 2 and those assumed for Approach 3 are given in Table 5.2.

TABLE 5.2 HERITABILITIES AND CORRELATIONS FOR APPROACHES 1, 2 AND 3

	APPROACH 1	APPROACH 2	APPROACH 3
Heritabilities			
ML1	0.202(0.083)	0.725(0.130)	0.178
ML2	0.061(0.078)	0.780(0.131)	0.159
FM1	0.588(0.094)	0.608(0.127)	0.608
FM2	0.433(0.090)	0.438(0.121)	0.571
Genetic correlations			
ML1 x ML2	0.950(0.680)	−0.233(0.136)	0.900
ML1 x FM1	−0.595(0.257)	−0.136(0.151)	−0.136
ML1 x FM2	−0.691(0.317)	0.138(0.171)	0.138
ML2 x FM1	0.435(0.433)	−0.120(0.146)	−0.120
ML2 x FM2	−0.280(0.460)	−0.488(0.174)	−0.136
FM1 x FM2	0.861(0.067)	0.908(0.097)	0.908
Environmental correlations			
ML1 x ML2	0.071	0.843	0.071
ML1 x FM1	−0.077	0.134	0.134
ML1 x FM2	−0.189	−0.055	−0.338
ML2 x FM1	−0.173	−0.011	0.242
ML2 x FM2	−0.194	−0.062	0.134
FM1 x FM2	0.341	0.530	0.130

NOTE: The values in parenthesis represent standard errors of the estimates not applicable for Approach 3.

Although it was at first attempted to select values from either Approach 1 or

2 for use in Approach 3, in some cases neither of these approaches yielded estimates which appeared to be biologically sound. In such cases arbitrary values, based on the general findings in the literature, were used. Values not obtained from Approach 1 or 2 are the following:

(i) In comparison with literature, the heritability estimates of ML1 and ML2 for Approach 2 (0.725 and 0.780) appeared to be too high while that of ML2 for Approach 1 (0.061) appeared to be too low. Arbitrary values of 0.178 and 0.159 were assigned for ML1 and ML2 respectively.

(ii) As there is no reason to believe that the heritability of FM1 and FM2 should differ appreciably, only a slightly lower arbitrary heritability (0.571) was assigned for FM2 in Approach 3.

(iii) A high positive genetic correlation can be expected between ML1 and ML2, the obvious reason being that they are two repeated measurements of the same trait determined by the same set of genes. The value for Approach 2 (-0.233) therefore seems to be entirely unrealistic. On the other hand, the positive correlation of Approach 1 (+0.950) although high (as can be expected) seems to be almost too perfect. An arbitrary value of +0.900 was therefore assigned for Approach 3.

(iv) The genetic correlation between ML1 and FM1 in Approach 2 (-0.136) appeared to be the most realistic (of those presented in Table 5.2) when compared to the general results in the review by Turner (1972). Biologically viewed, there is no apparent reason why the genetic correlation between ML2 and FM2 should be any different from that between ML1 and FM1 and therefore the same values were used.

(v) The estimates of the environmental correlations between ML1 and FM2 in the literature indicate a higher negative value than obtained in Approach 1 or 2 (-0.189 and -0.055). This is probably due to a carry-over effect of maternal stress on later wool production.

Therefore an arbitrary value of −0.338 was used in Approach 3.

(vi) The environmental correlations between ML2 and FM1 for both Approach 1 and 2 (−0.173 and −0.011) being negative, were obviously improbable in a biological sense. Whereas a high ML record in one year could directly lead to a lower FM record in the next, due to a physiological drain on the ewe (as explained in (v) above), a high FM1 record, induced by environment, is an indication of improved physiological abilities. This would well be manifested in improved lamb production in the following year. An arbitrary value of +0.242 was consequently used for Approach three.

(vii) The same reasoning as for (iv) was employed in adopting the environmental correlation of +0.134 between ML2 and FM2 in Approach 2, for the value of the correlation between both ML1 and FM1 and also between ML2 and FM2 in Approach 3.

(viii) An abitrary value of +0.130 was assigned for the environmental correlation between FM1 and FM2 as the values in Approach 1 and 2 (+0.341 and +0.530) are both unrealistically high, the obvious reason being the relative high heritabilities and genetic correlations between these two traits.

As mentioned in section 5.2, not many appropriate estimates of (co)variance structures including ML traits (as defined for the present study) are available in the literature. Notwithstanding this limitation, some of the results presented in Table 5.2 will be evaluated against the estimates available in the literature in order to explain the values assumed for Approach 3. The following results from similar analyses could well be obtained from the literature:

In a first report, More O'Ferral (1976) obtained heritability estimates of 0.25 and 0.30 for ML1 and ML2 and a genetic correlation of 0.27 between the two traits in Galway ewes. The heritability estimate of 0.3

increased to 0.5 when ewes not rearing lambs were excluded. In the present study an increase from 0.061 (ML2 in Approach 1) to 0.780 (ML2 in Approach 2) occurred. This far greater increase was probably due to the low reproduction encountered in the present study. More O'Ferral (1976), however, also states that the heritability estimates of total mass of lamb weaned for lambing opportunity one and two respectively (defined as ML1 and ML2 in the present study) are far higher than estimates obtained for weaning mass in Galway sheep. It must be noted that this was the only report found in literature employing the same technique on the same traits as in the present study.

In a second group of three reports, ML traits were defined as the average lifetime mass of lamb weaned per mating.

In the first of these reports, Fogarty, Dickerson and Young (1982), obtained heritability estimates of 0.06 and 0.15 for mass of lamb weaned per ewe joined in crosses with different breeds. Contrary to the result presented in Table 5.2 for Approach 2, as well as that by More O'Ferral (1976), this result seems to indicate a low heritability for ML traits. This finding is more compatible with the results reviewed by Turner (1972) which indicated the following general guidelines:

(i) Low heritabilities for body mass traits at weaning.

(ii) Low genetic correlations between these traits and wool production at 18 months of age.

Secondly, Basuthakur, Burfening, Van Horn and Blackwell (1973) reported heritability estimates ranging from 0.0 to 0.50 for weaning mass (ML) traits and 0.0 to 0.34 for fleece traits. These figures also indicates lower heritabilities than that of More O'Ferral (1976) and that presented for Approach 1 and 2. It must, however, be noted that the genetic correlations reported (Basuthakur,

Burfening, Van Horn and Blackwell, 1973) were outside the parameter space and they are therefore not considered in the following discussion.

In the third instance, Owen, Crees and Williams (1986) also reported low heritabilities (0.09 to 0.301) for ML traits. In the study of these authors, however, fleece traits were unfortunately not recorded.

Lastly, a report by Cundiff, Gregory and Koch (1982) on selection for increased survival from birth to weaning will be considered. Although survival rate is an indirect component of ML as defined for the present study, estimates of the heritability of suvival rate as a trait of the dam, was reported (Cundiff, Gregory and Koch, 1982). These estimates were extremely low and ranged from 0.00 to 0.20.

The logical deduction from the literature mentioned above is that taking values from literature alone, would be very speculative. Therefore, the results from Approach 1 and 2 were considered together with the rather scanty results from literature. Various other results on reproduction traits and general guidelines reported by Turner (1972), were additionally used to arrive at a result for Approach 3 which does seem biologically justified.

Comparing the heritability estimates for FM1 and FM2 to the heritability of maiden fleece mass is biologically important in the sense that accuracy of selection of young ewes may be verified in this manner. The heritability estimates for FM1 and FM2 obtained by using both Approach 1 and 2 (Table 5.2) are consistently higher than the heritabilities of 0.229 and 0.249 respectively, for both clean and greasy fleece mass at 18 months age obtained by Erasmus (1988) in the same flock. This could be due to the fact that, because of the harsh conditions, differences in rate of maturity were still prevalent at 18

months of age. This is an aspect that warrants future research, as the Merino is known to be a slow maturing breed, especially under poor conditions.

In a recent extensive review by Cloete (1986) the large order, and even sign differences, of estimates of genetic parameters for sheep are clearly illustrated. Some estimates quoted are not even in the allowable parameter space. This is also borne out in the review by Turner (1972). This stresses the need for either better design or better methods of computation or most probably both. The present study does not attempt to solve this problem and the results presented here should be seen merely as possible indications of the true situation and as a step in the attempt to evaluate how differences in these "nuisances" of Gianola, Foulley and Fernando (1986) will affect selection decisions.

The resulting matrices of genetic and environmental (co)variances (G_0 and R_0) are as follows:

APPROACH 1:

	G_0 Matrix					R_0 Matrix			
	ML1	FM1	ML2	FM2		ML1	FM1	ML2	FM2
ML1	5.012	-0.349	3.028	-0.442		94.059	-1.345	16.111	-2.428
FM1		0.069	0.162	0.064			0.398	-0.360	0.291
ML2	SYM		2.026	-0.114		SYM		130.727	-1.758
FM2				0.082					0.674

APPROACH 2:

	G_0 Matrix					R_0 Matrix			
	ML1	FM1	ML2	FM2		ML1	FM1	ML2	FM2
ML1	3.045	-0.079	-0.710	0.059		13.758	-0.083	1.229	-0.227
FM1		0.112	-0.070	0.075			0.622	0.031	0.263
ML2	SYM		3.048	-0.205		SYM		12.581	0.023
FM2				0.060					0.492

APPROACH 3:

| | G_0 Matrix | | | | | R_0 Matrix | | | |
	ML1	FM1	ML2	FM2		ML1	FM1	ML2	FM2
ML1	4.466	−0.079	3.465	0.059		95.654	−0.083	15.174	−0.227
FM1		0.112	−0.070	0.075			0.622	0.031	0.263
ML2	SYM		5.188	−0.079		SYM		125.609	−0.083
FM2				0.104					0.623

NOTE: For Approach 4 the variances of Approach 3 were used.

The elements of G_0 and R_0 are given to the nearest third decimal, but for computational purposes, eight decimals were used. Also, rows and columns of the matrices had to be rearranged for decomposition so that the elements of the diagonals of R_0 are arranged from small to large. For the two-trait model the corresponding rows and columns of the matrices obtained for Approach 3 were used.

The results on genetic and phenotypic (co)variances presented above is needed to perform canonical transformation (Appendix B) on the data set, Both R_0 and G_0 are used in the process of canonical transformation to arrive at a single matrix termed "L" in Appendix B. This matrix (and its inverse) contains the necessary values for transforming the data to canonical variates (and back transformation to the original scale) according to the method presented in Appendix B. The L-matrices resulting from the (co)variances (above) for the different approaches, are presented for verification purposes as follows:

APPROACH 1: Sequence = FM1; FM2; ML1; ML2

$$
L = \begin{bmatrix}
-0.08207219 & -0.01082192 & 0.04364035 & -0.63274329 \\
0.01581342 & -0.03538768 & -0.61653985 & -0.49087780 \\
-5.37157912 & 7.22579325 & 1.67467468 & 2.77230893 \\
8.77017311 & 6.69566419 & 1.98891280 & -0.52492186
\end{bmatrix}
$$

APPROACH 2:   Sequence = FM2; FM1; ML2; ML1

$$L = \begin{bmatrix} 0.47929855 & -0.18646354 & 0.41179378 & 0.24049195 \\ -0.21549354 & -0.35232645 & 0.66200723 & 0.11468419 \\ 0.94851501 & -2.27843376 & -0.64102699 & -2.46568167 \\ -0.55048281 & -2.28779249 & -2.09211055 & 1.96058198 \end{bmatrix}$$

APPROACH 3:   Sequence = FM1; FM2; ML1; ML2

$$L = \begin{bmatrix} 0.03558581 & 0.16213730 & -0.34886948 & -0.68754102 \\ -0.11256354 & -0.16316979 & 0.41872587 & -0.63871626 \\ 6.22230662 & 6.59846476 & 3.65615066 & 0.14402477 \\ -7.37480423 & 8.22749361 & 1.77653116 & 0.61140359 \end{bmatrix}$$

TWO-TRAIT MODEL: Sequence = FM1; ML1

$$L = \begin{bmatrix} 0.00000000 & 0.78865546 \\ 9.77925725 & -0.10557112 \end{bmatrix}$$

The different sequences for the L-matrices presented above are due to a rear-rangement of the matrices for Cholesky decomposition (Appendix B).

It is noticable that no L-matrix is presented for Approach 4. The reason is that no L-matrix is needed for Approach 4 in which only variances are used. Inclusion of the L-matrix for a two-trait model stems from the decision to test the possibility of using only the first lambing record (and corresponding fleece mass record) for breeding value determination.

In spite of the fact that the problem of obtaining correct variances is accen-tuated by specifying a multiple-trait analysis which demands the inclusion of covariances, it is the logical refinement of breeding value determination following a single-trait analysis. In a multiple-trait analysis it can truly be said that all possible information is being used – all relatives and all

traits. Little is to be gained in the case of, for instance, a sire that has a large number of recorded progeny on each trait (Quaas, Anderson and Gilmour, 1985) but it is obvious that in the present study, where there are four inter-related traits and small numbers of progeny, a multiple-trait analysis is the correct choice. The increased cost of a multiple-trait analysis can largely be reduced by the use of canonical transformations. The biggest disadvantage of a multiple-trait analysis is the number of parameters needed. For example, in four single-trait analyses, only four heritabilities are needed, but in a four-trait analysis, four heritabilities, four genetic correlations, four environmental correlations and four phenotypic variances - a total of sixteen parameters - are needed. As Quaas, Anderson and Gilmour (1985) point out, they are assumed to be known but have to come from somewhere. They conclude: "Anyone with some experience estimating genetic correlation will realise the problems that can be encountered".

6. RESULTS AND DISCUSSION

6.1 Introduction

The results of this study will be presented in the following sequence:

(i)   A general description of the breeding values obtained will be sup-
plied.   An attempt will also be made to show how the use of diffe-
rent (co)variance structures influences the distribution of breeding
values.

(ii)   The possibility of selecting both ewes and rams on the basis of the
EPI values of their dams will be investigated.   The accuracy of
prediction of EPI and its components will also be evaluated.

(iii) The possibility of selecting ewes on their EPI values before they
produce offspring will be investigated.   Additionally the accuracy
of using only ML1 and FM1 for selection will be investigated for the
purpose of determining the possibility of shortening the generation
interval.

(iv)   The investigation for (ii) and (iii) will additionally be used to
decide which (co)variance structure produced the most reliable set
of breeding values.

(v)   A comparison of the breeding values of EPI and its components with
the breeding values of 18 months traits (body mass, fleece mass and
fibre diameter determined by Erasmus (1988)) will be used to inves-
tigate possible antagonisms between selection on EPI and selection
practised at 18 months of age for the three traits mentioned.   The
effectiveness of selection for EPI in order to increase lifetime
reproduction will also be investigated.

6.2 Description of breeding value predictions

Breeding value predictions were obtained by using the three different (co)variance structures presented in Chapter 5. The most accurate method for comparing different results obtained for breeding value prediction, is to make use of prediction error variance (PEV). As stated in Chapter 3, PEV could not be determined in the present study and it was decided to use the following approach:

> Comparison of the distribution of predicted breeding values will be limited to the base population (base population defined as the original parents of the data set which did not appear as progeny themselves, comprised of 256 parents). This method of comparison has the advantage that the means of the base population are, theoretically at least, zero. Therefore the complication of possible differences in genetic trend is eliminated.

It must also be borne in mind that the ML traits are not normally distributed (on the original scale). This is another reason why it was decided to present the frequency distribution of breeding values in the base population only in Figure 6.1. Assuming that the largest deviations from the normal distribution could be expected for ML1, only results for this trait are presented (the graphs are arranged in descending order of expected superiority of the different approaches).

The distributions for all three approaches presented in Figure 6.1 are not deviant from the normal distribution according to the tests done for skewness and kurtosis. The variances are also not significantly different (P < 0.05) according to Bartlett's test. The homogeneity of these distributions could be indicative of the following:

> Accurate determination of the true (co)variance structure is not all that

critical for breeding value determination. When comparing this result with the effect of the data structure on the results (presented in Chapter 2), it seems as if accuracy of the data may be more important.
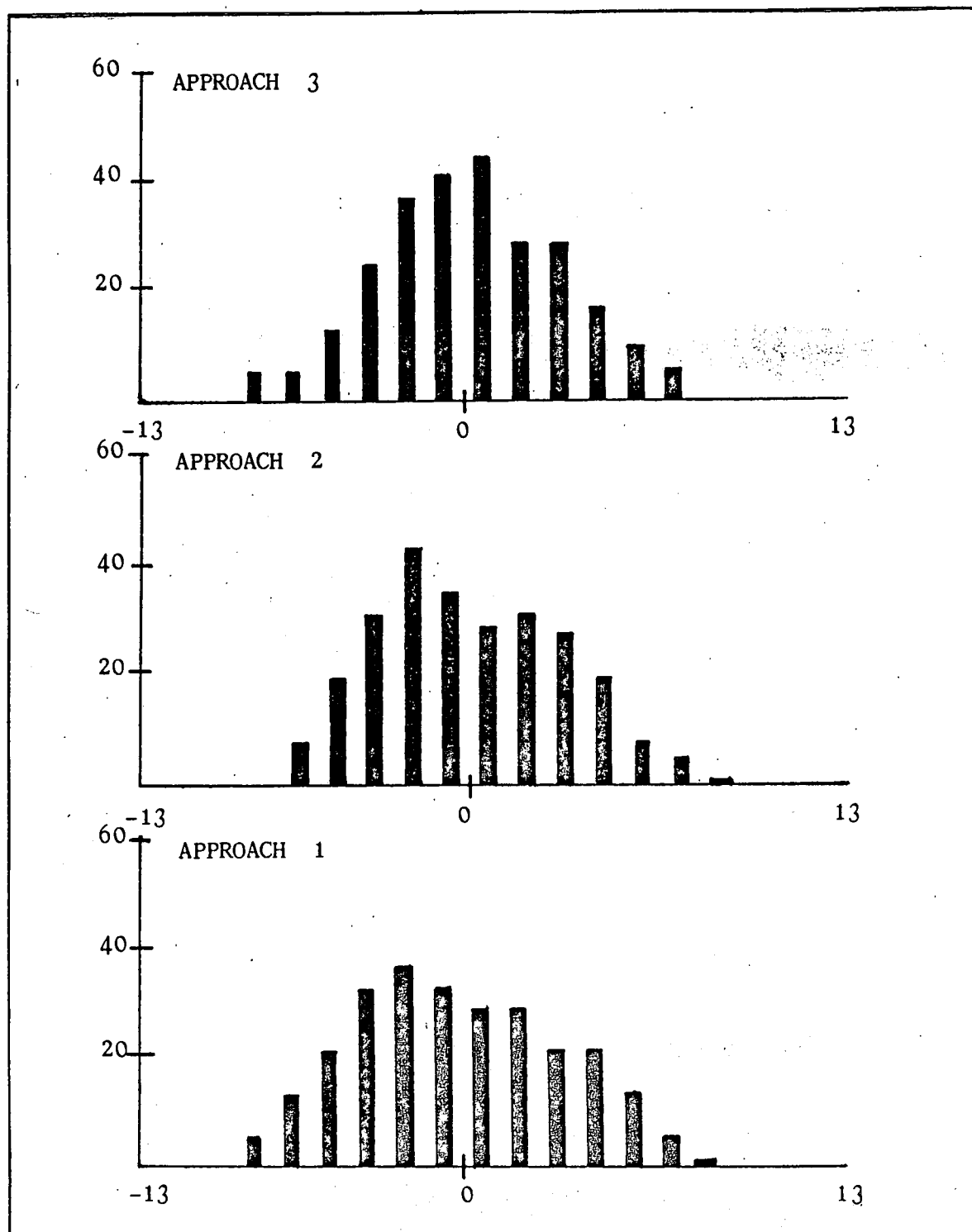

FIGURE 6.1   DISTRIBUTION OF BREEDING VALUE PREDICTIONS IN THE BASE POPULATIONS FOLLOWING THREE ANALYSES WITH DIFFERENT (CO)VARIANCE STRUCTURES FOR ML1

According to the results presented in Figure 6.1, it appears that inclusion of the full relationships matrix in the analysis and consequently also complete information from all available relatives (using a multiple-trait animal model) led to a more normally distributed measure of ML traits than that found with phenotypic values alone (Chapter 2). It must however be borne in mind that the use of canonical transformations may also have influenced the distribution of breeding value predictions.

In a simulation study by Sorensen and Kennedy (1986) on selection experiments, it is stated that "...bias in breeding value solutions due to different (co)variance structures is small". It was, however, decided to investigate how critical the use of different (co)variance structures is in practice, due to the difficulty encountered in the determination of an accurate (co)variance structure (Chapter 5). The (co)variance structures resulting from the first three different approaches (presented in Chapter 5) were used. The use of the different (co)variance structures had a negligible effect on the fixed effect solutions (differences occurred in the second decimal place only), therefore only differences in breeding value predictions will subsequently be presented.

The variances of predicted breeding values in the base population obtained using different (co)variances are presented in Table 6.1.

Although the distribution of breeding values are similar (Figure 6.1), the slightly larger differences in the variances of breeding value predictions (Table 6.1) for ML traits compared to FM traits, suggests that differential (co)variance structures may have some influence on the distribution of breeding value solutions for these traits.

In order to obtain some idea of why the different (co)variance structures could influence breeding value distribution, it may be reasoned as follows:

Increased PEV leads to larger errors in the estimates of individual breeding values and hence higher variances. The results presented in Table 6.1 indicate that the smallest variances generally are for Approach 3, a little larger variances for Approach 1 and the largest for Approach 2. The obvious conclusion therefore is that the (co)variance structure obtained by using Approach 3 provided the best result in terms of breeding value prediction.

TABLE 6.1 VARIANCES OF BREEDING VALUES IN THE BASE POPULATION USING DIFFERENT (CO)VARIANCE STRUCTURES (n = 256)

	APPROACH 1	APPROACH 2	APPROACH 3
ML1	14.153 (3.762)	16.683 (4.084)	8.629 (2.938)
ML2	11.818 (3.438)	15.759 (3.970)	13.267 (3.642)
FM1	0.079 (0.281)	0.155 (0.394)	0.072 (0.268)
FM2	0.053 (0.230)	0.183 (0.428)	0.095 (0.308)
NOTE: Standard deviations are given in parenthesis.			

Although this method of comparison can be regarded as a crude method to compare the accuracy of breeding value predictions when using different (co)variance structures, a more reliable substitute could not be found. One argument, which could give more credibility to this comparison may be that the base population (for which no own records exist) should be more sensitive to possible increased error variance, since these animals' breeding values are based only on information from relatives, which could be scanty.

The Pearson's product moment correlation between breeding values may provide additional information on the differences in breeding value predictions when applying different (co)variance structures. This relatively simple method was used in similar experimental conditions by Djemali, Berger and Freeman (1987)

and Preisinger, Claus and Kalm (1986) for comparative purposes. Lacking more sophisticated methods, this method will be applied in all subsequent sections when necessary.

The difference among the four different approaches expressed as correlations between BLUP breeding values, is presented in Table 6.2. Since the evidence on the distribution of breeding values suggests (co)variance structure to be non-critical, Approach 4 (four single-trait analyses) was included in this comparison, for the purpose of determining whether it is necessary to use multiple-trait analyses at all. The measure for ewe productivity (EPI) was included to ensure that the conclusions made with regard to the components of EPI also hold true for its overall measure.

The correlations between breeding value predictions (Table 6.2) were generally high for all possible approaches (even for the single-trait analysis). As expected, the lowest correlation (r = 0.811) was recorded in the case of EPI (a composition of four traits). This illustration, based on real data agrees with the algebraic evidence of Sorensen and Kennedy(1986).

In accordance with the discussion on Figure 6.1 the essential conclusion therefore, is that the exact determination of the true (co)variance structure for the specific data set is not all that critical for selection purposes. Although genetic gains will definitely not be optimised by using an erroneous (co)variance structure, major changes in the order of merit of individual animals will also not occur. The implications for quantifying genetic trends may however be somewhat different (Erasmus, 1988).

It can further be inferred from the correlation matrices (Table 6.2) that the values for the single-trait analysis (Approach 4) probably lie near the middle of the range of these values, the obvious reason being the relatively high

correlation between Approach 4 and all other approaches for all possible traits (Table 6.2).

TABLE 6.2 CORRELATIONS BETWEEN BREEDING VALUE PREDICTIONS FOR FOUR DIFFERENT APPROACHES TO (CO)VARIANCE STRUCTURE DETERMINATION

	APPROACH FOR ML1 (ABOVE) AND ML2 (BELOW)				
		1	2	3	4
APPROACH	1	–	0.967	0.925	0.895
	2	0.932	–	0.939	0.935
	3	0.924	0.944	–	0.882
	4	0.865	0.956	0.893	–
	APPROACH FOR FM1 (ABOVE) AND FM2 (BELOW)				
		1	2	3	4
APPROACH	1	–	0.950	0.976	0.997
	2	0.837	–	0.888	0.948
	3	0.922	0.931	–	0.967
	4	0.843	0.952	0.972	–
	APPROACH FOR EPI				
		1	2	3	4
APPROACH	1	–	0.979	0.945	0.848
	2	–	–	0.977	0.851
	3	–	–	–	0.811
	4	–	–	–	–

For illustrative purposes the linear regression of EPI based on Approach 3 on that based on Approach 4 (single-trait analysis), is presented in Figure 6.2. It is evident that this comparison between using only variances but no covariance structure at all and using the (co)variance structure considered to be

the most realistic, still reveals a reasonably close relationship. This relationship is however, not close enough to suggest that a single trait analysis, which is theoretically inferior, should be used for breeding value prediction. Approach 4 (using variances only) is therefore omitted in the succeeding sections.
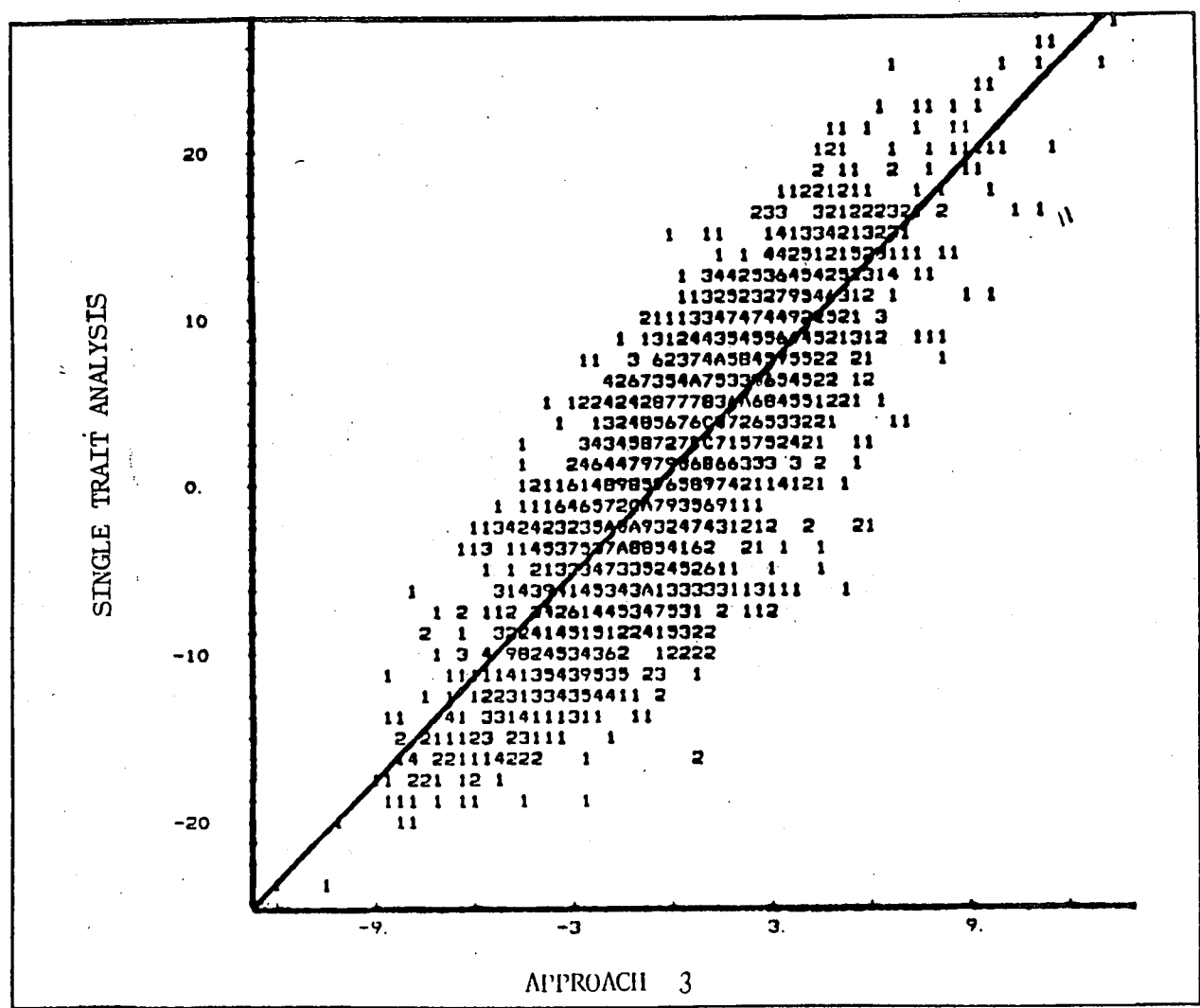

FIGURE 6.2   LINEAR REGRESSION OF EPI (NO (CO)VARIANCE STRUCTURE) ON EPI ((CO)VARIANCE STRUCTURE FOR APPROACH 3)

6.3 Possible selection of animals on the basis of relatives' performance

It is of great importance to know how accurately animals can be selected on the basis of the performance of their relatives when dealing with sex-linked

traits such as EPI and its components. Even FM1 and FM2, wool production while rearing lambs, are traits of the ewe only.

As the primary aim in this section, two possiblities of selecting animals on the basis of relatives' performance were investigated, namely:

(i) To reduce the generation interval it is important to know how accurately ewes can be selected before their own records are available.

(ii) The possibility of selecting rams on EPI which naturally have no own-performance records of EPI. They can only be selected for EPI on the basis of the performance of their female relatives.

To investigate the two possibilities mentioned above, Pearson's product-moment correlation coefficients were calculated between the dams' (and sires') predicted breeding values and that of their progeny for EPI and its components.

The results presented in Table 6.3 are only for ewes born in 1974 with known dams. Only 1974 born ewes were used for this comparison to bring this result in line with the results presented in the next section (section 6.4).

TABLE 6.3:   CORRELATIONS BETWEEN BREEDING VALUES OF DAMS AND BREEDING VALUES OF DAUGHTERS (n = 168)

APPROACH	ML1	FM1	ML2	FM2	EPI
1	0.404	0.621	0.501	0.646	0.451
2	0.392	0.360	0.522	0.459	0.515
3	0.495	0.656	0.504	0.627	0.513
Note: All correlations are highly significant (P < 0.01)					

Although these correlations seem to be low when used to indicate accuracy, they are similar to the correlations obtained by Olivier (1988) who compared

performance test results on young Merinos with their subsequent predicted breeding values. It therefore seems as if selection of young animals based on BLUP of breeding values was far superior to existing methods.

A preliminary selection of ewes, based on the breeding values of their dams, therefore seems feasible. A comparison of a ewe's breeding value prediction before she has had any progeny with the prediction after progeny records are available, is discussed in the next section (6.4).

The results of comparing breeding value solutions for males which later became sires (indicated as breeding values of sons in Table 6.4) with that of their dams, are presented in Table 6.4. The entire dataset was used.

TABLE 6.4:   CORRELATIONS BETWEEN BREEDING VALUES OF DAMS AND BREEDING VALUES OF SONS (n = 143)

APPROACH	ML1	ML2	FM1	FM2	EPI
1	0.055	0.086	0.250^{**}	0.279^{**}	0.077
2	0.014	0.059	0.256^{**}	0.178^{**}	0.091
3	0.063	0.082	0.259^{**}	0.268^{**}	0.069
Note: ** = highly significant (p > 0.01); all other correlations are non-significant.					

From Table 6.4 it is clear that selection of rams on the basis of ancestral information only is not reliable, especially as far as ML-traits are concerned, since all correlations are low.

As far as reproduction rate (indirectly a component of EPI) is concerned, Cloete (1986) came to the following conclusion: "The present results failed to reveal any justification for the selection of multiple born rams to increase

overall reproduction in the Tygerhoek flock." The results presented in Table 6.4 obviously lead to a similar conlusion for EPI since one of the primary aims of using EPI as a selection criterion, is to increase reproduction rate.

In order to investigate the possible effect of the number of progeny on the accuracy of breeding value prediction for sires, only Approach 3 was used since the different approaches should yield very similar results. The correlation between the sires' breeding value predictions (termed sons in Table 6.4) and average breeding value prediction of their ewe progeny, is given in Table 6.5.

TABLE 6.5:   CORRELATION BETWEEN THE BREEDING VALUES OF SIRES (n = 143) AND THE AVERAGE BREEDING VALUES OF THEIR PROGENY

NO. OF PROGENY	n	ML1	FM1	ML2	FM2	EPI
< 4	262	0.061	0.048	0.013	0.040	0.049
4 - 6	175	-0.002	0.035	0.049	-0.063	0.071
> 6	63	-0.042	0.122	-0.071	0.181	-0.090
Pooled	500	0.031	0.019	0.051	0.025	0.043

Note: All correlations are non-significant ($P > 0.05$)

According to the results presented in Table 6.5 the largest increase in the correlation between the breeding values of sires and that of the average of their daughters, with an increase in the number of daughters, occurred in respect of FM1 (from 0.048 to 0.122). It can therefore be concluded that where the number of progeny per ram is small, as in the present study, additional information from progeny did not contribute much to increase the accuracy of the prediction. It therefore seems appropriate to suggest that rams cannot be selected on the EPI values of their dams or daughters unless the number of daughters is much higher.

The difference obtained between rams and ewes as far as accuracy of prediction of breeding values of young animals without their own records or progeny is concerned (Tables 6.3 and 6.4) can readily be explained. Rams provide no additional information as they have no records of their own. The Mendelian Sampling effect of the genes they receive can therefore not be determined. Their own breeding values are predicted only on information from their female ancestors and female progeny. The accuracy of the rams' prediction is therefore expected to be lower than that of the ewes, whose Mendelian Sampling effect is known.

As mentioned in section 6.1, a secondary aim in this section is to ascertain which one of the three approaches yielded the most reliable (co)variance structure.

The results presented in Tables 6.3 and 6.4 suggest that the (co)variance structure obtained by Approach 3 is consistently slightly superior in depicting the effect of the actual (co)variances on breeding value prediction. The correlation obtained for EPI using Approach 3 is slightly higher than for Approach 1, which again points to a slight superiority of Approach 3. It therefore seems reasonable to assume that the results used for (co)variance determination were interpreted correctly in Chapter 5. Subsequently only the results obtained by using Approach 3, will be used for further investigations.

6.4 Use of Part-Records of ewes for Predictive Purposes

Pertinent questions to be answered when applying ewe productivity in practice, include the following:

(i)   Is it possible to select ewes after one record (ML1 plus FM1) only?

(ii) What is the accuracy of predictions based on two records?

A comparison was made between breeding value predictions obtained for ewes born in 1974 utilising information from ancestors and collateral relatives only (B74-2), and the breeding value predictions of the same ewes obtained by including progeny (B80-2). It was decided to truncate the dataset at 1974 to provide as much ancestral information as possible, while leaving at least one generation of progeny for an accurate analysis. Additionally only one lambing record consisting of ML1 and FM1 was used in a two trait animal model analysis (B74-1) to investigate question 1. The appropriate L-matrix specified in Chapter 3 for the two-trait model was used for the necessary canonical transformations. This analysis (B74-1) included ewes which were eliminated after the first record, and which therefore were excluded in the data set on which the four trait (ML1, FM1, ML2 and FM2) animal model (B80-2) was used. This resulted in a data set comprising 2248 records based on ML1 and FM1. The same ewes used in the analysis of both the total data set of 1907 records and the data set truncated after 1974, were used for comparative purposes.

The B80-2 analysis can only be regarded as a "prediction" of the true values on account of its dependence on the assumed (co)variance structure. The other two, more error-prone, analyses (B74-2 and B74-1) were compared with this analysis, since the true breeding values were not available.

Results are presented in Table 6.6 for the components of EPI.

The correlations between breeding values obtained by all three methods for the ML traits, except those between the B80-2 and B74-1 analyses (0.319), are reasonably high.

TABLE 6.6: CORRELATION COEFFICIENTS BETWEEN PART-RECORDS FOR PREDICTION AND COMPLETE RECORDS FOR PREDICTION OF BREEDING VALUES OF THE COMPONENTS OF EWE PRODUCTIVITY (n = 168).

1. ML TRAITS			
		ML1	ML2
B80-2 x B80-2	ML1	–	0.086
B80-2 x B74-2	ML1	0.976	0.777
B80-2 x B74-2	ML2	0.814	0.983
B80-2 x B74-1	ML1	0.758	0.319
B74-2 x B74-1	ML1	0.811	0.399

2. FM TRAITS			
		FM1	FM2
B80-2 x B80-2	FM1	–	0.879
B80-2 x B74-2	FM1	0.988	0.874
B80-2 x B74-2	FM2	0.863	0.986
B80-2 x B74-1	FM1	0.960	0.811
B74-2 x B74-1	FM1	0.974	0.815

It was hoped that use of the B74-1 analysis would increase the accuracy of the evaluation since the availability of more animals with one record only, led to more information included in the relationship-matrix. On the other hand, the accuracy gained by including the information of a second record (B80-2 and B74-2) will be lost. It was hopefully anticipated that the compromise between these two factors would be in favour of the use of one record. The practical advantage of fewer measurements and earlier final selection of ewes, is self-evident. As a result of the low correlation of B74-1 with B80-2 (r = 0.319), at least two measurements of ML for accurate breeding value predictions are required.

Unfortunately the correlations between both B80-2 and B74-2 with B74-1 (r = 0.319 and 0.339 respectively) are low. This result indicates that prediction of a ewe's second lambing record (ML2) from her first record (ML1) only is very inaccurate.

Contrary to the ML traits, the lowest correlation between any two analyses in the case of the FM traits, is 0.811 (Between B74-1 and B80-2). Therefore it seems as if one measurement of fleece mass should be sufficient for evaluating fleece production. It must, however, be remembered that information on correlated FM traits contributes towards the accuracy of prediction of breeding values of the ML traits. Consequently, it is difficult to contemplate what the precision of such a possible three trait animal model would be.

Correlations similar to those for the components of EPI (Table 6.6) are presented for EPI itself in Table 6.7, the objective being to obtain a better indication as to whether implementing a three trait animal model (ML1, ML2 and FM1) is a feasible proposition.

TABLE 6.7:   COMPARISON OF PART-RECORDS WITH COMPLETE RECORDS OF EPI BASED ON PRODUCT MOMENT CORRELATION COEFFICIENTS BETWEEN THE THREE DIFFERENT ANALYSES (n = 168).

	B80-2	B74-2
B74-2	0.986	–
B74-1	0.578	0.606

The low correlations between the B74-1 analysis and the other two analyses may be ascribed to the effect of the low accuracy of ML1 predictions obtained by B74-1 (according to Table 6.6).

The correlation between B80-2 and B74-1 which included FM1 only, was 0.578. In comparison, the correlation between ML1 (obtained by B74-1) and ML2 (obtained by B74-2) was 0.339 (Table 6.6). It is therefore clear that the difference between the two correlations (17.74%) brought about by combining the FM1 and ML1 values to obtain a selection index, did not increase the level of accuracy to an acceptable degree above that for ML1 alone. The norm was taken as the correlation between the B80-2 and the B74-2 analysis of 0.986. Following this reasoning, it seems as if the inclusion of FM2 in models recommended for the industry, may therefore be warranted.

The fact that the correlations indicated in Tables 6.6 and 6.7 are not closer to unity, can be ascribed to two main possible reasons.

Firstly, smaller numbers of observations in the subsets of data could lead to larger regressions to the mean.

Secondly, the use of a sub-optimal (co)variance structure could have lead to differences in the variances of the traits concerned.

It is interesting to note that Wilson (1984) reported correlation coefficients of 0.79 and 0.93 in a comparison of different approximations of PEV's of breeding values in a sire model. The results obtained in the present study in predicting breeding values based on full records from predicted breeding values derived from part-records therefore seem fairly accurate, especially in the case of fleece mass.

To illustrate how the theoretically most inaccurate analysis (B74-1) influences the order of merit of ewes in predicted breeding value, scatter plots of the lowest regressions between the B74-1 and B80-2 analyses for ML1, FM1 and EPI are presented in Figure 6.3.
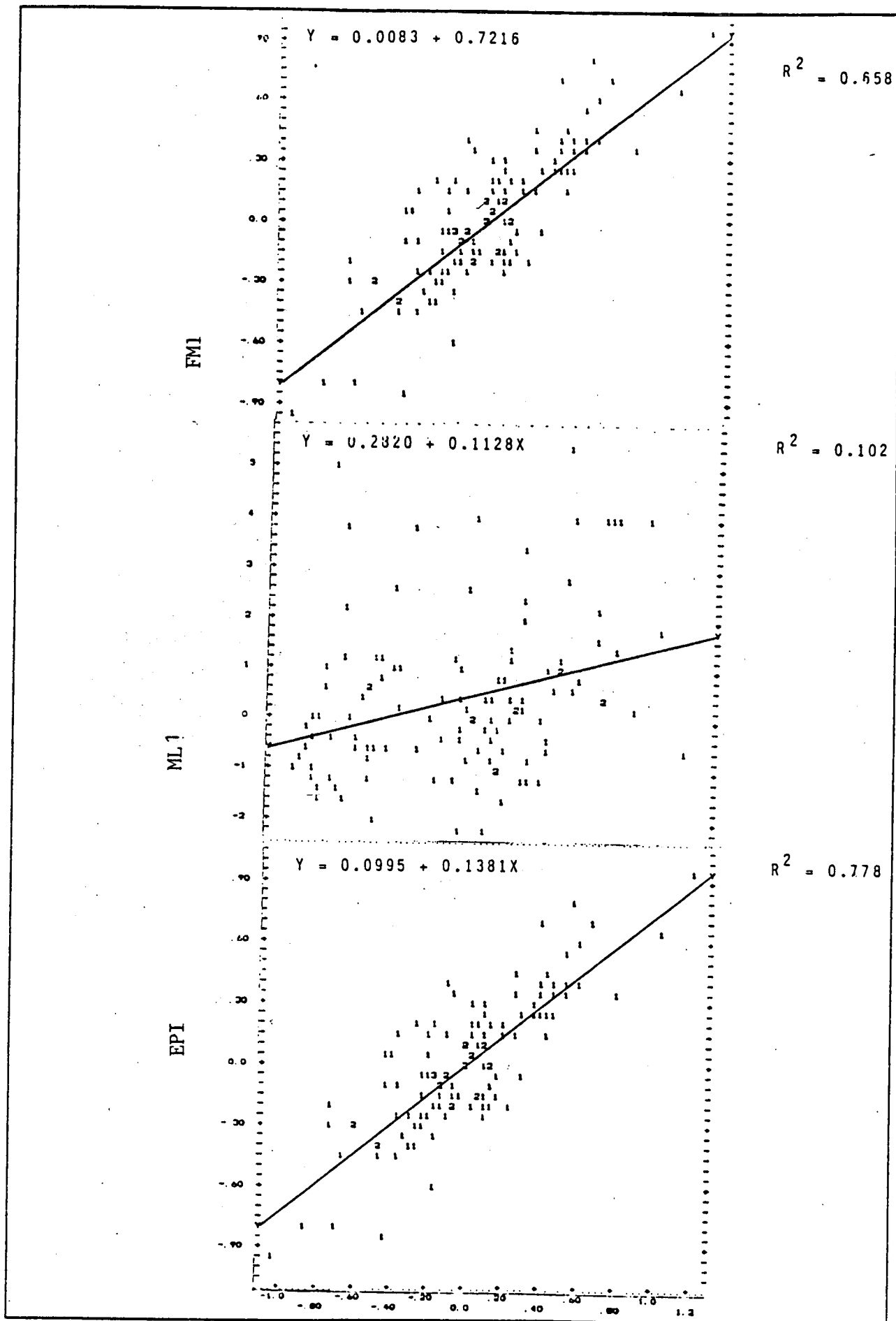
FIGURE 6.3   RECESSION OF B74-1 ANALYSES ON B80-2 IN CASE OF FM1, ML1 AND

EPI

The narrow distribution around the regression line of FM1 ($R^2 = 0.658$) compared to that of ML1 ($R^2 = 0.102$), is marked. The fact that reasonably accurate selection for fleece mass can be achieved from one measurement only is clearly demonstrated.

With regard to ML1, it is clear that a group of "outliers" occur above the general pattern of distribution. These predicted breeding values are representative of ewes which reared reasonably well-grown multiples.

6.5 Correlated changes

The main purpose of this section is to determine whether any adverse correlated changes may occur in any of the more important production traits traditionally selected for at 18 months of age, when selecting ewes on the basis of EPI.

Breeding values predicted for body mass, clean fleece mass and fibre diameter measured on maiden ewes at 18 months of age in the Klerefontein selection experiment, were available (Erasmus, 1988) and were consequently regarded as ideally suited to investigate possible correlated genetic changes with EPI.

In addition to these traditional selection criteria (mentioned above), the actual number of lambs weaned was used to investigate the relationship of EPI with reproduction because of the generally accepted significant influence of reproduction on income from the ewe flock in the form of lamb or mutton production.

Weaning mass *per se* was not compared to EPI as it forms an integral part of EPI. It is also doubtful whether the ewe's own weaning mass bears any significant direct relationship to her productive ability (other than mature body

mass and growth traits) during her lifetime.

The investigation was performed by making use of the following principles:

Although the correct method to undertake this investigation would be to make use of the theory on genetic correlations, the second best alternative, namely the determination of Pearson's product moment correlations between breeding value predictions, was used. The reason being that the iterative procedures (I-MIVQUE, MINQUE, REML and ML) can only be used if an inverse of the coefficient matrix can be obtained. In terms of the computing ability of the mainframe computer in use and the available algorithms, any analysis will be limited to a maximum of approximately 650 animals in the case of the animal model.

The correlations presented in this section are dependent on the (co)variance structure used for the particular analysis and although they conform closely to the general definition of genetic correlations, they can only be regarded as correlations between predictions and not true genetic correlations.

The breeding value predictions for body mass, clean fleece mass and fibre diameter used in this investigation of "correlated changes", were obtained from the study by Erasmus (1988). The heritabilities used for that analysis were the following:

Body mass   0.247

Clean fleece mass   0.229

Fibre diameter   0.369

The correlations between the breeding values of the traits measured at 18 months of age and EPI, are presented in Table 6.8. The correlations were pooled over years and selection flocks. All correlations were highly significant (P < 0.001).

TABLE 6.8:   CORRELATIONS BETWEEN THE BREEDING VALUES OF TRAITS MEASURED AT 18-MONTHS OF AGE AND EPI

BODY MASS	CFM	FIBRE DIAM.	n
+0.301	+0.136	+0.120	1893

NOTE: (1) CFM = Clean Fleece Mass.

(2) Although the data set used for this study contained 1907 records, some ewes were not measured at 18 months of age and hence the lower n of 1893.

The fact that 18-month body mass changes in a positive direction with increased ewe productivity is to be expected due to the relationship between body mass and reproduction normally found in Merino sheep. The fact that the Klerefontein experiment was conducted in semi-desert environmental conditions, probably also increased this relationship. The more robust males and females produced more offspring (Erasmus, 1988). The effect of both natural and artificial selection may therefore have been responsible for this relatively high correlation of +0.301.

Reproductive ability which is also included in an effort to determine "correlated changes", forms a part-whole relationship with total ewe productivity. The most suitable manner of handling this kind of relationship would be to employ partial regression techniques. Landis and Koch (1977) quoted by Rae and Anderson (1982), however, mention that variance and covariance estimation from categorical data has progressed only as far as the one-way classification model and that calculating covariances between discrete and continuous random variables is in need of further investigation. Therefore, it was decided to resort to an ordinary comparison of the animals constituting the two ends of the distribution curve. This method of comparison is also in accordance with

the use of the principles of selection differential theory to avoid the complexity of the determination of a correlation between a discrete and continuous trait (Yamada, 1977).

In the present study, the number of lambs weaned from the highest ten percent and lowest ten percent of ewes selected on EPI, were compared. The analysis was restricted to ewes born in 1974 and 1975. The ewes born in 1974 were selected so as to coincide with the procedures used in section 6.3 and 6.4. Inclusion of an additional year's (1975) data led to the advantage of comparing lifetime reproduction figures during a period of extreme fluctuations in average yearly reproduction rates (Figure 2.1). The comparison presented in Table 6.9 consisted of a total of 186 ewes from which the highest 20 and lowest 20, made up from both birth years, were selected on the basis of total ewe productivity.

TABLE 6.9: DIFFERENCE IN NUMBER OF LAMBS WEANED (NLW) FROM THE LOWEST AND HIGHEST PRODUCING EWES BORN IN 1974 AND 1975

| | AVERAGE NLW PER LAMBING RECORD | | | | | | | |
	1st	2nd	3rd	4th	5th	Mean	n	Deaths
1974 Low	0.00	0.00	0.67	0.55	1.00	0.42	12	2
High	0.83	1.33	0.50	0.73	1.18	0.91	12	1
1975 Low	0.00	0.00	0.50	1.20	0.80	0.45	8	3
High	1.00	1.13	1.13	1.25	1.38	1.18	8	0

The range in EPI (to indicate typical figures which may be expected in this criterion) were from -13.29 to +21.39. Ewes which died before the end of their productive lifetime of five lambing seasons are indicated as "deaths" in Table 6.9. These ewes were not taken into account in calculating mean total lambing performance.

These results clearly illustrate that EPI was effective in identifying ewes with relatively high lifetime reproductive abilities. The figure of 0.50 in Table 6.9 for the third lambing record of the 1974 born high producing ewes seems to be contradictory to expectation in that it is lower than that for the corresponding low producing ewes (0.67). The third lambing record of the ewes born in 1974, however, represents the lowest reproduction figures recorded in the entire experimental period (Figure 2.1). It can therefore be reasoned that the carry-over effect of the previous year's lamb production is expressed to a greater extent in harsher periods.

An important aspect, highlighted by Table 6.9, is the fact that some 1974 born ewes which did not lamb at two years of age (ML1 = 0) were included in the highly productive group since number of lambs weaned is not the only factor contributing to EPI. The average number of lambs produced per mating (0.83) is a clear indication that the implementation of EPI makes it possible to select potentially highly productive ewes from groups of ewes falling in the same lamb-rearing status category. Although this specific subset of data illustrates selection of the best ewes from those which did not rear lambs, a similar possibility is expected for ewes raising multiple lambs.

To indicate how selection on EPI could affect traits recorded at 18 months of age, differences between the breeding value predictions for body mass, clean fleece mass and fibre diameter of ewes with high EPI values and those with low EPI values (same ewes presented in Table 6.9), is depicted in Table 6.10.

It is interesting to note that all the breeding value predictions presented in Table 6.10 are positive which illustrates the positive selection response for all three traits obtained earlier as reflected by the ewes born in 1974 and 1975.

TABLE 6.10: DIFFERENCE IN BREEDING VALUES OF 18 MONTH TRAITS FOR 1974 AND 1975 BORN EWES.

	BODY MASS	CLEAN FLEECE MASS	FIBRE DIAMETER
Deviation in:	kg	kg	μ
1974 Low	1.700	0.063	0.290
High	2.282	0.149	0.366
1975 Low	0.024	0.126	0.174
High	3.394	0.134	0.459
TOTAL Low	1.089	0.124	0.244
High	3.049	0.143	0.403

Table 6.10 indicates the actual selection of ewes with substantially higher breeding value predictions for 18 month body mass (maximum difference = +3.39 kg). Only slightly higher predictions were indicated for clean fleece mass and fibre diameter (maximum difference = +0.09 kg and +0.285 μ). This is in accordance with the correlations presented in Table 6.8.

The results presented in this section indicate that positive selection for EPI should not have any serious deleterious effects on other important production traits. Although lambing performance is an important factor contributing to EPI the growth of the lamb(s) produced and wool production is also important in determining the total productivity of Merino ewes.

6.6 Genetic trends

The genetic trends as presented in Figures 6.4 and 6.5, were compiled from a multiple-trait analysis utilising the (co)variance structure of Approach 3. In comparison to the genetic trends (based on an analysis utilising variances

only) presented in section 3.2, the complete genetic and environmental (co)variance structures were utilised for the presentation of Figure 6.4. As far as the trends in the components of EPI are concerned, although not clearly evident from the presentation in Figures 6.4 and 6.5, significant (P < 0.05) positive trends in ML1 and ML2 for both the subjective and "control" flocks were obtained (Table 6.11). These trends may represent correlated changes as the result of positive natural and artificial selection for 18 months body mass which took place in both these two flocks (Erasmus, 1988).
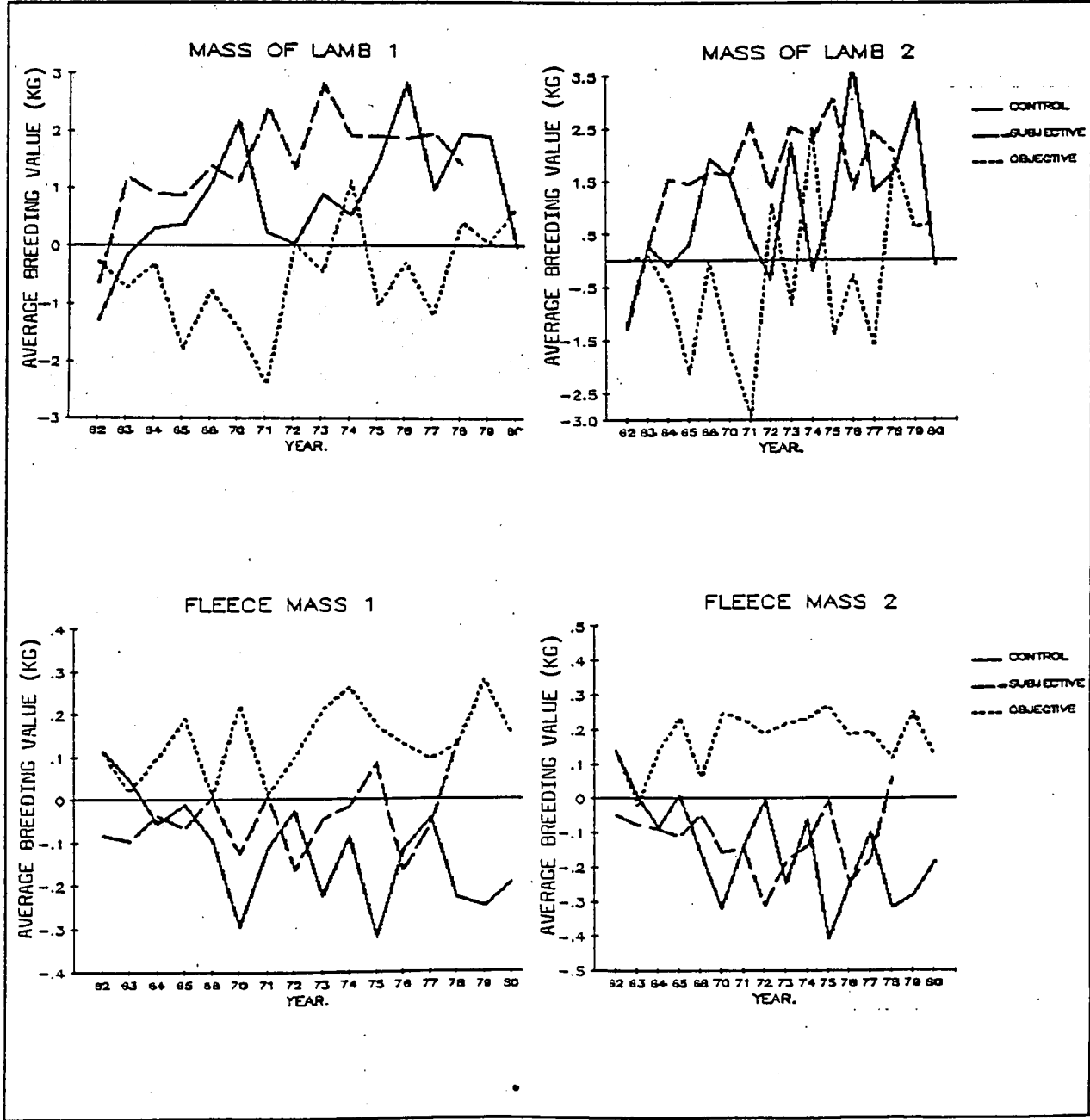
FIGURE 6.4   GENETIC TRENDS IN THE FOUR COMPONENTS OF EPI (THREE SELECTION FLOCKS)
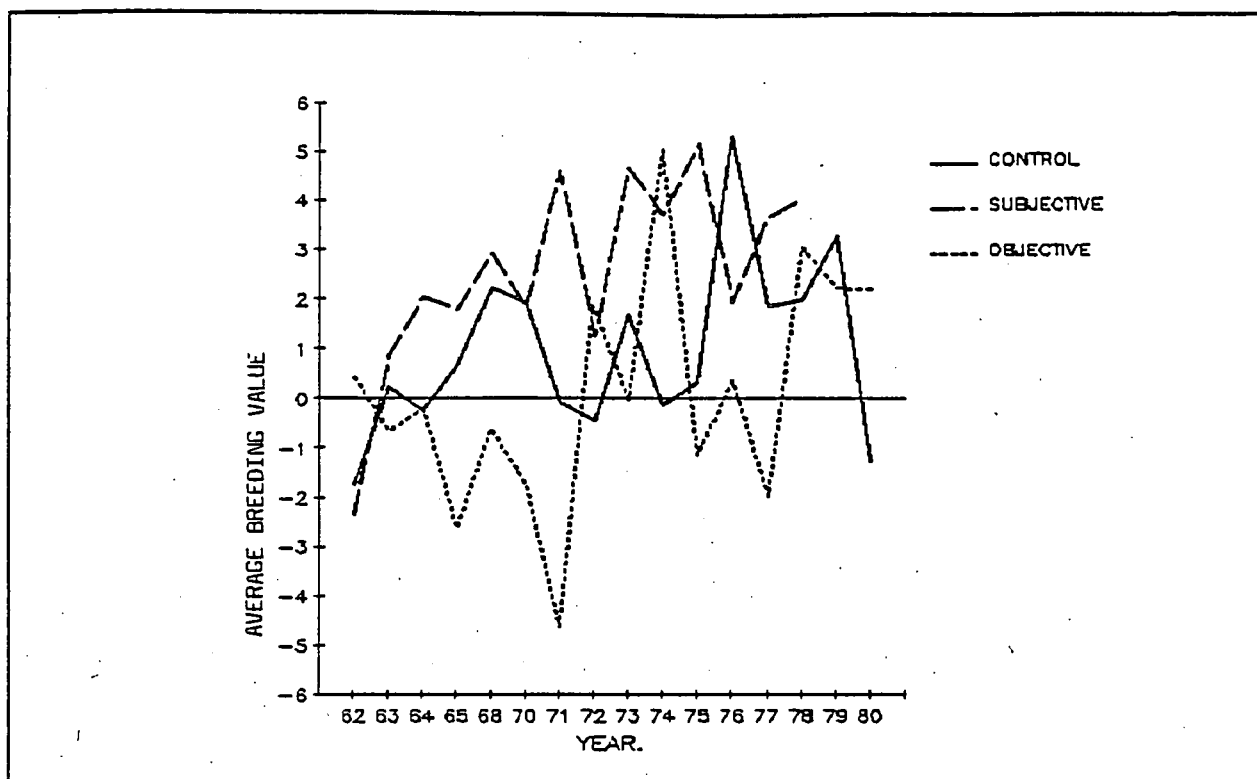
FIGURE 6.5   GENETIC TRENDS FOR EPI IN THE THREE SELECTION FLOCKS

Regression coefficient of yearly averages of breeding value predictions on time (expressed in years) are presented in Table 6.11.

TABLE 6.11:   REGRESSION COEFFICIENTS OF BREEDING VALUES OF EWE PRODUCTIVITY (EPI) AND ITS COMPONENTS ON TIME IN THE THREE SELECTION FLOCKS

FLOCK:	CONTROL	SUBJECTIVE	OBJECTIVE
EPI	0.121	0.256*	0.159
ML1	0.100*	0.105*	0.057
ML2	0.112*	0.144*	0.070
FM1	0.014*	0.005	0.006
FM2	−0.017*	−0.003	0.005
NOTE: * = P < 0.05			

The values obtained for ewe productivity (EPI) can strictly speaking not be

regarded as breeding values since EPI is a selection index compiled from the predicted breeding values of it's components. The utility value of the calculation and the presentation of the composite trait EPI in Table 6.11, however, stems from the fact that it is difficult to differentiate between highly and less productive animals by using breeding value figures of four different traits separately. It must, however, be stressed that although EPI is an important measure, this is not an attempt to reduce selection technique for ewe selection to a single figure.

The only significant ($P < 0.05$) positive trend in EPI was found in the subjectively selected flock ($b = 0.256$) which is most probably related to the genetic increase in body mass reported by Erasmus (1988). It must, however, be borne in mind that a definite possibility of positive changes in the reproduction ability of the subjectively selected flock and to a lesser extent of the control flock, was pointed out in Chapter 2.

It is interesting that Table 6.11 also indicates a significant positive genetic trend for FM1 in the control flock ($b = 0.014$), but a correspondingly negative trend for FM2 ($b = -0.017$).

Visual observations (J. M. Cloete, S.A. Wool Board, Pretoria,1986, personal communication) indicated an increase in skin folds in the objectively selected flock. This could have caused a correlated decline in reproduction rate (Dun and Eastoe, 1970). Unfortunately fold score was not measured in this experiment, thereby excluding any conclusive evidence of a relationship between fitness traits and wool production.

An apparent contradiction exists between the results presented for 18 month clean fleece mass in Table 6.8 (section 6.5) and those in this section for FM1 and FM2 (fleece mass after producing a lamb). The fact that FM1 and FM2 tend

to have a slightly negative regression coefficient on time in the control and subjectively selected flocks (b = -0.017 and -0.003 respectively) may be an indication of the negative genetic effect of gestation and lamb rearing on genetic potential for wool production. The slight positive correlation between EPI and 18 month clean fleece mass breeding values (r = +0.136, Table 6.8) may, on the other hand, be an indication of inherent superior genetic potential for ewe productivity. EPI therefore probably identified the genetically more robust animals for selection purposes. This low correlation between predictions for 18 month clean fleece mass and predictions for EPI may be indicative of another very important aspect, namely that selection on fleece mass in the ewe flock should take place only after the ewes have had an opportunity to rear lambs.

The same argument as for fleece mass, namely that EPI tends to identify animals which are physiologically more efficient at 18 months of age, and therefore produce more wool, also holds true for fibre diameter (which is higher) measured at the same age. The low correlation between EPI and breeding value for fibre diameter of 0.120 (Table 6.8) might be seen as an indication of a positive relationship between EPI and the production of thicker fibres.

The non-significant change in FM1 and FM2 which took place in the objectively selected flock (b = 0.006 and 0.005) may be an indication that the high selection pressure on maiden clean fleece mass (Erasmus, 1988) was ineffective in increasing fleece production later in the ewes' lifetime. The most probable reason is that selection took place too early in the ewes' life which is substantiated by the generally higher heritabilities obtained in the present study for FM1 and FM2 than the 0.241 for fleece mass at 18 months of age reported by Erasmus (1988).

CHAPTER 7

7. GENERAL CONCLUSIONS

The concept of ewe productivity, expressed as the total production of lamb and wool, is obviously a useful measure of expected income from the ewe flock and therefore needs serious consideration as a selection criterion. The present study has shown that by applying multiple-trait mixed model analyses, breeding value predictions can readily be obtained for this complex trait and its components. The most useful finding is undoubtedly that the combination of two lambing and fleece mass records as a single measure of ewe productivity, is both practical and feasible. Another positive result is that selection for ewe productivity appears to have no deleterious effect on maiden ewe performance as far as fleece mass and body mass is concerned. The slight positive relationship with fibre diameter should not pose a serious problem. Selection for ewe productivity can therefore be carried out after, and supplementary to, the normal preliminary selection before lambing.

Accurate prediction of breeding values for ewe productivity may lead to the exploitation of exciting new possibilities. Using this technique on a within-breed basis on ewes which produced at least two lambs after the first two lambing opportunities, may be an aid in identifying the "Elite" ewes in the breed. Multiple Ovulation and Embryo Transfer (MOET) technology may consequently lead to more rapid dissemination of this superior genetic material throughout the entire breed (Skjervold, 1984).

Some limitations in the applications of ewe productivity as a selection criterion have also been unveiled. Firstly, it is evident that one record only of total mass of lamb weaned is not a reliable basis for accurate predictions to be made. Until more extensive evidence is available, this first application

of a four-trait model using two records of mass of lamb weaned and two fleece mass records, seems to be the most realistic option.

Secondly, whereas evidence from the present study suggests that dam selection on the basis of breeding value predictions may be fairly accurate, the possibility of sire selection does not seem promising. Willham (1982), Wilson (1984) and others however, recommended the determination of maternal breeding values for sires. The fact that this recommendation was made for a beef industry where the use of AI is widespread, may warrant its implementation in that situation. Under a system of natural mating with few progeny per sire, the value of these estimates is doubtful. Depending on future use of MOET (implying more research on maternal breeding value estimations) in the sheep industry, the situation might well change.

The fact that one record of a ewe for ewe productivity consists of two traits (both known), means that the computing strategy using canonical transformations, is ideally suited to meet the conditions of the model specified. Although basic computer algorithms for the execution of this method have been written, considerable refinement for broad application is needed. Firstly, a database for the orderly collection of data should be developed. Secondly, an algorithm based on the Simple Method (Schaeffer and Kennedy, 1986) will have to be developed for the early identification of highly productive ewes. A method for the calculation of predicted error variance and its incorporation into the Simple Method, needs urgent attention.

The computer programmes developed initially to give the author the neccessary insight and confidence in applying the advanced methodology, have already proved to be useful in research and practice. The sire model using the "Simple Method" of Schaeffer and Kennedy (1986) is currently used to evaluate Dairy bulls on a National basis in South Africa. The programme for a single

trait animal model has been used in the analysis of selection experiments (Erasmus, 1988; Cloete, Delport, Erasmus & Olivier, 1989) and in separating genetic and environmental effects in a commercial Merino stud (Olivier, 1989). An indirect consequence of this study, was the development of a programme for microcomputers to determine inbreeding according to the algorithm by Quaas (1976). Application of the computing strategy using canonical transformations to other situations such as fleece analysis, where the prerequisites of all traits being known and the same design matrix prevail, can also be envisaged.

Also, future research should be directed at developing a multiple-trait analysis for continuous traits to be combined with a threshold trait. Rae and Anderson (1982), however, warn that these procedures are extremely intricate.

The first determination of the (co)variance structure used in the present study can be regarded as the best "calculated guess" possible. Future research implementing new sophisticated methods of estimation (REML and other iterative techniques) should be a high priority. This research will naturally depend heavily on the availability of accurate data. Accurate records of parentage will be one of the critical success factors determining the quality of such research.

Although it is accepted that the last word has certainly not been said on the possible improvement of the productivity of the ewe flock, it is hoped that this dissertation will make some contribution towards existing knowledge.

ABSTRACT

1. The possibility of using Mixed Model Methodology in the selection of Merino sheep for ewe productivity was investigated. Ewe productivity, defined as a function of both the mass of lamb weaned and the mass of wool produced by the ewe, presented a situation ideally suited to the use of canonical variates in a multiple-trait model.

2. The methodology and computer algorithms for the application of the mathematical model were validated by using a data set (1907 ewes with two successive records) obtained from the Klerefontein selection experiment of the Department of Agriculture and Water Supply. The experiment consisted of three flocks, one selected for high clean fleece mass, another for overall visual excellence and an unselected control flock.

3. Computer programmes developed for the purpose of this study proved to be useful for other situations of determining breeding values, separating genetic and environmental effects and inbreeding calculation.

4. The fact that no (co)variances between mass of lamb weaned and wool production could be obtained from literature led to the determination of the necessary parameters from the available data (although not ideally suited to this purpose).

5. The effect of using different (co)variance structures was investigated. Results indicate that adjustment to these structures does not lead to selection of vastly different ewes. The lowest correlation between predicted breeding values of any of four different structures was 0.811. The best one of these structures was selected on the basis of the distribution pattern in the base population as well as the accuracy of

predicting breeding values.

6. It is possible to make a reasonably accurate preliminary selection of ewes on their dams' breeding value predictions. The dam-daughter correlations (between breeding values) were as high as 0.66 in the case of the chosen (co)variance structure. The possibility of selecting sires on the basis of their daughters' predicted breeding value in ewe productivity does, however, not seem to be promising.

7. The evidence presented points to no significant adverse effects on 18-month performance when selecting for ewe productivity. The correlation with BLUP on ewe productivity with BLUP breeding values for body mass ($r=+0.301$), and clean fleece mass ($r=+0.136$) seems to fit in with current selection practices. The correlation of ewe productivity values with breeding value predictions for fibre diameter ($r=+0.120$) may present a problem in the sense that negative selection for fibre diameter is currently a high priority in the industry. The fact that the correlation is very low indicates that slight selection pressure on fibre diameter will take care of this relationship.

8. Genetic trends in ewe productivity (EPI) and the components thereof are presented. Being correlated responses to both artificial and natural selection for body mass, genetic changes were slight. The highest regression coefficient for ewe productivity (EPI) was 0.256 ($P<0.05$).

9. The general conclusion is that the concept of ewe productivity poses a practical possibility for increasing returns from the ewe flock. Applying the technique of multiple-trait analysis on canonical variates, may be a viable proposition in the solution of many other problems.

ACKNOWLEDGEMENTS

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APPENDIX A

PERCENTAGE OF LAMBS WEANED PER EWE MATED

(From data supplied by Olivier, unpublished)

YEAR	CONTROL	SUBJECTIVE	DEVIATION	OBJECTIVE	DEVIATION
1962	74	69	-5	70	-4
1963	69	74	5	78	9
1964	53	63	10	66	13
1965	70	80	10	75	5
1966	64	70	6	64	0
1967	67	66	-1	66	-1
1969	81	96	15	68	-13
1970	58	64	6	54	-4
1971	88	86	-2	81	-7
1972	65	69	4	64	-1
1973	78	93	15	72	-6
1974	74	85	11	63	-11
1975	82	83	1	75	-7
1976	62	54	-8	44	-18
1977	75	89	14	84	9
1978	45	50	5	42	-3
1979	56	56	0	44	-12
1980	93	92	-1	83	-10
1981	74	75	1	67	-7
1982	91	-	-	80	-11

Note: deviations are given from control

APPENDIX B

METHOD FOR MULTIPLE-TRAIT ANALYSIS WITH CANONICAL TRANSFORMATION

Referring to the model specified in section 4.3 and using the general notation for specifying a multiple-trait model in matrix notation (Henderson and Quaas, 1976), the following equations may be set up :

$$
\begin{bmatrix} Y \\ Y \\ Y \\ Y \end{bmatrix} = \begin{bmatrix} X & 0 & 0 & 0 \\ 0 & X & 0 & 0 \\ 0 & 0 & X & 0 \\ 0 & 0 & 0 & X \end{bmatrix} \times \begin{bmatrix} B \\ B \\ B \\ B \end{bmatrix} + \begin{bmatrix} Z & 0 & 0 & 0 \\ 0 & Z & 0 & 0 \\ 0 & 0 & Z & 0 \\ 0 & 0 & 0 & Z \end{bmatrix} \times \begin{bmatrix} U \\ U \\ U \\ U \end{bmatrix} + \begin{bmatrix} e \\ e \\ e \\ e \end{bmatrix}
$$

In this form animals are ordered within traits.

At this point, it may be appropriate to mention two different possible approaches for setting up and solving the mixed model equations (MME) specified above.

Following the first approach, mixed model equations are set up in the form of traits within animals. Solutions are obtained from solving the MME for all traits simultaneously. The algorithm by Schaeffer (1984), using block iteration, is ideally suited for calculating breeding values when following this approach. Arnason (1984) also followed this approach for solving MME, but with the difference that canonical transformations were applied. In Arnason's (1984) case the inverse of the numerator relationship matrix still appears four times in the set of MME when dealing with two traits, the reason being to make provision for covariance between traits.

The second approach, namely that followed by Quaas, Anderson and Gilmour (1985) implies reduction of the MME to that for separate single-trait

analyses. Although this method reduces to separate computer runs for each trait, it was decided to follow this approach, the main reason being that Schaeffer and Kennedy's (1986) Simple Method could be employed thereby saving more computing effort than with the use of block iteration.

The essential difference between a single-trait model and a multiple-trait model is that the covariance structures for the general model above may be described as follows:

$$
VAR \begin{bmatrix} U_1 \\ U_2 \\ U_3 \\ U_4 \\ e_1 \\ e_2 \\ e_3 \\ e_4 \end{bmatrix} = \begin{bmatrix} G_{11} & G_{12} & G_{13} & G_{14} & & & & \\ G_{21} & G_{22} & G_{23} & G_{24} & & & \phi & \\ G_{31} & G_{32} & G_{33} & G_{34} & & & & \\ G_{41} & G_{42} & G_{43} & G_{44} & & & & \\ & & & & R_{11} & R_{12} & R_{13} & R_{14} \\ & & & & R_{21} & R_{22} & R_{23} & R_{24} \\ & \phi & & & R_{31} & R_{32} & R_{33} & R_{34} \\ & & & & R_{41} & R_{42} & R_{43} & R_{44} \end{bmatrix} \cdot \sigma^2
$$

Factoring out σ^2 from all matrices does not leave one with $R = I$ as in the case of a single-trait model (Quaas, Anderson and Gilmour, 1985).

In order to make use of canonical transformations the following assumptions must be made:

i)   for every element in Y_1, and therefore e_1, there are corresponding elements in Y_2 to Y_4 and e_2 to e_4.

ii) $X_1 = X_2 = X_3 = X_4 = X_0$. This implies that all traits are affected by the same fixed effects (exactly the same fixed effect design matrix is being used for all traits).

The model may now be denoted as:

$$
\begin{bmatrix} Y_1 \\ Y_2 \\ Y_3 \\ Y_4 \end{bmatrix} = \begin{bmatrix} X_0 & 0 & 0 & 0 \\ 0 & X_0 & 0 & 0 \\ 0 & 0 & X_0 & 0 \\ 0 & 0 & 0 & X_0 \end{bmatrix} \times \begin{bmatrix} B_1 \\ B_2 \\ B_3 \\ B_4 \end{bmatrix} + \begin{bmatrix} Z_0 & 0 & 0 & 0 \\ 0 & Z_0 & 0 & 0 \\ 0 & 0 & Z_0 & 0 \\ 0 & 0 & 0 & Z_0 \end{bmatrix} \times \begin{bmatrix} U_1 \\ U_2 \\ U_3 \\ U_4 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \\ e_3 \\ e_4 \end{bmatrix}
$$

with covariance structure in matrix notation of:

$$
G_0 = \begin{bmatrix} G_{11}A & G_{12}A & G_{13}A & G_{14}A \\ G_{21}A & G_{22}A & G_{23}A & G_{24}A \\ G_{31}A & G_{32}A & G_{33}A & G_{34}A \\ G_{41}A & G_{42}A & G_{43}A & G_{44}A \end{bmatrix}
$$

Where G_0 is the additive genetic covariance matrix in the case of the animal model:

$$
R_0 = \begin{bmatrix} r_{11}I & r_{12}I & r_{13}I & r_{14}I \\ r_{21}I & r_{22}I & r_{23}I & r_{24}I \\ r_{31}I & r_{32}I & r_{33}I & r_{34}I \\ r_{41}I & r_{42}I & r_{43}I & r_{44}I \end{bmatrix}
$$

R_0 is the residual covariance matrix for the four traits.

The MME now become:

$$
\begin{bmatrix} R_0^{-1*} X_0'X_0 & R_0^{-1*} X_0'Z_0 \\ R_0^{-1*} Z_0'X_0 & R_0^{-1*} Z_0'Z_0 + G_0^{-1*} A^{-1} \end{bmatrix} \begin{bmatrix} \hat{B} \\ \hat{U} \end{bmatrix} = \begin{bmatrix} (R_0^{-1*} X_0')Y \\ (R_0^{-1*} Z_0')Y \end{bmatrix}
$$

where $*$ = Kroenecker product (see Searle, 1966).

This system of equations may be simplified by linear transformation at the variates. By using canonical variates Quaas, Anderson and Gilmour (1985) inferred a linear model in the form:

$$(L^{-1*} I)Y = (I^* X_0)B^* + (I^* Z_0)U^* + e^*$$

with

$$\text{var } U^* = L^{-1} G_0(L^{-1})'^* A^{-1}$$
$$\text{and} \quad \text{var } e^* = L^{-1} R_0(L^{-1})'^* I$$

This model implies calculation of a matrix L, characterised by the following:

$$L^{-1} G_0 L^{-T} = D \quad \text{(diagonal matrix)}$$
$$\text{and} \quad L^{-1} R_0 L^{-T} = I$$

Interestingly enough, these two conditions coincide with that specified by Cue and Hayes (1984) for accommodating both continuous and discrete traits in one selection index value. It is therefore apparent that this transformation will lead to a normal distribution of transformed observations.

According to Quaas, Anderson and Gilmour (1985) L may be found as follows:

i) Decompose R_0 as:
$$R_0 = TT^T$$

where T = the triangular Cholesky decomposition.

ii) Then form $B = T^{-1} G_0 T^{-T}$

iii) Decompose B as:
$$B = PDP^{-T}$$

where D is a diagonal matrix containing the eigen values of B.

also $PP^T = P^TP = I$

This implies that the columns of P are the orthonormal eigen vectors of B.

In the present study this step involved calculation of the eigen values and eigen vectors of B with a subroutine (EIGRS) in the IMSL Library of Mathematical subroutines. Hereafter, the matrix containing the eigen vectors was normalised in the usual way to find P.

iv) Then L = TP

The correctness of L may be verified using the following equations (characteristic of the definition of L in step 1):

$$G_0 = LDL^T$$
$$\text{and} \quad R_0 = LL^T$$

After determination of L, the Y values used in the model may be transformed in the following way:

$$Y_i^* = X_0 B_i^* + Z_0 U_i^* + e_i^*$$

where $i = 1$ to 4

and $\text{var } U_i^* = d_i A^{-1}$

$\text{var } e_i^* = I$

Transformed Y-value

$$(Y_i^*) = l^{i1} y_1 + l^{i2} y_2 + l^{i3} y_3 + l^{i4} y_4$$

where

$$L^{-1} = \begin{bmatrix} l^{11} & l^{12} & l^{13} & l^{14} \\ l^{21} & l^{22} & l^{23} & l^{24} \\ l^{31} & l^{32} & l^{33} & l^{34} \\ l^{41} & l^{42} & l^{43} & l^{44} \end{bmatrix}$$

After solving MME for canonical variates, back-transformation is achieved as

follows:

$$\hat{U}_i = l_{11} \hat{U}_1^* + l_{12} \hat{U}_2^* + l_{13} \hat{U}_3^* + l_{14} \hat{U}_4^*$$

$$\hat{B}_i = l_{11} \hat{B}_1^* + l_{12} \hat{B}_2^* + l_{13} \hat{B}_3^* + l_{14} \hat{B}_4^*$$

where

$\hat{U}_i$ = back transformed breeding value for animal

$\hat{U}_i^*$ = breeding value for the i-th animal in canonical form

$\hat{B}_i$ = backtransformed solution for fixed effect

$\hat{B}_i^*$ = solution for fixed effect in canonical form

where

$$L = \begin{bmatrix} l_{11} & l_{12} & l_{13} & l_{14} \\ l_{21} & l_{22} & l_{23} & l_{24} \\ l_{31} & l_{32} & l_{33} & l_{34} \\ l_{41} & l_{42} & l_{43} & l_{44} \end{bmatrix}$$

From the explanation above it is clear that this method involves little more computational labour than four single-trait models. The deduction, therefore, is that the compromise between computational labour and increased accuracy might have been met for testing the possibility of a measure for ewe productivity in the present study.

APPENDIX C

EFFICIENCY OF SCHAEFFER'S SIMPLE METHOD IN COMPARISON WITH RAM

In a comparison of RAM with the Simple Method applied on Canadian swine data, Schaeffer and Kennedy (1986) found that although both methods were computationally demanding, the Simple Method required 43% of the total computing time of RAM, but 175% of the total amount of the computer memory used. In order to enlighten the reader further on firstly the rate of increase in computing time when expanding the size of data set and secondly, the effect of analysing different traits, measured on different scales on computational labour, a few local results, obtained by using both methods, are presented. When evaluating the results it must obviously be borne in mind that a Unisys B7900 mainframe computer was used for all computations.

i) The aim of presenting the first two results below is to illustrate how computation time increases when increasing the size of data sets.

The first analysis (preliminary analysis for Erasmus, unpublished) involved constructing a coefficient matrix with order of 1246 for RAM. Solutions for the RAM equations were obtained by iterating the mixed model equations to a degree of accuracy of 0.0001. Ordinary Gauss-Seidel iteration was used.

Solutions were obtained for 129 fixed effects, 1117 parents and a further 1676 non-parents by back-solving. This run required 15.7 minutes Central Processing Unit (CPU) time.

Using RAM for analysing a second even larger set of data of the Grootfontein Merino Stud (Olivier, 1988), 85.15 minutes CPU time was required. In this case 254 fixed effects, 1923 parents and 3707

non-parents were involved.

In comparison with the first analysis, the second analysis was done on a 50.34% larger set of data but used 81.56% more computing time. When interpreting these results it must, however, be taken into account that different numerator relationship matrices, which could influence the sparcity of the coefficient matrices, were used. It is, however, hoped that an idea can be formed of the non-linear increase in computing time when expanding data set to larger proportions.

Two possible reasons (other than the size of the data set.) for the extremely slow rate of convergence in these analyses were:

(a) The accuracy level which was set at 0.0001.

(b) The sparcity of the numerator relationship matrix naturally made an additional contribution towards this slow rate of convergence.

ii) The second principle, namely that different traits measured on different scales can affect computational labour, is illustrated by the computing times used for the following analyses done for the present study:

Using canonical variates and iterating to an accuracy level of 0.00001, CPU times of a maximum of 9.15 minutes and 19.9 minutes for four traits on two data sets consisting of 2157 and 2881 animals (including the base population) respectively, were recorded. In this case only the Simple Method was employed.

When comparing these results with any other results it must be remembered that canonical transformation of the data to canonical variates, transforms the data to the same scale.

The results in terms of computing time for the present study can readily be compared with that for the first analysis mentioned

above, since both problems were approximately of the same size (± 3000 mixed model equations).

Despite the fact that the Simple Method, which should be more time efficient than RAM, was employed, analyses for the present study required 26.75% more computing time than that for the first data set (above). Although the nature of the numerator relationship matrix may have influenced this comparison, it seems as if the scale on which data is measured does have an appreciable influence on computing time.

Unfortunately, both RAM procedures and the Simple Method were not used on the same set of data for the purpose of direct comparison of the efficiency of the two methods. This is understandable in view of the considerable computational costs involved.

In order to obtain some idea of the efficiency of the Simple Method, computing times for a third analysis, also for Erasmus (unpublished) will be presented. The data set for the second analysis (above) was expanded to include nearly twice as many animals. This expanded data set was analysed using the Simple Method. Solutions for a total of 28 fixed effects, 7410 animals and a further 638 base population parents were computed. Using the same level of accuracy as for RAM (above), 135 rounds of iteration using 70.43 minutes of CPU time were required.

In spite of the fact that this problem solved was 37.25% larger than the second analysis (above), computation time needed was 17.29% less.

The essential conclusion, therefore, is that the Simple Method's increased efficiency in terms of CPU time (Schaeffer and Kennedy, 1986) holds true for the locally developed Fortran 77 algorithms.