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A MIXED MODEL ANALYSIS OF A SELECTION EXPERIMENT WITH MERINO SHEEP IN AN ARID ENVIRONMENT

by

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in

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Promotor: Professor A.O. de Lange

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CHAPTER 1 INTRODUCTION

Selection experiments are normally conducted to evaluate direct and possible correlated genetic response to the selection applied. Selection experiments with Merino sheep were first initiated in Australia around 1950 (Turner, 1977) making them among the earliest selection experiments with domestic livestock. Since then many single and multi-trait selection lines have been established in Australia and the results have been extensively reviewed by Ferguson (1976), Turner (1977), McGuirk (1979) and Rogan (1984). The main objective in most of these experiments has been to increase wool production through selection for increased fleece mass and in many cases the additional aim was to at least maintain wool quality and reduce such faults as excessive skin fold and face cover (Turner, 1977). Selection experiments provided a means of checking the prediction that mass selection for traits such as fleece mass would be effective (McGuirk, 1979) and one can assume that additionally, the results could be used to demonstrate the effectiveness of selection on objective measurements of these traits.

In South Africa, only two selection experiments for production traits with Merino sheep have yet been undertaken. The first of these was started in 1962 at the Grootfontein College of Agriculture, Middelburg C.P. and shortly afterwards moved to the Klerefontein Research Station at Carnarvon. This experiment was terminated in 1984. Another was initiated in 1969 at the Tygerhoek Research Station near Riviersonderend which, with some modifications, is still continuing. The former consisted of a single trait (high clean fleece mass) selection group as well as a group selected for subjectively evaluated overall excellence (Olivier, 1980). The latter experiment included selection for higher clean fleece mass and higher secondary to primary wool follicle ratio as single traits and in combination with 42-day body mass (Heydenrych, 1975). In both these experiments, as in many such experiments in Australia, an unselected control line was, or is, kept to measure response.

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From the literature cited above, it is evident that although the degree and consistency of the responses obtained varied, initial responses, at least, were not far from expectations. An exception is the selection experiment at Klerefontein, Carnarvon, which showed virtually no response (0.12% per annum) in clean fleece mass in either the subjectively or objectively selected groups when measured against the control group (Olivier, 1980). Ferguson (1976) and Rogan (1984) report an apparent plateauing of response in clean fleece mass in some of the Australian selection experiments but, as far as could be established, the Klerefontein experiment is the only one which failed to show any meaningful response from the outset.

McGuirk (1979) reports on work done in Australia, showing a decline in sulphur content of wool in lines selected for higher fleece mass. Supplementing sulphur-containing amino acids, cystine and methionine, dramatically widened the gap between lines selected for high and low fleece weight (McGuirk, 1979). Methionine-supplementation at Klerefontein, however, failed to produce a significant result (Jacobs G.A., 1982 – personal communication). The possibility that the selected lines were incapable of expressing their superior genotype because of sub-optimum sulphur levels in the diet was therefore practically ruled out.

The experiment can therefore justly be seen as a failure if the aim was to prove or demonstrate that mass selection for fleece mass is effective and is probably one of the reasons why it was terminated. It is, however, imperative that the reasons for the apparent lack of response be found, and that prompted the present study. The possible reasons generally cited for low response include:

- 1) Inbreeding depression
- 2) Genetic drift in the random control
- 3) Opposing natural selection
- 4) Insufficient additive genetic variation
- 5) Genotype x environment interaction

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When genetic and environmental trends are separated using a control, it must, of course, be assumed that the control has remained genetically stable. Control populations can be designed to minimise the possibilities of random genetic drift and directional genetic change as discussed by Hill (1972). As no effort was made to achieve this in the Klerefontein experiment, it is obvious that possible genetic changes in the control line should first be studied. A control line not designed to minimise genetic change has the important advantage of providing a population in which natural selection could freely operate. It is therefore possible to study the traits favoured by natural selection in a harsh environment (see description in Chapter 2) in a breed which has been subjected to some form of artificial selection for more than a century.

A method of separating genetic and environmental trends without the use of a control is provided by C.R. Henderson's mixed model methodology which he started developing at Cornell University in 1949 (Henderson, 1984). It has become widely used in the analysis of field data where controls are normally not available. It has also been used to estimate genetic trend in a selection experiment with sheep with and without the use of a control population (Blair & Pollak, 1984).

The success of the method in separating genetic and environmental effects is partly dependent on genetic connectedness across environments (different years, for instance, in a selection experiment). The genetic ties arise through genotypes being completely or partially (through relatives) represented in the different environments (years). Sires are often used only once and this necessitates the utilisation of all relationships between animals to establish genetic ties across the years. Mixed model methodology makes provision for the inclusion of all possible relationships (Henderson, 1984).

The methodology evolved by Henderson was initially directed at providing more sophisticated and accurate progeny testing across environments (including years) which subsequently became known as a "sire model" in contrast to an "animal model" developed later (Quaas & Pollak, 1980). Although it is generally accepted that the term "animal model"

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was coined by Quaas and Pollak (1980) in their paper presenting the reduced animal model (RAM), Henderson (1987) claims that its first application was most probably by Henderson (1949).

The procedures are not simple and are computationally demanding, but the estimators have a number of well-defined statistical properties (Sorensen & Kennedy, 1986). Recently, genetic properties of mixed model methods have also been defined (Kennedy and Sorensen, 1987). When applied to performance test data, the most important shortcoming of conventional methods, *viz.* that comparisons cannot be made across environments, can be overcome. This, in itself, provides enough motivation for developing and testing programmes on experimental data which could later be applied on a much wider scale.

The purpose of the present study was to re-analyse the data obtained from the Klerefontein selection experiment using mixed model methodology in an effort to explore the reasons for an apparent lack of response. It is also envisaged that the knowledge obtained in developing and applying these methods will be utilised for more widespread use in performance testing programmes.

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CHAPTER 2 MATERIAL AND METHODS

2.1 Introduction

A detailed description regarding the environment, animals, management and experimental procedures pertinent to the present study has been supplied by Olivier (1980). An attempt will be made to highlight only some of the more important aspects for the sake of clarity and completeness.

2.2 Environment

The experiment was initiated at the Grootfontein College of Agriculture, Middelburg C.P. in 1962, but moved to the Klerefontein Research Station, Carnarvon in 1964 until termination, which is the experimental environment. Klerefontein is situated approximately 18 km west of Carnarvon in the arid Karoo and the veld type is described as False Desert Grassland (Acocks, 1953). The average annual rainfall during the experiment was 235 mm (SD = 108). The stocking rate applied is five hectare per small stock unit and is largely dependent on the rainfall. The vegetation consists mainly of sparsely populated shrubs and some annual grasses. Temperatures are typical of a semi-desert climate and vary between -9° C and 39° C.

2.3 Animals

A total of 500 Merino ewes were visually selected from an available 700 belonging to the Grootfontein College of Agriculture Merino flock. These were randomly divided (within age groups) into two selection lines comprising 200 ewes each and one control line of 100 ewes. For the first two matings 50 rams from the Grootfontein Merino stud were used. These rams were randomly devided among the three lines.

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2.4 Procedure

The three lines were subjected to three different treatments (selection procedures) and are denoted, for the sake of brevity, as follows:

- Objective Line: Ram and ewe replacements were selected on the basis of the highest clean fleece mass. Sheep with overstrong wool and excessive skin folds were, however, culled.
- Subjective Line: Replacements were selected subjectively in an effort to increase production by a trained Merino judge, Mr J.A.A. Baard and from 1977 onwards by Mr J.M. Cloete.
- 3) Control Line: Replacements were counted off at random.

All measurements were taken at 18 months of age, after which replacements were selected or merely counted off in the case of the control line. In all three lines sheep with defects faults were removed. The number of ewes in the first two lines was kept at roughly 200 each and from 1965 the size of the Control Line had been gradually enlarged from the initial 100 to 200 ewes as well. Ewes were replaced after five matings and after 1963, rams were replaced annually, except in 1980 and 1981 when only 50% of the rams were replaced. In 1969 no progeny was available as all the ewes were used for the development of a new breed (Afrino). Initially 10% rams were used, but this was decreased to 5% from 1967 onwards. This meant that 10 rams were selected for each line while an additional five were kept in reserve in case any of the selected rams could not be used.

The effective population size is, of course, in the case of discreet generations, related to the harmonic mean of the numbers in the two sexes. Given that each selection line consisted of ten rams and 200 ewes and generations did not overlap, the effective population size in each case would roughly be 38. There is voluminous evidence that selection response can readily be obtained in populations of this effective size.

The three lines were run together and managed as one, except at mating when ewes were

hand-mated to a randomly allocated sire of the relevant line. Full pedigrees were recorded. Lambs were weaned at approximately 120 days and the sexes separated after first shearing approximately two months later. All sheep were kept on the veld throughout, but in times of drought an energy-lick consisting of 70% maize meal and 30% salt was provided. An innoculation and drenching programme prescribed by the State Veterinarian was followed.

2.5 Observations

The following measurements recorded during the duration of the experiment were used in the study:

2.5.1 Clean fleece mass: greasy fleece mass was recorded after the second shearing when the sheep were 18-months old with roughly 12-months wool growth. All fleece mass records were adjusted to an exact 365-days wool growth. A mid-rib fleece sample taken from every sheep for determining clean yield percentage and fibre diameter. Clean yield percentage was determined by normal scouring procedures and calculated as follows on the basis of a 16% moisture regain:

CLEAN YIELD $\% = \frac{\text{bone-dry sample mass after scouring x 116}}{\text{sample mass before scouring}}$

The clean fleece mass was calculated by multiplying the clean yield percentage by the greasy fleece mass.

2.5.2 Fibre diameter: the mean fibre diameter of each sample was determined by the air-flow procedure using a WIRA fineness meter. Fibre diameter is expressed in micrometers (μm). Fleece samples were initially analysed by the Wool Research Section of the Karoo Region and since 1966 by the South African Fleece Testing Centre.

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2.5.3 Body mass: the body mass of all available sheep was recorded at 18 months of age immediately after shearing.

2.6 Statistical Analyses

2.6.1 Heritability estimates.

Heritability estimates were obtained by half-sib analysis of variance using Henderson's Method 3 (Henderson, 1952) with the library computer programme LSML-76 (Harvey, 1960). For comparison, two traits, clean fleece mass and body mass were analysed by the restricted maximum likelihood (REML) procedure (Patterson & Thompson, 1971) using the mixed model analysis of variance programme in the BMDP package. To facilitate use of the latter programme which has no absorption option, least-square means were calculated for combinations of sex, age of dam (maiden or mature) and birth status (single- or twin born) in a fixed effects model and records adjusted within year of birth. The following mixed model was then fitted for both procedures:

$$\mathbf{y}_{ijk} = \boldsymbol{\mu} + \mathbf{a}_i + \mathbf{s}_j + \mathbf{e}_{ijk}$$

Where: $y_{ijk} =$ the adjusted record on the k-th individual of the j-th sire in the i-th year,

It should be pointed out that such a priori adjustments of records for fixed effects are commonly made to reduce the size of the coefficient matrix and the resulting mixed model equations. This does not necessarily lead to bias, but the solutions no longer have minimum sampling variance (Henderson, 1984).

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The heritability estimates were obtained by:

$$h^2 = \frac{4 \sigma_s^2}{\sigma_s^2 + \sigma_e^2}$$

where:

 σ_s^2 = the observed sire variance,

 $\sigma_{\rho}^2 =$ error variance.

Henderson (1984) also points out that even when σ_s^2 and σ_e^2 are unbiased, this could be a biased estimator of h^2 .

Genetic and environmental correlations between the three traits were calculated by Henderson's Method 3 only. The estimates of genetic correlations were used to compare with the genetic responses obtained.

2.6.2 Genetic and environmental trends

The following linear mixed model was fitted to the data:

 $\mathbf{y}_{ijk} = \mathbf{\mu} + \mathbf{b}_i + \mathbf{c}_j + \mathbf{u}_k + \mathbf{e}_{ijk}$

where:

 $y_{ijk} =$

a measurement on the k-th individual born in the i-th year and belonging to the j-th handicap class,

 μ = the population mean,

 $b_i = the fixed effect of the i-th year of birth,$

 c_{j} = the fixed effect of the j-th handicap class,

 $u_k =$ the random effect (additive breeding value) of the k-th individual, $e_{ijk} =$ random error.

A handicap class was defined (as by Turner and Young, 1969) as a group of animals of the same sex, rearing status (single or twin) and age of dam (mai-

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den or mature). As there were only seven triplets in the whole data set, they were grouped with the twins. The fixed effects constituting a handicap class were identified by Olivier (1980) as being significant for the data used.

A general formulation of this model in matrix notation (Henderson, 1963) is as follows:

$\mathbf{y} = \mathbf{X}_1 \underline{\mathbf{b}}_1 + \mathbf{X}_2 \underline{\mathbf{b}}_2 + \mathbf{Z} \underline{\mathbf{u}} + \underline{\mathbf{e}}$

where:

Y

vector of observations,

 $\underline{\mathbf{b}}_1$ = vector of unknown fixed birth year effects,

 \underline{b}_2 = vector of unknown fixed effects other than birth years and fitted as combined effects, *i.e.* sex, rearing status, age of dam, representing a handicap class,

 X_1 and X_2 = known incidence matrices relating records to fixed effects,

 $\underline{\mathbf{u}}$ = an unknown random vector representing breeding values,

Z = a known incidence matrix relating elements of <u>u</u> to elements of <u>y</u>,

 $\underline{\mathbf{e}}$ = a vector of random error (environmental factors particular to each record).

It is assumed that $E(u_i) = 0$ and $E(c_i) = 0$ and that \underline{u} and \underline{e} are uncorrelated to each other. Furthermore,

$$\operatorname{Var} \left[\begin{array}{c} \mathbf{u} \\ \mathbf{e} \end{array} \right] = \left[\begin{array}{c} \mathbf{A}/\mathbf{\alpha} & \mathbf{0} \\ \mathbf{0} & \mathbf{I} \end{array} \right] \sigma_{\mathbf{e}}^{2}$$

where:

 $\alpha = \sigma_{\rm e}^2/\sigma_{\rm a}^2,$

- A is a matrix of Wright's numerator relationships among animals ignoring inbreeding,
- I is an identity matrix.

Solutions to the mixed model equations were obtained using an animal model adaptation of the "simple" method devised by Schaeffer and Kennedy (1986). With this method fixed and random effect solutions can be obtained without setting up the mixed model equations explicitly. For obvious reasons the author prefers the alternative term "indirect approach" used by the same authors (Schaeffer and Kennedy, 1986a). No equations were absorbed, *i.e.* the full animal model was used and the only constraint imposed was $\mu = 0$. The three selection lines were analysed together in a single analysis for each trait. Since the three lines were selected from the same genetic base and no significant (P<0.05) selection line x sex, rearing status or age of dam interactions were found by Olivier (1980), a combined analysis should yield estimates of fixed and random effects with smaller sampling variance (Sorensen and Kennedy, 1984). Analysing each line separately would also not have afforded the opportunity of detecting possible random sampling in the base population where related but different rams were initially used in each line.

Equations for clean fleece mass and fibre diameter were iterated to an accuracy of 0.0001 which took 71 and 135 rounds respectively, while body mass was iterated 240 rounds, leading to an accuracy of 0.0018.

Blair and Pollak (1984) used the direct approach of estimating genetic trend (calculating average breeding values of animals born in each year) as well as two other approaches simulating the traditional method of expressing yearly genetic superiority as a deviation from the control by calulating predicted yearly phenotypes as the average breeding value prediction added to the corresponding year effect estimate. One of the major issues in the present study was the evaluation of possible genetic trend in the control line and therefore only the direct approach was used. Blair and Pollak (1984) obtained identical "realised heritabilities" using the direct approach and an indirect approach accounting for genetic drift in the control by expressing response as the deviation of the predicted yearly phenotype for the selected line from the year estimate of the control line. The direct approach, however, yielded a much smoother representation of the genetic trend.

Annual genetic trend in the present study was estimated as the regression of the average predicted breeding value on year of birth. Genetic trends, expressed as a deviation from the control line, were calculated on the same set of data by Olivier (1980 and 1984). Where applicable, these results are also presented for comparison.

In the analysis of selection experiments the primary objective of partitioning phenotypic trend into its genetic and environmental components is to obtain unbiased estimates of genetic trend. Sorensen and Kennedy (1984) have shown that a mixed model analysis without a control population and ignoring selection can adequately partition these trends even after several cycles of selection, provided certain conditions are met. These conditions are:

1) the model used is the correct one;

- 2) the ratios of the variances of the trait are known before selection;
- 3) selection is on a linear function of the records and is invariant to the fixed effects in the model, namely, L'X = 0 (Henderson, 1975) where X is an incidence matrix and L' is a matrix describing selection; and
- 4) the relationship matrix is complete.

The model applied in the present study is an animal additive genetic model and assumes that the sole genetic effect on the traits is a large number of additive loci, in which case, selection followed by random mating causes only small departures from normality (Bulmer, 1971). Sorensen and Kennedy (1984) have shown that with finite numbers of loci that move towards fixation, this assumption will not hold. The most important assumption is, of course, that a linear model is correct. (Henderson, 1984). The assumptions as far as the second condition is concerned will be referred to in the next chapter. The most important possible violation of the third condition in the present study could be due to natural selection and is discussed under the appropriate heading (3.4). There is some comfort in the fact that the relationship matrix is, as far as practically possible, complete and that the fourth condition is fully met in this study.

2.6.3 "Realised heritabilities"

A common feature of the analysis of selection experiments is the estimation of "realised heritabilities". This is normally done by regressing the mean of groups of contemporaries on the cumulative selection differential of their parents, both values usually being expressed as deviations from a control line. It is also occasionally estimated as the ratio of total response to total cumulative selection differential but the former has been shown by Hill (1972a) to be slightly superior both when a control line is maintained or when the environment is kept stable in an effort to measure genetic response.

A "realised heritability" is a very useful descriptive parameter since it makes provision for changes in response due to changes in selection intensity (Thompson, 1979) and it also allows comparisons among experiments with different selection intensities (Falconer 1960). It does, however, suffer from difficulties of interpretation when generations overlap as pointed out by James (1986). On the one hand effective selection creates genetic differences between parental age groups, with a resulting increase in genetic variance within a group of progeny. On the other hand, selection can also establish linkage disequilibrium (Bulmer, 1971) which in turn will reduce genetic variance. The ratio of response to selection will depend on the balance of these effects and may not be suitable for estimating base population heritability or for comparison with a prior estimate (James, 1986). Falconer (1960) points out that upward and downward selection for a trait could yield different estimates of "realised heritability". Both are valid descriptions of the effect of selection but neither could be a valid estimate of the actual heritability of the base population. Lerner (1958) does not use the term "realised heritability" but refers to the principle of estimation as "probably the most informative technique for depicting the course of selection experiments".

When response to selection is estimated without the use of a control population it is more difficult to disentangle genetic and environmental contributions (Thompson and Cameron, 1986). By using a mixed model analysis, predictions of the genetic merit of animals born in each year can be made. Blair and Pollak (1984) suggested regressing the predicted genetic merit on the cumulative selection differential to derive an estimate of "realised heritability". This is analogous to the definition of heritability as the regression of breeding value on phenotypic value but where the breeding value is merely a best linear unbiased prediction of the true breeding value. As the predictions of breeding values obtained depend largely on the value of the heritability used in the mixed model equations, "realised heritability" estimates obtained in this manner could be even more misleading as a measure of the true heritability in the population. An example of the effect of using different heritabilities is provided in section 3.4.2.

Notwithstanding these shortcomings, "realised heritabilities" were calculated in the same manner (Blair and Pollak, 1984) in the present study with the sole intention of expressing changes in predicted genetic merit over time in terms of the amount of selection applied. The standard error of these "realised heritability" estimates is given as the standard error of the regression coefficient. To enable the calculation of "realised heritabilities", cumulative selection differentials had to be calculated. In the present study, as is the case in most selection experiments with livestock, generations overlapped and care had to be taken in calculating cumulative selection differentials since the parents of each set of progeny could have different numbers of generations of selection behind them. Several methods have been evolved in an effort to circumvent this problem. A technique used by Pattie (1965) and described by Turner and Young (1969), has been shown to be biased by James (1986), tending to overestimate the cumulative selection differential and therefore underestimate "realised heritability". In the present study, cumulative selection differentials were calculated for each individual by adding each individual's own phenotypic deviation from its birth year group and handicap class to the average mid-parent cumulative selection differential of its birth year group and handicap class, similar to the method used by Newman, Rahnefeldt and Fredeen (1973). The procedure not only accounts for overlapping generations, but also for differential use of sires and dams.

2.6.4 Generation interval

Generation intervals were calculated as the actual average age of the parents of the lambs born in each year.

2.6.5 Inbreeding

Inbreeding coefficients were computed for each animal using the algorithm reported by Quaas (1976). The inbreeding coefficient of the i-th animal was calculated as $F_i = d_{ii} - 1$, where F_i is the inbreeding coefficient and d_{ii} is the diagonal element of the i-th animal in the numerator relationship matrix (Wright, 1922). The base population was assumed to be non-inbred.

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CHAPTER 3 RESULTS AND DISCUSSION

3.1 Genetic parameters

3.1.1 Data description

The least square means, standard deviations and coefficients of variation in the control line (n = 2265) of the five traits recorded are given in Table 3.1. Only the control line was used for estimation of genetic parameters since it was assumed that no selection had taken place.

TABLE 3.1LEAST SQUARE MEANS (X), STANDARD DEVIATIONS (SD)AND COEFFICIENTS OF VARIATION (CV%) OF TRAITSRECORDED IN CONTROL LINE.

TRAIT	X	SD	CV%
Body mass (kg)	32.51	3.81	11.72
Greasy fleece mass (kg)	4.70	0.61	12.98
Clean yield (%)	56.02	4.43	7.91
Clean fleece mass (kg)	2.64	0.36	13.64
Fibre diameter (µm)	19.64	1.21	6.16

The mean are far lower than those reported for the Tygerhoek selection experiment (Heydenrych, 1975), but the coefficients of variation are in close agreement. Compared with the 4.70 kg for greasy fleece mass given in Table 3.1, the national average wool production per Merino sheep (greasy fleece mass) is 5.63 kg (de Klerk, Duvel and Terblanche, 1983).

3.1.2 Correlations between traits

The phenotypic and environmental correlations between the three traits analysed in the present study is supplied in Table 3.2. (Note that greasy fleece mass and clean yield percentage were not analysed but merely used to estimate clean fleece mass).

TABLE 3.2PHENOTYPICANDENVIRONMENTALCORRELATIONSBETWEEN TRAITS IN CONTROL LINE

PHENOTYPIC CORRELATIONS	ENVIRONMENTAL CORRELATIONS
0.333*	0.369
0.138*	0.161
0.147*	0.184
	PHENOTYPIC CORRELATIONS 0.333 0.138 0.147

NOTE: BM = Body Mass, CFM = Clean Fleece Mass,

FD = Fibre Diameter, * P < 0.01

All the phenotypic correlations are highly significant (P<0.01), which is in agreement with most published results, although reasonably large differences in the magnitude of the estimates occur.

Of particular interest in a study of this nature are estimates of genetic correlations, as they indicate which possible correlated responses to selection could be expected. The low accuracy of many estimates of genetic correlations, as indicated by large standard errors relative to the parameter estimates, reduce their usefulness in predicting correlated responses. Also, published estimates are characterised by large order and even sign differences. The estimates of genetic correlations obtained in the present study, together with

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that of two other South African studies, and the ranges obtained in several Australian studies on Merino sheep, are given in Table 3.3.

TABLE 3.3ESTIMATES OF GENETIC CORRELATIONS BETWEEN TRAITSIN CONTROL LINE

			R	ANGE OF EST	IMATES ON	
SO	OUTH AFRICAN MERINOS				AUSTRALIAN	MERINOS
	1		2	3		
TRAITS						
BM-CFM	0.21	8	0.50	0.380	-0.12 TO 0.30	(4)
SE	(0.1	72)		(0.181)		
BM-FD	0.08	8	0.68	0.127	-0.08 TO 0.12	(4)
SE	(0.1	57)		(0.208)	с	
CFM-FD	0.06	3	0.03	0.291	-0.06 TO 0.40	(5)
SE	(0.1	62)		(0.167)		
NOTE:	SE	=	Standar	d Error	···-···	
	1	=	Present	study		
	2	=	Bosman	(1958) – No sta	andard errors were cal	culated
Degrees of f				of freedom roug	hly 1300	
	3	=	Heyden	rych (1975)		
Pango of A	netre	lion d	etimator	rom reviews by	Turner (1077) and Be	(1084)

Range of Australian estimates from reviews by Turner (1977) and Rogan (1984). The number of references is given in parenthesis. Two of the estimates in the present study, those between body mass and fibre diameter and between clean fleece mass and fibre diameter, and one in the study by Heydenrych (1975), that between body mass and fibre diameter, have standard errors higher than the parameter estimates and can therefore be regarded as non-reliable.

From Table 3.3 it is evident that estimates of genetic correlations of the three traits are data-dependent. Discrepancies could in part be due to the inconsistency of present methods of estimation. This is discussed briefly under heritability in 3.1.3.

Multiple trait reduced animal models for predicting breeding values, first introduced by Quaas and Pollak (1980), utilise not only information of all available relatives with respect to a specific trait, but information on correlated traits as well. It stands to reason that this extra information could greatly enhance the reliability of breeding value predictions, especially in the case of sequential culling (Quaas and Pollak, 1980), but, as Henderson (1984) points out, the additional advantage obtained depends on how closely the estimated values (correlations or covariances) used resemble their true values. From Table 3.3 it is clear that selecting appropriate *a priori* estimates for these traits from the literature is an extremely difficult, if not impossible, task.

In the present study the estimates of genetic correlations were used to compare with the genetic response patterns obtained.

3.1.3 Heritability estimates

The heritability estimates (h^2) obtained by using Restricted Maximum Likelihood (REML) and Henderson's Method 3 (H-3) are given in Table 3.4. TABLE 3.4 HERITABILITY ESTIMATES USING RESTRICTED MAXIMUM LIKELIHOOD (REML) AND HENDERSON'S METHOD 3 (H-3) IN CONTROL LINE

TRAIT	H–3	(SE)	REML	(SE)
Body mass	0.247	(0.058)	0.252	(0.051)
Clean fleece mass	0.229	(0.056)	0.249	(0.048)
Fibre diameter	0.369	(0.066)	-	

Published heritability estimates of the three traits cover almost the entire parameter space, but the median values obtained from Bosman (1958), Heydenrych (1975) and the references cited in the reviews by Turner (1977) and Rogan (1984), are roughly 0.50 for body mass, 0.40 for clean fleece mass and 0.45 for fibre diameter. The heritability estimates obtained in the present study are therefore generally much lower than expected.

In practice, Henderson's mixed model methodology is normally used to predict breeding values and estimate fixed effects on the assumption that genetic and environmental variances and covariances, in the case of multiple trait models, are known or that good estimates are available (Henderson, 1984). However, estimation of these (co)variances can be done jointly with prediction of breeding values when solving the mixed model equations. For single trait models, for instance, prior knowledge of h^2 is not required to obtain predictions of breeding values. The resulting predictions are not best linear unbiased predictions (BLUP), but are good approximations (Gianola, Foulley & Fernando, 1986). The two estimators most commonly cited as possibilities for obtaining genetic parameters in this manner are Rao's (1971) minimum variance quadratic unbiased estimator (MIVQUE) or Patterson and Thompson's (1971)

REML (Sorensen and Kennedy, 1986). In contrast to Henderson's Method 3, MIVQUE and REML on an animal model makes use of all the data available. All animal records and all the relationships among them can be used to compute estimates of genetic parameters (Sorensen & Kennedy, 1986). In the present study however, REML was used on a sire model that ignores all but half-sib relationships. This does not yield unbiased estimates of the base population additive variance, because the model does not account for the entire correlated structure in the data (Sorensen and Kennedy, 1984). As is normally the case with half-sib analyses, it was assumed in the present study that $Var(u) = I\sigma_s^2$, $Var(e) = I\sigma_e^2$ and $Var(y) = ZZ'\sigma_s^2 + I\sigma_e^2$, where σ_s^2 is the variance component between half-sib progeny groups, σ_{e}^{2} is the error variance and I is an identity matrix. This variance structure assumes that sires are unrelated and that the only covariance present is among half-sib groups. All non-collateral relationships are ignored. Ignoring relationships over generations has important implications if selection has been present. The correct variance structure of the observations is: $Var(y) = ZAZ'\sigma_a^2 + I\sigma_e^2$, where A is the complete relationship matrix and σ_a^2 and σ_e^2 is the additive genetic variance in the base population and the environmental variance respectively. MIVQUE and REML can utilize this variance structure. Use of MIVQUE or REML on an animal model yields unbiased estimates of the base population additive genetic variance, provided that the initial sample was drawn at random (Sorensen & Kennedy, 1986), seemingly even when used on data that have been generated by several cycles of selection and mating (Sorensen and Kennedy, 1984a).

The problem is that the use of MIVQUE or REML on an animal model is currently computationally prohibitive even on reasonably small data sets. The major problem is that both require a generalised inverse of the coefficient matrix. Recently, however, Graser, Smith and Tier (1987) presented a REML algorithm for the estimation of variance components in single trait animal or reduced animal models that does not use matrix inversion but utilises the principle of Gaussian-elimination. Developments such as this and the increasing power of computers are making these methods more practical computationally and, as Sorensen and Kennedy (1984a) have pointed out, they ought to be considered as alternatives to some of the more traditional methods.

Blair and Pollak (1984) illustrated the effect, in practice, of different heritability values used in a mixed model analysis to determine genetic trend. The estimated genetic change in greasy fleece mass over 20 years was 1.06 kg using $h^2 = 0.30$, 0.77 using $h^2 = 0.20$ and 0.42 kg using $h^2 = 0.10$. Monte Carlo simulation studies by Sorensen and Kennedy (1984a) indicated that a 40% departure from the true heritability introduced a bias of only 8% in the estimated response after two cycles of selection. When the heritability is over-estimated the response is biased upwards and vice versa.

The use of REML, even on a sire model as in the present study, is computationally more demanding and far more costly than Henderson's Method 3. As the results obtained for the first two traits (Table 3.4) are in close agreement, there seems little point in using REML unless all relationships among animals can be utilised. It was therefore decided that the estimates obtained by Henderson's Method 3 would suffice for use in the mixed model equations. There is, however, no doubt that methods that avoid sampling and selection bias are to be preferred and that the search for more efficient algorithms that are computationally more feasible is indeed warranted.

Quite by accident, all three traits were initially analysed using a heritability value of 0.142. This is the value used in a worked example kindly provided by Professor Larry Schaeffer to test the computer programme used. This rather expensive mistake provided the opportunity to illustrate the effect of using different heritabilities on the response curve. An illustration of the different genetic trends obtained for fibre diameter, the trait for which the two initial heritabilities used differed most (0.142 vs 0.369), is presented in Figure 3.1. The graph depicts response in the subjectively selected line where the genetic gain was greatest.



FIGURE 3.1 COMPARISON OF GENETIC TREND IN FIBRE DIAMETER IN THE SUBJECTIVELY SELECTED LINE USING TWO DIFFERENT INITIAL HERITABILITY VALUES.

3.2 Generation interval

The generation intervals obtained in the three selection lines are given in Table 3.5.

The generation intervals in the three lines are almost identical. That of the objectively selected line is slightly larger due to the fact that in some years the required number of replacement ewes was not available as a result of low reproduction. The average number of lambs weaned per ewes mated during the experimental period was only 69.7% (Olivier, 1980). The generation intervals obtained indicate that the experiment represented rough-

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ly six and a quarter generations of selection.

	Rams	Ewes	Average
Objectively selected line	2.1	4.5	3.3
Subjectively selected line	2.1	4.3	3.2
Control line	2.1	4.3	3.2

TABLE 3.5AVERAGE GENERATION INTERVAL IN THE THREE LINES

3.3 Partitioned phenotypic trends

3.3.1 Introduction

Having partitioned mean annual phenotype into its two causal components (genotype and environment), these can be presented and discussed separately. The environmental trends spanning the duration of the experiment are presented and discussed first, followed by a presentation of the genetic time trends and a discussion of response to selection in the different selection lines.

Whereas the primary emphasis in the analysis of selection experiments is normally placed on obtaining unbiased estimates of genetic trends as mentioned earlier, Wilson and Willham (1986) have shown that environmental trend lines could be as important to a commercial breeder to monitor management effects and/or climatic changes. Even in the analysis of selection experiments, environmental trends can be useful in providing additional useful information as shown in the following section.

3.3.2 Environmental trends

The estimates of fixed year effects as a measure of environmental trends in all

three lines, for the three traits are presented in Figures 3.2, 3.3 and 3.4.



FIGURE 3.2 YEAR EFFECTS FOR CLEAN FLEECE MASS.



FIGURE 3.3 YEAR EFFECTS FOR FIBRE DIAMETER.



FIGURE 3.4 YEAR EFFECTS FOR BODY MASS.

All three traits exhibit typical annual fluctuations due to environment but no distinct overall trend (non-significant regression coefficients) in any of the traits is depicted. The annual environmental fluctuations normally present in sheep have led Turner and Young (1969) to suggest that deviations from a control should be expressed as a percentage and not in actual units.

An interesting aspect is illustrated in Figure 3.3. The environmental trend lines for fibre diameter prior to 1966 is more than one μ m lower than for the following years. This is due to the change in laboratories measuring fibre diameter as mentioned in Chapter 2. The WIRA fineness meters of the Wool Research Section of the Karoo Region were calibrated with local raw wool samples while the Fleece Testing Centre uses standard wool tops supplied by the International Wool Testing Authority (IWTA) to bring the results supplied to breeders in line with international standards. The effectiveness of mixed model methodology in highlighting such changes in measurement as an environmental effect is clearly illustrated. In order to provide a comparison of how annual environmental differences influenced the three traits, the mean annual percentages of the overall mean (environmental) was plotted for each trait. The results are presented in Figure 3.5.



FIGURE 3.5 MEAN ANNUAL PERCENTAGES OF OVERALL MEAN (ENVI-RONMENTAL) FOR CLEAN FLEECE MASS (CFM), FIBRE DIAMETER (FD) AND BODY MASS (BM).

Figure 3.5 provides a graphic illustration of what can be deduced from some of the parameter estimates for fibre diameter supplied earlier. The relatively higher heritability of fibre diameter (Table 3.4) in spite of a relatively low coefficient of variation (Table 3.1) compared to the other two traits studied, implies that the environmental variation in fibre diameter is relatively low. From Figure 3.5 it is clear that fibre diameter is relatively less prone to environmental fluctuations than either body mass or clean fleece mass. This fact has a very important practical implication: Fibre diameter is by far the most important physical property affecting the price of clean wool in South Africa (Erasmus and Delport, 1987) and efforts are being made to produce finer wool (Erasmus, 1986). An obvious method of achieving this is by restricted feeding. It is, however, evident that decreasing fibre diameter by manipulation of the environment will have a far more drastic deleterious effect on clean fleece mass and body mass than on fibre diameter.

From Figure 3.5 it is also evident that environmental differences produce roughly the same pattern of influence on all three traits but that the extent to which each is influenced is not consistent. The high values for clean fleece mass in the three years, 1979 to 1981, relative to the other two traits are difficult to explain since the favourable environmental influence was obviously through other components of clean fleece mass than the two recorded in this study, *viz* fibre diameter and body mass. The most likely explanation is an over-adjustment to 365-days wool growth due to incorrect shearing dates being supplied, a common problem encountered at the Fleece Testing Centre (fibre diameter and body mass are not adjusted). Although this is impossible to verify, the fact that the shearing dates applicable to these three birth years differed markedly from the previous years, points to a distinct possibility of such an error.

3.4 Genetic trends

3.4.1 Clean fleece mass

The genetic response curves for clean fleece mass in the two selection lines and the control, expressed as the mean breeding value prediction per annum, are illustrated in Figure 3.6.

The trend lines are purposely not forced through the origin to illustrate random sampling in the base. Olivier (1980) showed that the mean phenotypic value of the base ewes were the same for all three lines. The breeding value predictions of the first lamb drop (1962), however, show differences among the lines that are most likely due to sampling bias of the initial rams used. It can generally be accepted that, because of relatively small numbers, the initial sires allocated to the different lines are the biggest source of potential sampling bias. This possibility could have been largely overcome by using the same sires on all three lines which would have had the added advantage of supplying genetic ties between the lines.



FIGURE 3.6 MEAN ANNUAL BREEDING VALUE PREDICTIONS IN THE THREE LINES FOR CLEAN FLEECE MASS.

In order to compare the results of mixed model analyses (MM) with those obtained by Olivier (1984), who expressed genetic trend as a deviation from the control (DEV), the different regressions of genetic merit on birth year are diagrammatically presented in Fig 3.7. For comparative purposes, all regression lines are forced through the origin. The regression coefficient of +0.0007obtained for the control line by MM is non-significant, while all those presented are highly significant (P<0.001). Non-significant values are omitted from all subsequent tables and figures.



FIGURE 3.7 COMPARISON OF SELECTION RESPONSE AS MEASURED BY MIXED MODEL ANALYSIS (MM) WITH DEVIATION FROM CON-TROL (DEV) FOR CLEAN FLEECE MASS IN THE OBJECTIVELY (OBJ) AND SUBJECTIVELY (SUB) SELECTED LINES.

The genetic trends obtained by MM are slightly larger than those obtained by DEV. This could be due to the possibility that the heritability used in the mixed model equations, although lower than expected (sect. 3.1.3), is still slightly higher than the true heritability in the base population. In any event, both methods indicate very low responses. The 0.014kg or 0.53 percent per annum obtained for single trait selection in the objective selected line is far lower than the estimates of between 0.75 and 2.08 percent per annum reported by Rogan (1984) or the roughly 1.0 persent obtained by Heydenrych, du Plessis and Cloete (1984) in the Tygerhoek experiment. The trend is however, linear, as indicated by the high value of $R^2 = 0.919$. The lower fit ($R^2 =$

0.776) obtained in the subjectively selected line is most probably due to more inconsistant selection decisions.

As Thompson (1979) has pointed out, genetic time trends alone are difficult to interpret, since differences in genetic response is also a function of differences in the selection applied. The cumulative selection differentials and "realised heritabilities" are presented in Table 3.6. For ease of comparison, the heritability estimates for clean fleece mass, presented in Table 3.4, are repeated. As discussed in section 2.6.3, comparing the estimated to the "realised" heritabilities should not be seen as a comparison of different methods of estimation of the same parameter.

TABLE 3.6CUMULATIVE SELECTION DIFFERENTIALS (CSD), "REALISED
HERITABILITY" ESTIMATES (REAL h²) AND HERITABILITY
ESTIMATES OBTAINED BY HENDERSON'S METHOD 3 (H-3)
AND REML FOR CLEAN FLEECE MASS.

	Objective	Subjective	Control
CSD	1.44	0.970	0.29
REAL h ²	0.187	0.138	-
SE	0.001	0.001	-
H-3 h ²	_ ·	· _	0.229
REML h ²	-	-	0.249

Note: Since the subjectively selected line was terminated two years before the other two lines, the CSD was adjusted by multiplying the mean annual CSD by the number of years in the other two lines.

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The slow rate of genetic improvement for clean fleece mass can be ascribed to two factors, namely a low selection intensity and a low heritability. The low selection intensity can, in turn, be ascribed to the low rate of reproduction (see sect. 3.2). Whereas Blair and Pollak (1984) obtained a cumulative selection differential of 4.25 kg greasy fleece mass in Romney sheep after 18 years of selection, the corresponding figure for clean fleece mass in the present study after 20 years is only 1.44 kg. The estimate obtained by Blair and Pollak (1984) could, however, be sligtly biased upwards because of the method used (James, 1986).

If Falconer's (1960) argument that the same trait measured in different environments can be influenced by different genes is taken to its full consequence, it simply means that estimates of heritability of a trait can only be compared if estimated in the same environment if there is any genotype x environment interaction. Gene frequencies may also differ in different lines but one is inclined by one's human nature to ascribe the lower-than-expected estimated and "realised heritability" to a difference that is visible, namely an extreme environment.

The "realised heritabilities" obtained are even slightly lower than the initial estimates (Table 3.4). This is in accordance with the findings of Heydenrych, du Plessis and Cloete (1984) who estimated a heritability of 0.31 and obtained a "realised heritability", estimated as the regression of mean annual deviation from the control on cumulative selection differential, of 0.24 in the Tygerhoek experiment. Although the control line showed a non-significant genetic change in clean fleece mass, the slight positive CSD (Table 3.6) is possibly due to its phenotypic and genetic correlation with body mass (Table 3.2 and 3.3), a trait which did undergo selection as discussed later (sect. 3.4.3):

3.4.2 Fibre diameter.

The genetic response curves for fibre diameter in the two selection lines and the control are given in Figure 3.8.



FIGURE 3.8 MEAN ANNUAL BREEDING VALUE PREDICTIONS FOR FIBRE DIAMETER IN THE THREE LINES.

The regression of predicted breeding value for fibre diameter on birth year was highly significant (P<0.01) in the subjectively selected line, significant (P<0.05) in the objectively selected line and non-significantly deviant from zero in the control line. In the analysis by Oliver (1984), the regression in the objectively selected line was non-significant, while that for the subjectively selected line was highly significant (P<0.01). The results are presented diagrammatically in Figure 3.9.

The much poorer fit ($R^2 = 0.221$) than for clean fleece mass obtained in the objectively selected line($R^2 = 0.919$) is understandable as there was no direct selection for fibre diameter and the trend obtained represents a correlated

response. The slightly better fit for fibre diameter than for clean fleece mass $(R^2 = 0.823 \ vs \ 0.776)$ obtained in the subjectively selected line points to greater consistency in visual evaluation of fibre diameter. It seems as if the judges placed more emphasis on fibre diameter than on fleece mass even though the objective must have been to improve the latter. This aspect is discussed later.



FIGURE 3.9 COMPARISON OF SELECTION RESPONSE AS MEASURED BY MM WITH DEV FOR FIBRE DIAMETER IN THE OBJ AND SUB SELECTED LINES.

The cumulative selection differentials, "realised" and estimated heritabilities are given in Table 3.7. To illustrate the effect of using a different heritability in the mixed model equations, the "realised heritability" using an initial heritability of 0.142 is also included. TABLE 3.7 CUMULATIVE SELECTION DIFFERENTIALS (CSD) "REALISED HERITABILITY" (REAL h²) AND HERITABILITY ESTIMATES OBTAINED BY HENDERSON'S METHOD 3 (H-3) FOR FIBRE DIAMETER.

	OBJECTIVE	SUBJECTIVE	CONTROL
CSD	0.92	2.5	0.20
REAL h ²	0.282	0.401	_
SE	0.038	0.011	_ .
REAL h ² B	_	0.273	-
SE	_	0.004	-
H-3 h ²	-	-	0.369
Note:	REAL h^2B = "realised heri	tability" obtained	using an as-

sumed initial heritability of 0.142

When an initial heritability of 0.142 is used, the estimated genetic trend and resulting "realised heritabilities" in the objectively selected line become non-significant. In the subjectively selected line, the use of this initial heritability value decreased the obtained "realised heritability" from 0.401 to 0.273, in other words, a decrease of 0.227 in the assumed base population heritability led to a decrease of 0.128 in the "realised heritability". The difference in the "realised heritability" obtained therefore represents approximately 56% of the difference in the assumed heritability used in the mixed model equations. Thompson and Cameron (1986) give two simple examples to substantiate their view (supported by Dempfle, (1982)) that "realised heritabilities" obtained by using predicted breeding values from mixed model analyses without the use of a control population, is more a function of the heritability used to generate the predictions than the heritability in the population. They argue that "In a sense, two predictions are being compared rather than a prediction with a response". The results obtained with different assumed heritabilities presented in Table 3.7 indicate that reasonably good estimates of the base population heritability is needed if genetic trend is to be quantified to a useful level of accuracy. This should not be seen as a limitation of mixed model methodology. It merely stresses the need for reliable heritability estimates which would also enhance the other uses of this frequently estimated parameter.

Contrary to the result obtained for clean fleece mass, the "realised heritability" obtained for fibre diameter is slightly higher than the initial heritability used. It is interesting to note that this holds true for both initial heritabilities used and that the difference between the "incorrect" heritability and the resulting "realised heritability" is 0.131, while the difference when using the Henderson Method 3 estimate is only 0.032.

The genetic response in fibre diameter in the objectively selected line was only slight. This points to the fact that the culling of overstrong animals (Chapter 2) was reasonably successful in maintaining fibre diameter at a constant level and that the low genetic correlation between clean fleece mass and fibre diameter (Table 3.3) is in accordance with the result obtained.

An expected but somewhat alarming result, is the positive trend for fibre diameter in the subjectively selected line. The belief that wool production cannot be increased without an increase in fibre diameter (determined subjectively by the size of the crimp and feel of the wool) has led to indirect selection for fibre diameter in an effort to increase wool production. This tendency is, however, in the process of being reversed. The general recommendation to sheep breeders until recently has been to adopt a selection policy aimed at increasing clean fleece mass and keeping fibre diameter from changing (Turner and Young, 1969). However, the price premium currently being paid for finer (low fibre diameter) wool has most probably made a reversal of this policy a more profitable prospect (Erasmus and Delport, 1985). At current prices, the subjectively selected line, in spite of the slight increase in clean fleece mass, would generate a lower wool income at the end than at the beginning of the experiment because of the increased fibre diameter.

3.4.3 Body mass

The genetic response curves for body mass are given in Figure 3.10. Olivier (1980 and 1984) found no significant genetic trend in body mass in either of the two lines measured against the control. In the present study, however, all three lines showed a highly significant (P<0.01) genetic trend. The results are diagrammatically illustrated in Figure 3.11.



FIGURE 3.10

MEAN ANNUAL BREEDING VALUE PREDICTIONS FOR BODY MASS IN THE THREE LINES.



FIGURE 3.11 REGRESSION OF MEAN ANNUAL PREDICTED BREEDING VALUE FOR BODY MASS ON BIRTH YEAR FOR THE OBJEC-TIVELY SELECTED (OBJ), SUBJECTIVELY SELECTED (SUB) AND CONTROL LINE (CON).

> Figure 3.11 illustrates that the largest response for body mass was obtained for the subjectively selected line, followed by the control line. This led Olivier (1984) to conclude that, although non-significant, the objectively selected line showed a slight correlated response in body mass to selection for clean fleece mass which is contrary to the results of Heydenrych, du Plessis and Cloete (1984) and that generally found in the literature (Olivier, 1984). Figure 3.11, however, illustrates a positive correlated response in body mass which was found to be highly significant (P < 0.01).

> The relatively large positive trend for body mass in the subjectively selected line points to the importance judges place on size as a means of increasing production. At present, the emphasis placed on size by the stud breeding industry is even greater, as the general tendency is to breed bigger, plainer

(less skin folds) and finer (low fibre diameter) sheep (Erasmus and Delport, 1985; Erasmus, 1986).

The cumulative selection differentials, "realised heritabilities" and heritability estimates using Henderson's method 3 and REML are given in Table 3.8.

From Table 3.8 it is evident that the "realised heritabilities" obtained in the three different lines are in close agreement and only slightly lower than the estimated values.

TABLE 3.8 CUMULATIVE SELECTION DIFFERENTIALS (CSD), "REALISED HERITABILITIES" (REAL h²) AND HERITABILITY ESTIMATES FOR BODY MASS OBTAINED BY HENDERSON'S METHOD 3 (H-3 h²) and REML (REML h²) FOR THE OBJECTIVELY SELEC-TED (OBJ), SUBJECTIVELY SELECTED (SUB) AND CONTROL LINE (CON).

	OBJECTIVE	SUBJECTIVE	CONTROL
CSD	9.68	14.30	12.99
REAL h ²	0.205	0.234	0.210
SE	0.025	0.021	0.013
H-3 h ²	_	-	0.247
REML h ²	-	. –	0.252

It is interesting to note that, not only in body mass, but also in the two traits previously discussed, a higher cumulative selection differential consistently led to a higher "realised heritability". Also, in all cases, a higher cumulative selection differential led to a better fit being obtained when a linear regression

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was used to describe annual response. This emphasizes the importance of purposeful and consistent selection in maximising genetic gains.

3.4.4 Relative Trends

In order to draw a comparison among the three traits as far as selection applied and response obtained is concerned, the cumulative selection differentials and annual genetic gains in standardised units (phenotypic and genetic standard deviations respectively) are given in Table 3.9.

TABLE 3.9

CUMULATIVE SELECTION DIFFERENTIALS (CSD) AND ANNUAL GENETIC GAIN (Δ G) BOTH IN STANDARDISED UNITS FOR CLEAN FLEECE MASS (CFM), FIBRE DIAMETER (FD) AND BODY MASS (BM) IN THE THREE SELECTION LINES.

		OBJECTIVE	SUBJECTIVE	CONTROL
CFM:	CSD	4.00	2.69	0.81
	ΔG	0.062	0.035	0.000
 FD:	CSD	0.76	2.07	0.09
	ΔG	0.023	0.059	0.000
BM:	CSD	2.53	3.75	3.41
	ΔG	0.037	0.080	0.071

As is to be expected, the highest selection pressure applied was for clean fleece mass in the objectively selected line. However, the largest response obtained was for body mass in the subjectively selected line followed by body mass in the control line. The positive selection pressure and resulting genetic trend in all three traits in the subjectively selected line is in keeping with selection for visual "overall excellence" normally applied by Merino judges.

The fact that the control line remained genetically stable as far as clean fleece mass and fibre diameter were concerned, but showed an appreciable genetic gain in body mass, which cannot be explained by random genetic drift alone, points to the distinct possibility of natural selection. This possibility is now discussed.

3.5 Natural selection

Natural selection differs from artificial selection in that its goal cannot be defined in any way except by saying that it favours the fitter individuals. Dobzhansky (1951), showed that fitness is a property of all phenotypic expressions including subtle differences at the physiological or biochemical level. If there is an increase in a trait like body mass due to natural selection, it could merely be the outward manifestation of many other undetectable changes.

In interpreting the results of the present study, another important inherent property of natural selection must be borne in mind, namely that it operates even in the presence of artificial selection. "The latter, generally speaking, does not exist in pure form" (Lerner, 1958). This implies that if natural selection had been operative, it would have been equally intense in all three selection lines irrespective of the artificial selection practised. Natural selection has the final say as to which animals will survive and leave progeny, even if artificial selection has already operated.

When examining the results presented in Table 3.9 it appears strange and rather unlikely that the control line should exhibit a slightly higher genetic response and cumulative selection differential for body mass than the objectively selected line. A positive cumulative selection differential and genetic response for body mass, in the absence of natural selection, in the objectively selected line is expected due to the positive phenotypic and genetic correlation (Tables 3.2 and 3.3) of body mass with clean fleece mass, the trait under selection. In contrast no response is expected in the control line, in the absence of natural selection and random genetic drift.

The cumulative selection differential, as calculated in the present study, measures the joint effect of artificial and natural selection since it makes provision for differential number of progeny per selected parent. Falconer (1960) suggests comparing this "effective selection differential" with the "expected selection differential" which is merely the mean deviation of the individuals selected as parents from their contemporary group mean. In order to arrive at some measure of the relative "expected selection differentials" for body mass in the three lines, the mean deviation of the individuals selected or used as parents from their birth-year mean was calculated within each "generation". A "generation" was taken as every two years in the case of rams and every four years in the case of ewes. (The actual generation intervals are given in section 3.2). These mean deviations were summed to provide a relative measure of the amount of intentional or unintentional artificial selection applied without making provision for different numbers of progeny. The values obtained in this way cannot be compared to the realised cumulative selection differentials as suggested by Falconer (1960) for discreet generations. It does, however, provide a relative measure of the amount of artificial selection applied in the three selection lines. The results are presented in Table 3.10.

Table 3.10 indicates that animals with above-average values for body mass were eventually selected in all three lines. The small positive deviation of the ewes in the control line could have been unintentional but it is doubtful whether the deviation of the rams in the control line, which is approximately equal to that for the objectively selected line, is entirely unintentional. Mr J.J. Olivier, Senior Research Officer, Karoo Region, Middelburg C.P. (1987 – personal communication) who was stationed at Klerefontein towards the end of the experiment; is of the opinion that selection bias in the control could have been caused as a result of not using some of the small rams originally selected but rather one or two bigger reserve rams. Apparently the smaller rams had difficulty in serving the ewes. If this was the case, it can be seen as a form of simulated natural selection because if hand-mating had not been practised, these smaller rams would, in all probability, have served few, if any, ewes. However, this selection was more intense than in the objectively selected line and an overestimation of possible natural selection was obtained.

TABLE 3.10CUMULATIVE DEVIATIONS (kg) IN BODY MASS OF SELECTEDPARENTS IN THE THREE SELECTION LINES.

Sires	Dams	Mid-parent	
•			
20.47	2.41	11.44	
33.84	3.26	18.55	
20.54	1.75	11.15	
	Sires 20.47 33.84 20.54	Sires Dams 20.47 2.41 33.84 3.26 20.54 1.75	

It is a well-known fact that ewes below a sub-optimum body mass do not readily conceive. A minimum body mass of 36 kg is generally recommended for Merino sheep (Pamphlet on sheep production compiled by Department of Agriculture and Water Supply, 1976) but the average body mass at mating age in this selection experiment was only 32.5 kg (section 3.1.1). This was most probably the reason for the low lambing percentage in this experiment and it is therefore quite reasonable to accept that natural selection for body mass did take place and was partly responsible for the positive trend. This leads to the question of how effectively mixed model analyses can accommodate natural selection.

Under certain conditions, the mixed model equations ignoring selection lead to BLUE of the fixed effects and BLUP of the random effects even if there has been selection (Sorensen and Kennedy, 1984). As seen earlier (2.6.1), two of these conditions are that selection is based on a linear function of the records and L'X = 0. Henderson (1980) has given examples of types of selection that yield L'X = 0. He shows that if selection is based on records adjusted for fixed effects using unbiased estimators, ignoring selection, L'X will be nil.

In the present study it can be assumed that artificial selection by definition was based on a linear function of the records. Records were not adjusted for fixed effects prior to selection. In the objectively selected line, however, selection was based on within-year ratios and therefore some adjustment (not necessarily unbiased) for year effects can be assumed. Natural selection can seriously violate both these conditions. It does not necessarily favour maximum values but optimum or "adequate" values in a specific trait. The direction of selection is also not always constant. Scholtz (1985), for instance, explains contradictory results obtained in correlations between body mass and fertility (a fitness trait) in beef cattle on the grounds of Sewall Wright's genetic landscape as presented by Lush (1945). This implies that the correlation can be positive or negative, depending on the position of the population on the genetic landscape. It must be accepted that natural selection is seldom on a linear function of the records. Natural selection is also not invariant to the fixed effects normally specified in any model. In fact, fixed environmental effects can be more important in deciding the selection fate of an animal than its breeding value. It can favour animals with lower breeding values but a higher phenotypic expression in a trait as a result of a fixed effect.

It is not known how much bias these violations can introduce and little or no work has been done on the effects of natural selection in mixed model analyses.

3.6 Variance of predicted breeding values

In the analysis of selection experiments it is important to know how selection has effected the available genetic variation. Analogous to the determination of actual genetic varian ce, it seems of interest to know, in a practical situation, how selection will effect the variance of the breeding value predictions obtained by a mixed model analysis using a constant estimated base population variance ratio (heritability). The annual variances of the breeding value predictions for clean fleece mass in the objectively selected line are presented in Figure 3.12.



FIGURE 3.12 ANNUAL VARIANCE IN PREDICTED BREEDING VALUES IN CLEAN FLEECE MASS IN THE OBJECTIVELY SELECTED LINE.

Figure 3.12 shows a slightly positive time trend in variance in clean fleece mass. The other two traits show no apparent time trend (Appendix A). A decline in genetic variance is not to be expected considering the time span of the experiment. Breeders like to believe that selection increases genetic uniformity but in reality, supported by genetic theory, this happens at an almost imperceptibly slow rate.

Plotting histograms of the annual distributions of breeding value predictions, provides a clear illustration of the primary effect of selection, namely to shift the population mean. An example is provided in Figures 3.13 and 3.14, deputing the distributions in the first

and last year of the experiment.

The effect of using different heritabilities on the variance of the breeding value predictions for the objectively selected line is illustrated in Appendix A.



FIGURE 3.13 DISTRIBUTION OF PREDICTED BREEDING VALUES FOR CLEAN FLEECE MASS IN THE OBJECTIVELY SELECTED LINE.



FIGURE 3.14 DISTRIBUTION OF PREDICTED BREEDING VALUES FOR BODY MASS IN THE OBJECTIVELY SELECTED LINE.

3.7 Inbreeding

In any selection experiment it is normally assumed that the rate of inbreeding in all the divergent lines is identical. Figure 3.15 provides the mean annual percentage inbreeding calculated for the three lines.



FIGURE 3.15 ANNUAL PERCENTAGE INBREEDING IN THE THREE LINES.

The differences in inbreeding among the three lines were non-significant. Inbreeding could therefore not have had a significant influence on the differences in response obtained among the three selection lines. However, as shown in Fig 3.15, there is an inevitable increase in the amount of inbreeding as is expected in any closed population of finite size. Figure 3.15 indicates no distinct plateauing of the percentage inbreeding and a first order regression fitted to the objectively selected line produced an almost identical fit ($R^2 = 0.701$) to a second order regression ($R^2 = 0.690$). A mean inbreeding coefficient of roughly two percent during the last three years (Figure 3.15) can be considered low, but the relatively large standard deviations (Appendix B) indicate that the influence of individual inbreeding coefficients on natural and artificial selection cannot be ruled out. The effect

of inbreeding on production and reproduction traits in Merino sheep has been the subject of many studies and reviews (Morley, 1954; Doney, 1957; Lax and Brown, 1967; Turner and Young, 1969; Dolling 1970). These studies show a decline of varying degree in all three traits recorded in the present study with an increase in inbreeding. As is to be expected, however, the largest decline found was in lambing performance, a decrease of roughly one percent lambs weaned with every one percent increase in inbreeding. The levels of inbreeding obtained in the present study could therefore not have been responsible for the low overall production and reproduction encountered.

CHAPTER 4 GENERAL CONCLUSIONS

The question which immediately arises is: Was a mixed model approach in the analysis of the Klerefontein Selection Experiment successful in the sense that it provided information that would not have been obtained by simple traditional estimators? The answer to this must be positive, as traditional methods used by Olivier (1980) did not, and in fact, could never have unmasked the positive genetic trend for body mass in the control line. Because of this, the positive genetic trend for the same trait in the other two selection lines also remained undetected or at least seriously underestimated in the case of the subjectively selected line.

To argue that the basic reason for traditional estimators being unsuccessful is an inadequate experimental design is rather naive. One cannot change the design of an experiment initiated 26 years ago and merely write off all the time, effort and money that has been spent in its execution. If alternative estimators are available which can better handle poor experimental design, it is obvious that they should be used. It must be stressed, however, that there is still no true substitute for proper design. As a result of the time involved, medium and even short-term selection experiments are, in many cases, analysed by different people with different resources at their disposal than those who initiated them. It is inevitable that some discrepancy between the initial design and the requirements of the eventual analysis will exist.

Apart from the fact that the actual heritabilities in the base population were not known, some of the other conditions, such as that selection must be on a linear function of the records and invariant to the fixed effects, under which mixed model methodology will adequately separate genetic and environmental effects were clearly not met in the present study. It is doubtful whether all these conditions will ever be met in practice under field conditions. The amount of bias introduced by a violation of these conditions will have to be quantitatively known before the results obtained by mixed model analyses can be interpreted with confidence.

In the present study, selection was carried out in a harsh environment. Merino sheep in South Africa are normally selected under favourable conditions as was the case with the sheep used before the experiment was initiated. It can therefore be assumed that the sheep used were not fully adapted to the experimental environment and this could have had a marked influence on the results obtained. As far as this aspect is concerned, a major shortcoming of the experiment was that skin fold score, or some measure of skin folds, was not recorded. Selection for skin folds was widely practiced in the past in an effort to increase wool production. Selection for this "external" trait has produced a sheep showing a series of classical constitutional faults (Dun and Eastoe, 1970). Although rather harsh, these authors claim that, "The physiology of the sheep has been wrecked in a way that no one could possibly have predicted." If skin fold score had been recorded much light could have been shed on how this important trait could have influenced selection response.

The control line of the Tygerhoek selection experiment (Chapter 1) is used by some South African Merino breeders to evaluate the relative genetic merit of their studs and to measure genetic progress (Erasmus, 1976; van der Merwe and Poggenpoel, 1977). With the advent of mixed model methodology, this method could well become redundant. It is doubtful, however, whether control populations will ever become redundant in selection experiments. Control populations can be used to good effect in detecting correlated changes in traits not recorded from the onset and in determining the possible establishment of genotype x treatment interactions such as the effect of cystine and methionine supplementation by McGuirk (1979) referred to in Chapter 1. Mixed model analyses can, however, be used to good effect to check their stability. In such cases prior knowledge of the true base population heritability is not as important since a slightly inflated value could be used to make sure that no genetic trend is present.

Overwhelming evidence of the superiority of objective vs subjective selection has put this issue beyond doubt and results obtained in the Klerefontein selection experiment in this regard (present study and Olivier, 1980) have nothing new to offer. The present study has, however, illustrated how Merino judges place as much or more emphasis on components of wool production (body mass and fibre diameter) than the trait they are actually attempting to improve (clean fleece mass). The emphasis placed on body mass is not unwarranted since it has been suggested by the results presented that natural selection also favoured higher body mass. The emphasis placed on high fibre diameter in an effort to increase wool production raises the question if subjective selection could ever be effective in decreasing fibre diameter (a serious present consideration as discussed) without an inevitable equally serious decline in clean fleece mass. The problem is that, in subjective selection, the trait in question is not necessarily directly evaluated but components that are, or made out to be, the most important and which are normally more visible are used. Having to reverse the direction of selection in one of the most important components used to increase wool production, a reversal in the direction the latter will respond seems most likely. Add to this that the present tendency is also to select for less skin folds (Erasmus, 1986) the other important component used in the past to increase wool prodution subjectively, increasing or maintaining wool production by subjective selection alone when the direction in these components is reversed, seems impossible. On the other hand, Poggenpoel and Van der Merwe (1987) give evidence to suggest that by using obective measurements in a selection index, clean fleece mass can be increased genetically while decreasing both fibre diameter and skin fold score. Using objective measurements in a multiple trait mixed model could be even more effective.

The adverse effect of low reproduction rate on possible genetic progress has been clearly demonstrated. Low reproduction is generally considered as one of the major problems in the South African sheep industry (De Klerk, Duvel and Terblanche, 1983). Although the situation encountered in this study is not even remotely typical of that in the Merino studs, where lambing percentages of over 100 are common, due to better nutrition and management, it does point to the restrictions that can be encountered when attempting to

raise the genetic level of production under less favourable conditions. Escalating input costs have prompted many breeders to practise selection in a low cost environment in an effort to breed sheep capable of increasing production under such conditions (Erasmus, 1986). It is evident that the necessary attention to reproduction rate will have to be given if these attempts are to be successful.

Finally, Van Vleck (1987) suggests that the true model describing a vector of observations, $\underline{\mathbf{y}}$, can be written as:

$$\mathbf{y} = \mathbf{f}(\mathbf{g}, \mathbf{e}, \mathbf{people})$$

i.e. the observations are a function of the genotype, the environment and the people managing the animals and collecting the data. The linear mixed model $\mathbf{y} = \mathbf{X}\mathbf{b} + \mathbf{Z}\mathbf{u} + \mathbf{e}$ is normally used as an approximation of the true model as it is virtually impossible to quantify the "people" – effect. Experience has taught that this "people" – effect can be of overriding importance in the analysis of field data. However, experience gained in the present study has clearly indicated that it also cannot be ignored in the analysis of experimental data.

ABSTRACT

- 1. A mixed model analysis of a selection experiment with Merino sheep carried out at the Klerefontein Research Station, Carnarvon, C.P., from 1962 to 1982 was undertaken. The experiment consisted of three selection lines: One objectively selected for high clean fleece mass, another selected subjectively for "overall excellence" and an unselected control line. The generation interval was almost identical (3.3 years) in all three lines and the experiment represented roughly six and a quarter generations of selection.
- Heritability estimates of 0.247 for body mass, 0.229 for clean fleece mass and 0.369 for mean fibre diameter were obtained using Henderson's Method 3. REML estimates on a sire model yielded almost identical estimates.
- 3. The line selected for high clean fleece mass showed a genetic response of 0.014 kg per annum in this trait. The low response is ascribed to a low heritability and a low cumulative selection differential due to low reproduction rates. The "realised heritability" was 0.187. Small annual genetic changes of 0.098 kg and 0.016 micrometer in body mass and mean fibre diameter, leading to "realised heritabilities" of 0.205 and 0.282 respectively, also occurred.
- 4. The largest response in the subjectively selected line was for body mass (0.189) and fibre diameter (0.042), while clean fleece mass increased by 0.008 kg per annum. "Realised heritabilities" obtained were 0.234 for body mass, 0.138 for clean fleece mass and 0.401 for fibre diameter.
- 5. The control line remained genetically stable for clean fleece mass and fibre diameter, but showed a significant response of 0.168 kg per annum for body mass. The "realised heritability" obtained was 0.210. This response is ascribed partly to natural

selection in a harsh environment where some sheep were at a sub-optimum body mass.

- 6. An illustration of how lower heritability values in the mixed model equations leads to smaller predicted gains and hence lower "realised heritabilities" and also lower variances of predicted breeding values is provided.
- 7. The average inbreeding coefficient was roughly 0.02 at the end of the experiment and no significant differences in inbreeding among the three lines existed.
- 8. It is concluded that a mixed model analysis of selection experiments provides useful information especially if there is reason to believe that the control is not genetically stable.

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APPENDIX A

YEAR	BODY MASS		CLEAN FLEECE MASS		FIBRE DIAMETER	
	h ² =0.142	h ² =0.24	h ² =0.142	h ² =0.229	h ² =0.142	h ² =0.369
62	0.977	1.437	0.077	0.106	0.260	0.520
63	0.906	1.310	0.069	0.092	0.246	0.489
64	1.230	1.800	0.086	0.117	0.290	0.516
65	1.218	1.671	0.063	0.082	0.266	0.506
66	1.187	1.580	0.069	0.096	0.317	0.597
67	1.347	1.738	0.075	0.098	0.296	0.545
68	1.398	1.865	0.074	0.099	0.335	0.584
70	1.365	1.808	0.092	0.125	0.300	0.535
71	1.327	1.720	0.069	0.089	0.323	0.523
72	1.502	2 .049	0.074	0.100	0.379	0.655
73	1.619	2.152	0.087	0.113	0.362	0.623
74	1.113 ,	1.528	0.085	0.110	0.316	0.506
75	1.179	1.580	0.064	0.087	0.292	0.493
76	1.109	1.540	0.080	0.108	0.291	0.513
77	1.344	1.798	0.076	0.103	0.304	0.513
78	1.003	1.360	0.085	0.110	0.344	0.641
79	1.261	1.714	0.082	0.113	0.385	0.591
80	1.086	1.445	0.104	0.137	0.394	0.618
81	1.178	1.597	0.101	0.139	0.299	0.487
82	0.980	1.407	0.091	0.121	0.331	0.556

Annual variance of breeding value predictions in the objectively selected line.

APPENDIX B

Average annual inbreeding percentage in the three lines (base population inbreeding assumed to be zero, years 62 to 64 omitted because of zero inbreeding).

YEAR	OBJECTIVE		SUBJECTIVE		CONTROL	
	F	SD	F	SD	F	SD
65	0.0	0.0	0.2	1.6	0.2	1.7
66	0.9	3.9	0.0	0.0	0.7	2.4
67	0.3	1.4	0.3	1.8	0.8	2.5
68	1.0	3.9	0.4	1.8	0.6	1.6
70	0.5	2.3	0.9	2.9	1.1	2.6
71	0.9	2.7	0.7	2.6	0.7	2.0
72	1.2	2.2	1.0	2.4	1.5	3.3
73	1.4	2.2	0.8	2.0	1.2	1.5
74	2.1	4.1	1.0	2.1	1.5	2.6
75	1.5	2.1	1.4	1.9	1.6	1.9
76	1.5	2.4	1.8	4.0	1.4	1.4
77	2.4	4.2	1.6	2.0	2.0	3.9
78	2.3	2.4	1.9	2.4	2.5	2.2
79	1.5	1.4	. <u> </u>	_	2.6	2.3
80	2.0	2.4	-	-	2.3	1.6