Genetic and phenotypic parameter estimates of production traits of Merino sheep in an arid environment

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Genetic and phenotypic parameters were estimated in the control line of the Klerefontein Merino sheep selection experiment. The heritability estimates of 0,247 for body mass, 0,229 for clean fleece mass and 0,369 for fibre diameter are generally lower than other published estimates. Henderson's Method 3 and REML on a sire model produced almost identical estimates. Phenotypic, environmental and genetic correlation between the three traits were all positive low. As with many other published results, genetic correlations were characterized by large standard errors of estimation. The limitations of traditional estimators is briefly discussed.

Genetiese en fenotipiese parameters is in die kontrolelyn van die Klerefontein Merinoseleksie-eksperiment beraam. Die oorerflikheidsberamings van 0,247 vir liggaamsmassa, 0,229 vir skoonvagmassa en 0,369 vir veseldikte is oor die algemeen laer as ander gepubliseerde beramings. Henderson se Metode 3 en REML op 'n vaarmodel het bykans identiese beramings gelewer. Fenotipiese, omgewings- en genetiese korrelasies tussen die drie kenmerke was almal positief laag. Soos met baie ander gepubliseerde resultate, is genetiese korrelasies deur hoë standaardfoute gekenmerk. Die leemtes van tradisionele beramers word kortliks bespreek.

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Introduction

Genetic and phenotypic parameters are commonly used to predict direct and correlated response to selection. Estimates of these parameters are also needed for multiple-trait mixed model methods for prediction of breeding values. Single-trait models require heritability estimates of the specific trait in the base population. Control populations, used to monitor genetic change in selection experiments, are normally favoured for the estimation of genetic parameters since they are assumed to be unselected and genetically stable. Bias due to selection is therefore minimized when traditional estimators, that do not make provision for selection, are used.

The aim of this study was to estimate genetic and phenotypic parameters of production traits in the control flock of the Klerefontein selection experiment. The experiment was conducted in an extremely harsh environment and the estimates obtained under such conditions can be compared to other published values. Accurate estimates of genetic parameters in different environmental and production systems are necessary to predict response to selection. Estimates of heritabilities were also needed to perform single-trait mixed model analyses to determine genetic trends.

The efficiency of the commonly used least squares type of procedures for estimating genetic parameters is generally not known and this has partly been the impetus for research into other methods with more desirable statistical properties. The Restricted Maximum Likelihood (REML) procedure (Patterson & Thompson, 1971) is one such method and it was decided to compare heritability estimates obtained using this and the more traditional method on the same available data.

Material and Methods

Environment

The experiment was initiated at the Grootfontein College of Agriculture at Middelburg in the Cape Province in 1962, but moved to the Klerefontein Research Station at Carnarvon in 1964 until termination in 1984. 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, with a standard deviation of 108 mm. 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 and 39°C.

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.

Procedure

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 obvious cull 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 form 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 randomly allocated to the control line while five were kept in reserve.

Ewes were hand-mated to a randomly allocated sire. 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 and 30% salt, was provided. An inoculation and drenching programme, prescribed by the State Veterinarian, was followed.

Observations

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

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 was 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:

$$\text{Clean yield \%} = \frac{\text{bone-dry sample mass after scouring} \times 116}{\text{sample mass before scouring}}$$

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

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.

Body mass The body mass of all available sheep was recorded at 18 months of age, immediately after shearing.

Statistical analysis

Heritability estimates

Heritability estimates were obtained by half-sib analysis of variance using Henderson's Method 3 (Henderson, 1953) with the library computer program LSML–76 (Harvey, 1960). For comparison two traits, clean fleece mass and body mass, were analysed by the REML procedure using the mixed model analysis of variance program in the BMDP package. To facilitate use of the latter program which has no absorption option, least-square means were calculated for combinations of sex, age of dam (maiden or mature) and birth status in a fixed effects model and records were adjusted within year of birth. The following mixed model was then fitted for both procedures:

$$Y_{ijk} = \mu + a_i + s_j + e_{ijk}$$

where Y_{ijk} = adjusted record on the k-th individual of the j-th sire in the i-th year,
   μ = population mean,
   a_i = fixed effect of the i-th year,
   s_j = random effect of the j-th sire,
   e_{ijk} = random error.

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).

The heritability estimates were obtained by:

$$h^2 = \frac{4\sigma^2 s}{\sigma^2 s + \sigma^2 e}$$

where $\sigma^2 s$ = observed sire variance,
   $\sigma^2 e$ = error variance.

Henderson (1984) also points out that, even when $\sigma^2 s$ and $\sigma^2 e$ are unbiased, this could still be a biased estimator of h^2.

Genetic and environmental correlations were calculated by Henderson's Method 3 only.

Results and Discussion

Data description

The least squares means, standard deviations and coefficients of variation in the control line (n = 2265) of the five traits recorded, are given in Table 1.

Table 1 Least squares means ($\bar{X}$), standard deviations (SD) and coefficients of variation (CV%) of traits recorded

Trait	$\bar{X}$	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 means 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 1, the national average wool production per Merino sheep (greasy fleece mass) is 5,63 kg (De Klerk, Duvel & Terblanche, 1983).

Correlations between traits

The phenotypic and environmental correlations between the three traits analysed are given in Table 2 (note that greasy fleece mass and clean yield percentage were not analysed but merely used to estimate clean fleece mass).

All the phenotypic correlations are positive, which is in agreement with most published results, although reasonable large differences in the magnitude of the estimates occur.

Table 2 Phenotypic and environmental correlations between traits

Traits	Phenotypic correlations	Environmental correlations
BM[a]—CFM[b]	0,333	0,369
BM —FD[c]	0,138	0,161
CFM —FD	0,147	0,184

[a] Body mass.

[b] Clean fleece mass.

[c] Fibre diameter.

Of particular interest 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 characterized by large order and even sign differences. The estimates of genetic correlations obtained in this study, together with those of two other South African studies, and the ranges obtained in several Australian studies on Merino sheep, are given in Table 3.

Table 3 Estimates of genetic correlations between traits

Traits	Range of estimates on			
	South African Merinos			
	1[a]	2[b]	3[c]	Australian Merinos[d]
BM—CFM	0,218	0,50	0,380	–0,12—0,30 (4)
SE[e]	(0,172)		(0,181)	
BM—FD	0,088	0,68	0,127	–0,08—0,12 (4)
SE	(0,157)		(0,208)	
CFM—FD	0,063	0,03	0,291	–0,06—0,40 (5)
SE	(0,162)		(0,167)	

[a] Present study.

[b] Bosman (1958) – no standard errors were calculated. Degrees of freedom roughly 1300.

[c] Heydenrych (1975).

[d] From reviews by Turner (1977) and Rogan (1984). Number of reference is given in parenthesis.

[e] Standard error.

Two of the estimates in this 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 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.

Multiple-trait reduced animal models for predicting breeding values, first introduced by Quaas & Pollak (1980), utilize 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 & 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 it is clear that selecting appropriate *a priori* estimates for these traits from the literature is an extremely difficult, if not impossible, task.

Heritability estimates

The heritability estimates (h^2) obtained by using REML and Henderson's Method 3 (H–3) are given in Table 4.

Table 4 Heritability estimates using Restricted Maximum Likelihood (REML) and Henderson's Method 3 (H–3)

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 0,5 for body mass, 0,4 for clean fleece mass and 0,45 for fibre diameter. The heritability estimates obtained in this 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 the 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 predictors (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 & Thompson's (1971) REML (Sorenson & Kennedy, 1986). In contrast to Henderson's Method 3, MIVQUE and REML on an animal model make use of all the data available. All animal records and all the relationships among them can be used to compute estimates of genetic parameters (Sorenson & Kennedy, 1986). In this 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 (Sorenson & Kennedy, 1984a). All non-collateral relationships are ignored. Ignoring relationships over generations has important implications if selection has been present. However, use of the 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 (Sorenson & Kennedy, 1984a), seemingly even when used on data that have been generated by several cycles of selection and mating (Sorenson & Kennedy, 1984b).

The problem is that use of MIVQUE or REML on an animal model is currently computationally prohibitive even on reasonable small data sets. The major problem is that both require a generalized inverse of the coefficient matrix. Recently, however, Graser, Smith & 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 utilizes the principle of Gaussian elimination. Developments such as this and increasing power of computers are making these methods more practical computationally and, as Sorenson & Kennedy (1984b) have pointed out, they ought to be considered as alternatives to some of the more traditional methods.

The use of REML, even on a sire model as in this study, is computationally more demanding and far more costly than Henderson's Method 3 (H-3). As results obtained for the first two traits (Table 4) are in close agreement, there seems little point in using REML unless all relationships among animals can be utilized. It was therefore decided that the estimates obtained by H-3 would suffice for use in mixed model equations to determine genetic trend. 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.

Conclusions

Although gene frequencies, and therefore heritability estimates, can differ among populations, one is inclined to ascribe the low heritability estimates obtained in this study to the harsh environment under which the animals were kept. There is, however, evidence that genetic progress in all three traits can be made under such conditions and that deleterious correlated responses should not pose any serious problems.

Best linear unbiased prediction of breeding values by mixed model procedures require unbiased and derivative-free estimates of genetic parameters. High priority should be given to finding such estimators that are computationally more feasible than those presently available.

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