Estimates of genetic parameters and genetic trend for fur traits in a Karakul stud flock

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Heritability estimates were obtained by using a unitrait derivative-free animal model REML programme. Estimates of heritability for curl type \( h^2 = 0.46 \) and pattern score \( h^2 = 0.27 \) followed expectations as derived from literature. The estimate for hair quality score \( h^2 = 0.14 \) was, however, lower than expected. An unexpected negative correlation \( r = -0.37 \) was obtained between pattern score and hair quality score as estimated by simple correlation of individual predicted breeding values (PBVs) between traits. Environmental trends were influenced by changes in the system of score allocation to the subjectively evaluated traits, which possibly indicate the sensitivity of the procedure. A positive genetic trend was evident for both pattern score \( b = 0.011 \pm 0.002 \) and hair quality score \( b = 0.013 \pm 0.001 \).

Keywords: Animal model, fur traits, genetic parameters, Karakul, trends.

Introduction
Estimates of genetic parameters such as heritabilities and genetic correlations are important in the design of appropriate breeding programmes. They provide an indication of the relative genetic importance of traits, as either direct genetic response or correlated response to selection. Heritability estimates are also needed for the prediction of breeding values through uni- or multitrait mixed model methods (Sorensen & Kennedy, 1984).

The objective of this study was to obtain heritability estimates in the Lovedale Karakul stud flock. This flock is regarded as the single most important flock which makes a contribution to the genetic make-up of the Karakul industry of Southern Africa (Albertyn, 1990). By employing these heritability estimates, BLUP technology (Henderson, 1973) can be used to quantify genetic progress. The procedure includes a study of relationships among animals to provide the necessary genetic ties across years which make the separation of genetic and environmental effects possible (Blair & Pollak, 1984).

Material and Methods
Source of data
Data from the Lovedale Karakul stud flock in Namibia were used for the analysis. The data consisted of 4,746 records of animals which were born between 1968 and 1983. Only 21.8% or 1035 of the animals were selected, while the others (3711) were culled and slaughtered soon after birth. The number of base animals, which had no available records or pedigree information, totalled 1042. Sixty-four sires were used. The number of offspring per sire varied from 1 to 563, with an average of 74.09. Only black lambs, born from black X black matings, were included. Twin-born lambs, which made up only 2.1% of all lambs born, were also excluded.

Observations
Traits considered and included were curl type, pattern score and hair quality score. These traits are regarded to be economically the most important in Karakul breeding (Nel, 1966; Schoeman & Nel, 1969; Van Niekerk, 1972).

The three traits were evaluated subjectively according to the procedure laid down by the Karakul Breeders Association of Southern Africa (Anonymous, 1982). Each curl type classification is converted to a numerical code from 1 (smooth or no curl development) to 9 (pipe curl or fully developed). Curl type scores for the data set varied from 1 to 7, whereas scores for pattern and hair quality varied from 3 to 8 and from 4 to 9 respectively. All three traits were considered to be continuous.

Statistical analysis
The General Linear Models of the Statistical Analysis System (SAS, 1985) were initially used in the analyses of the data to determine the significance of each fixed effect (year of birth, season of birth, age of dam and sex of lamb) and their two-way interactions. Most traits were significantly \( P \leq 0.05 \) affected by the fixed effects, except hair quality score which was not significantly \( P > 0.05 \) affected by sex of lamb. The influence of interactions was also non-significant \( P > 0.05 \) and i: was assumed that the fixed effects were uncorrelated.
Heritability estimates were subsequently obtained by using the unitrait derivative-free animal model REML programme (DFREML) of Meyer (1989). This model includes all animals, even those without records, but as parents in the base population. It therefore takes all information into account for the estimation of variance components (Sorensen & Kennedy, 1986). The same model was fitted on all three traits. The general formulation of the mixed model fitted on the observations, comprised the following:

\[ Y_{ijklm} = \mu + A_i + B_j + C_k + D_l + Z_m + e_{ijklm} \]

where

- \( Y_{ijklm} \) is the individual observation for the appropriate trait,
- \( \mu \) is the population mean for the appropriate trait,
- \( A_i \) is the fixed effect of the \( i \)-th year of birth (1968—1983),
- \( B_j \) is the fixed effect of the \( j \)-th season of birth, with levels for summer- and winter-born lambs respectively.
- \( C_k \) is the fixed effect of the \( k \)-th dam age group (2 to 10 years of age),
- \( D_l \) is the fixed effect of the \( l \)-th sex of lamb,
- \( Z_m \) is the random genetic (breeding value) effect of the \( m \)-th animal (number of animals = 5788), and
- \( e_{ijklm} \) is the random error.

The formulation of the model in matrix notation is as follows:

\[ \mathbf{y} = \mathbf{Xb} + \mathbf{Zu} + \mathbf{e} \]

where

- \( \mathbf{y} \) is a vector of 4746 observations,
- \( \mathbf{b} \) is vectors of unknown fixed effects for year of birth, month of birth, age of dam and sex of lamb respectively (\( b_1 \) — \( b_6 \)),
- \( \mathbf{X} \) is known incidence matrices relating the records to fixed effects (\( \mathbf{X}_1 = \mathbf{X}_2 = \mathbf{X}_3 = \mathbf{X}_4 = \mathbf{X}_5 = \mathbf{X}_6 \)),
- \( \mathbf{u} \) is vector of unknown random effects fitted which represent breeding values of the animals,
- \( \mathbf{Z} \) is known incidence matrix relating the records to the unknown random effects (\( u \)), and
- \( \mathbf{e} \) is a vector of random residual errors.

The more general estimation programme (DFUNIS), which is suitable for all models, was used. This programme employs the Simplex method (Nelder & Mead, 1965) to locate the maximum of the likelihood function as has been discussed. Solutions for the mixed model equations were obtained by using an animal model adaptation (Delport, 1989) based on the so-called ‘Simple Method’ for single trait sire models of Schaeffer & Kennedy (1986), which presents predicted breeding values (PBVs) for each animal in each trait. The solutions were considered to be converged when a criterion of 0.001 has been reached.

Simple correlation coefficients were estimated between the PBVs for all animals in the three traits. PBVs were averaged within year of birth and these averaged values, regressed on year of birth, represent the genetic trend for each trait.

### Results and Discussion

#### Description of data

Means, standard deviations, coefficients of variation and Pearson's coefficients of skewness are presented in Table 1.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Curl type</th>
<th>Pattern score</th>
<th>Hair quality score</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean (( \bar{X} ))</td>
<td>3.86</td>
<td>5.60</td>
<td>6.89</td>
</tr>
<tr>
<td>SD</td>
<td>1.26</td>
<td>0.92</td>
<td>0.74</td>
</tr>
<tr>
<td>CV%</td>
<td>32.54</td>
<td>16.41</td>
<td>10.72</td>
</tr>
<tr>
<td>Skewness</td>
<td>0.69</td>
<td>0.65</td>
<td>-0.16</td>
</tr>
</tbody>
</table>

The mean value of 3.86 for curl type represents a watersilk (underdeveloped) type, which is the most popular type in Karakul breeding. The coefficient of variation for curl type is in close agreement to those values reported by Schoeman (1968) and Botma (1981), but is much lower for both pattern and hair quality scores compared to the corresponding parameters in the cited literature. This reduction in variation could have been the result of prolonged directional selection for these two traits or differences in procedure of scoring.

Pearson's coefficient of skewness (Steyn et al., 1984) indicated an almost normal distribution for hair quality score, with both curl type and pattern score showing a small positive deviation from normality. This may have been a result of the subjective assessment procedure. It was, however, decided to analyse the data on the original scale without any transformation.

### Estimates of heritability

Variance components and resulting heritability estimates, compared to those reported in the literature, are given in Table 2.

The heritability value of 0.46 for curl type is in good agreement with those values reported in other studies, which varied from 0.25 to 0.77 (Yao et al., 1953; Malan, 1959; Nel, 1966; Federson, 1968; Van Niekerk et al., 1968; Van Niekerk, 1972; Greeff et al., 1991a), with a median value of 0.51.
Published estimates (Nel, 1966; Federson, 1968; Van Niekerk et al., 1968; Van Niekerk, 1972; Botma, 1981; Greeff et al., 1991a) of genetic correlations vary considerably and cover almost the entire parameter space.

The genetic correlations obtained between curl type and pattern score varied between -0.55 and 0.77 with a median value of 0.11, which closely resembles the present correlation of 0.15. The genetic correlations between curl type and hair quality score are negative in all cases, with the present correlation \( r = -0.22 \) not too much different from the median value of the estimates obtained from the cited literature \( (r_E = -0.34) \).

Of particular interest is the correlation between pattern score and hair quality score, since these are economically the most important traits (Nel, 1966; Schoeman, 1968; Van Niekerk, 1972). These values varied from -0.32 to 0.61, but were in most cases negligible. Differences in genetic correlations between flocks may have been due to lamb evaluation peculiarities or to genetic differences between flocks. The fixation of pleiotropic genes as a result of selection on both traits may eventually change a positive genetic correlation into a negative one (Sheridan & Baker, 1974). This may probably have been one of the most important reasons for the negative correlation in the specific flock, as compared to a positive genetic correlation obtained by Greeff et al. (1991a) in the Upington control flock.

### Solutions for fixed effects

Generalized least squares (GLS) for the fixed effects (age of dam, season of birth and sex of lamb) are presented in Table 4.

All three traits were significantly \( (P < 0.001) \) influenced by age of dam. Curl development of lambs increased with increasing age of the dam, whereas pattern score deteriorated.

### Table 4 Solutions (generalized least squares) of age of dam, season of birth and sex of lamb for curl type, pattern and hair quality scores

<table>
<thead>
<tr>
<th>Fixed effects</th>
<th>Curl type</th>
<th>Pattern score</th>
<th>Hair quality score</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age of dam (years)</td>
<td>***</td>
<td>***</td>
<td>***</td>
</tr>
<tr>
<td>2</td>
<td>-0.26</td>
<td>0</td>
<td>0.05</td>
</tr>
<tr>
<td>3</td>
<td>-0.06</td>
<td>0.04</td>
<td>0.03</td>
</tr>
<tr>
<td>4</td>
<td>-0.06</td>
<td>0.11</td>
<td>-0.06</td>
</tr>
<tr>
<td>5</td>
<td>0.12</td>
<td>0</td>
<td>-0.14</td>
</tr>
<tr>
<td>6</td>
<td>0.13</td>
<td>0.02</td>
<td>-0.15</td>
</tr>
<tr>
<td>7</td>
<td>0.31</td>
<td>0.09</td>
<td>-0.21</td>
</tr>
<tr>
<td>8</td>
<td>0.28</td>
<td>-0.05</td>
<td>-0.18</td>
</tr>
<tr>
<td>9</td>
<td>0.39</td>
<td>-0.19</td>
<td>-0.16</td>
</tr>
<tr>
<td>10</td>
<td>0.23</td>
<td>-0.28</td>
<td>-0.27</td>
</tr>
<tr>
<td>Season of birth</td>
<td>***</td>
<td>***</td>
<td>***</td>
</tr>
<tr>
<td>Summer</td>
<td>-0.35</td>
<td>-0.13</td>
<td>0.13</td>
</tr>
<tr>
<td>Winter</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Sex of lamb</td>
<td>*</td>
<td>***</td>
<td>NS*</td>
</tr>
<tr>
<td>Rams</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Ewes</td>
<td>0.11</td>
<td>-0.11</td>
<td>0.19</td>
</tr>
</tbody>
</table>

* Non-significant \( (P > 0.05) \).
* \( P < 0.05; \) *** \( P < 0.001 \).

### Genetic correlations

Estimates of simple correlations between PBVs and genetic correlations among the three traits recorded, are presented in Table 3.

### Table 3 Estimates of simple correlation between PBVs and genetic correlations among the three traits recorded

<table>
<thead>
<tr>
<th>Traits</th>
<th>Present study*</th>
<th>Genetic correlations*</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Minimum</td>
<td>Maximum</td>
</tr>
<tr>
<td>Curl type &amp; pattern score</td>
<td>0.15</td>
<td>-0.55</td>
</tr>
<tr>
<td>Curl type &amp; hair quality score</td>
<td>-0.22</td>
<td>-0.06</td>
</tr>
<tr>
<td>Pattern score &amp; hair quality score</td>
<td>-0.37</td>
<td>-0.32</td>
</tr>
</tbody>
</table>

* Correlations obtained through simple correlations between individual breeding values.

from eight years of age onward. Hair quality scores gradually deteriorated from four years onward. This confirms a general trend which has also been found by Nel (1966), Le Roux & Van der Westhuizen (1970), Van Niekerk (1972) and Greeff et al. (1991b). It is thus clear that ewes were retained for too long and that they should have been culled after six or seven years of age.

Summer-born lambs have less curl development and lower pattern scores compared to winter-born lambs, but have superior hair quality. In addition, ewe lambs have more curl development than ram lambs, but have inferior pattern score. Hair quality score was, however, not significantly \( (P > 0.05) \) affected by sex of lamb. These effects were confirmed by Mostert (1963), Nel (1966), Van Niekerk (1972) and Greeff et al. (1991b).

The solutions of the fixed year effects on year of birth as environmental trends for curl type, pattern score and hair quality score are presented in Figures 1—3 respectively.

The curl type score exhibits the typical fluctuating nature owing to environment (Figure 1). The year-to-year fluctuations could have been associated with years of high and low rainfall respectively, e.g. 1970, 1973 and the early eighties which were extremely dry years compared to 1974 to 1976 which were years with an above-average rainfall. Steyn (1974) obtained differences in curl development between lambs born from ewes on different nutritional levels.

Figure 1 Generalized least squares by year of birth for curl type.

Figure 2 Generalized least squares by year of birth for pattern score.

Figure 3 Generalized least squares by year of birth for hair quality score.

An interesting feature of the year effects on pattern score (Figure 2) is the sharp decrease which occurred from 1968 to 1980, followed by a sharp increase. This change might have resulted from an adjustment in the score allocation system introduced by the Karakul Breeder's Association in 1980, when higher scores were allocated to more 'open' pattern types and lower scores to the traditional precious vertical types. Prior to this change in 1980, sires in the Lovedale flock had already been selected on this basis, but without allocating the higher scores.

The relatively sharp decrease in environmental trend for hair quality score (Figure 3) could, irrespective of year-to-year fluctuations, only be explained to be the result of the inconsistent nature of subjective evaluation. The sharp drop in environmental values between 1972 and 1974 corresponds with the period when the son took over management from his father, which indicates a change in evaluation standards applied by the two individuals. This highlights the sensitivity of mixed model methodology as a technique in the evaluation of environmental effects. This is confirmed by Erasmus (1988) who illustrated an environmental change in fibre diameter in Merino sheep resulting from an adjustment in laboratory measuring procedures.

Genetic trends

The genetic trends for the three traits are illustrated in Figures 4—6.
practiced for many years. In this study an unexpected low have been attributed to inaccurate subjective assessment of the PBV of 0.259 for pattern score. It is interesting that, in both Although computationally demanding, an individual animal produced 563 offspring in this flock. This ram had a PBV of 0.379 for hair quality score. There was also a relatively sharp increase in genetic improvement for pattern score since 1975, (Figure 6) with an annual increase of 0.013 score units during the period of investigation. The same applied to hair quality score. The sharp increase since 1977 was (r = -0.22) as a result of directional selection on maximum values for hair quality score. The full implications of subjective evaluation and changes in the score allocation procedure was illustrated. The authors express their gratitude to Dr Karin Meyer, Animal Genetics and Breeding Unit, University of New England, Armidale, Australia for using her DFREML unitrait programme. The assistance from Mr Adrian Thome, Bureau of Computer Services, University of Pretoria is also acknowledged. The authors also thank Dr G.J. Delport, Fleece Testing Centre, Grootefontein for the use of his BLUP programme.

A negative genetic trend for curl type was evident since 1972 (Figure 4). Theoretically, the relative strong change could have been expected as a result of the high heritability estimate for this trait, but it could also have been partly due to a correlated response ($r = -0.07$) as a result of directional selection on maximum values for hair quality score. The genetic trend for pattern score (Figure 5) was positive. It suggested an annual increase of 0.011 score units for the period of investigation. The same applied to hair quality score (Figure 6) with an annual increase of 0.013 score units during the period of investigation. The sharp increase since 1977 was brought about by the ram CLX1342, born in 1973, which produced 563 offspring in this flock. This ram had a PBV of 0.379 for hair quality score. There was also a relatively sharp increase in genetic improvement for pattern score since 1975, which was probably caused by the same ram, which had a PBV of 0.259 for pattern score. It is interesting that, in both cases, hardly any further progress has been made since 1978 when the ram was sold.

Conclusions

Although computationally demanding, an individual animal REML model provides heritability estimates by using all available data in a flock in which directional selection has been practiced for many years. In this study an unexpected low heritability was evident for hair quality score, which could have been attributed to inaccurate subjective assessment of the trait. An unexpected moderate negative correlation was obtained between pattern score and hair quality score. These unexpected parameters underline the need for flock-specific parameters as a pre-requisite in the design of appropriate breeding programmes.

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The authors express their gratitude to Dr Karin Meyer, Animal Genetics and Breeding Unit, University of New England, Armidale, Australia for using her DFREML unitrait programme. The assistance from Mr Adrian Thome, Bureau of Computer Services, University of Pretoria is also acknowledged. The authors also thank Dr G.J. Delport, Fleece Testing Centre, Grootefontein for the use of his BLUP programme.

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