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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 ± 0.002) and hair quality score (b = 0.013 ± 0.001).

Oorerflikheidsberamings is verkry deur van 'n afgeleide-vrye dieremodel REML-program met 'n enkeleienskap gebruik te maak. Oorerflikheidsberamings vir krultipe (h^2 = 0.46) en patroonpunt (h^2 = 0.27) was soos verwag uit bestaande literatuur. Die beraming vir haarkwaliteitspunt (h^2 = 0.14) was egter laer as verwag. 'n Onverwagte negatiewe korrelasie (r = −0.37) is tussen patroonpunt en haarkwaliteitspunt aangetoon, soos beraam deur middel van enkelvoudige korrelasie van individuele voorspelde teelwaardes (VTW's) tussen eienskappe. Omgewingstendense is beïnvloed deur veranderinge in die stelsel van puntetoekenning aan die subjektief-beoordeelde eienskappe, wat moontlik op die sensitiwiteit van die prosedure dui. 'n Positiewe genetiese tendens is vir beide patroonpunt (b = 0.011 ± 0.002) en haarkwaliteit (b = 0.013 ± 0.001) aangetoon.

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 (Sorenson & 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 4746 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 × 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 it was assumed that the fixed effects were uncorrelated.

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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 (Sorenson & 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} = the individual observation for the appropriate trait,

μ = the population mean for the appropriate trait,

A_i = the fixed effect of the ith year of birth (1968 — 1983),

B_j = the fixed effect of the jth season of birth, with levels for summer- and winter-born lambs respectively. Ewes were mated within fixed mating seasons which ranged from 1 December to 28 February, and from 15 April to 15 August,

C_k = the fixed effect of the kth dam age group (2 to 10 years of age),

D_l = the fixed effect of the lth sex of lamb,

Z_m = the random genetic (breeding value) effect of the mth animal (number of animals = 5 788), and

e_{ijklm} = the random error.

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

$$\underline{y} = X_1\underline{b}_1 + X_2\underline{b}_2 + X_3\underline{b}_3 + X_4\underline{b}_4 + Z\underline{u} + \underline{e}$$

where

$\underline{y}$ = a vector of 4 746 observations,

$\underline{b}_i$ = vectors of unknown fixed effects for year of birth, season of birth, age of dam and sex of lamb respectively (b_1 — b_4),

X_i = known incidence matrices relating the records to fixed effects (b_i) (X_1 — X_4),

$\underline{u}$ = vector of all unknown random effects fitted which represent breeding values of the animals,

Z = known incidence matrix relating the records to the unknown random effects (u), and

$\underline{e}$ = 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 by Meyer (1989). The convergence criterion was set at 0.1×10^{-9} and was reached after 10 iterations for the three traits. The number of likelihoods evaluated were 24, 27 and 26 for the three traits curl type, pattern score and hair quality score respectively. The programme does not, however, present individual predicted breeding values of animals. Solutions for the fixed effects (generalized least squares) are presented and discussed.

Variance component estimates obtained from this derivative-free REML programme were subsequently used to determine genetic trends by fitting the following linear mixed model:

$$\underline{y} = X_1\underline{b}_1 + X_2\underline{b}_2 + Z\underline{u} + \underline{e}$$

where

$\underline{y}$, $\underline{u}$, Z and $\underline{e}$ are as previously defined, and

$\underline{b}_1$ = a vector of unknown fixed effects other than birth years and fitted as combined effects, *i.e.* age of dam, season of birth and sex of lamb,

$\underline{b}_2$ = a vector of unknown birth year effects,

X_1, X_2 = incidence matrices of fixed effects.

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 1 Means ($\bar{X}$), standard deviations (*SD*), coefficients of variation (CV%) and Pearson's coefficient of skewness for the three traits recorded (*n* = 4746)

	Trait		
	Curl type	Pattern score	Hair quality score
$\bar{X}$	3.86	5.60	6.89
SD	1.26	0.92	0.74
CV%	32.54	16.41	10.72
Skewness	0.69	0.65	−0.16

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.

Table 2 Variance components and heritability (h^2) estimates of the three traits recorded

	Trait		
	Curl type	Pattern score	Hair quality score
Phenotypic variance (σ_p^2)	1.58	0.84	0.55
Additive genetic variance (σ_a^2)	0.73	0.23	0.08
Error variance (σ_e^2)	0.85	0.62	0.47
h^2	0.46	0.27	0.14
Other studies[a]			
Range in h^2 estimates	0.25—0.77	0.02—0.39	0.12—0.49
Median value	0.51	0.20	0.31

[a] Estimates taken from Yao *et al.* (1953), Malan (1959), Nel (1966), Federson (1968), Van Niekerk *et al.* (1968), Van Niekerk (1972), Botma (1981), Greeff *et al.* (1991a).

Estimates of heritability for pattern score varied according to the cited literature from 0.02 to 0.39 with a median value of 0.20, which is lower than the present value of 0.27. Contrary to the heritability for pattern score, the median value of heritabilities for hair quality score (which varied from 0.12 to 0.49) is 0.31.This value is higher than the present estimate of only 0.14. The low heritability as well as the low coefficient of variation (10.72%) for hair quality score, which may have been the result of the inaccuracy of subjective evaluation, indicates limited scope for genetic improvement in this trait. It also applies, to a lesser degree, to pattern score. The low heritability for hair quality score also may have resulted from a reduction in the additive genetic variance (Table 2) as a result of long-term directional selection. On the other hand, Albertyn *et al.* (1991) suggested a departure from linearity in the scale of evaluation for hair quality. It is not evident what the contribution of such departure from linearity could have been towards a possible decreased heritability estimate.

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

Traits	Present study[a]	Genetic correlations[b]		
		Minimum	Maximum	Median
Curl type & pattern score	0.15	−0.55	0.77	0.11
Curl type & hair quality score	−0.22	−0.06	−0.55	−0.34
Pattern score & hair quality score	−0.37	−0.32	0.61	0.15

[a] Correlations obtained through simple correlations between individual breeding values.

[b] Published estimates of genetic correlations taken from Nel (1966), Federson (1968), Van Niekerk *et al.* (1968), Van Niekerk (1972), Botma (1981), Greeff *et al.* (1991a).

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.

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_g = −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

	Traits		
Fixed effects	Curl type	Pattern score	Hair quality score
Age of dam (years)	***	***	***
2	−0.26	0	0.05
3	−0.06	0.04	0.03
4	−0.06	0.11	−0.06
5	0.12	0	−0.14
6	0.13	0.02	−0.15
7	0.31	0.09	−0.21
8	0.28	−0.05	−0.18
9	0.39	−0.19	−0.16
10	0.23	−0.28	−0.27
Season of birth	***	***	***
Summer	−0.35	−0.13	0.13
Winter	0	0	0
Sex of lamb	*	***	NS[a]
Rams	0	0	0
Ewes	0.11	−0.11	0.19

[a] Non-significant (P > 0.05).

* $P \leq 0.05$; *** $P \leq 0.001$.

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.

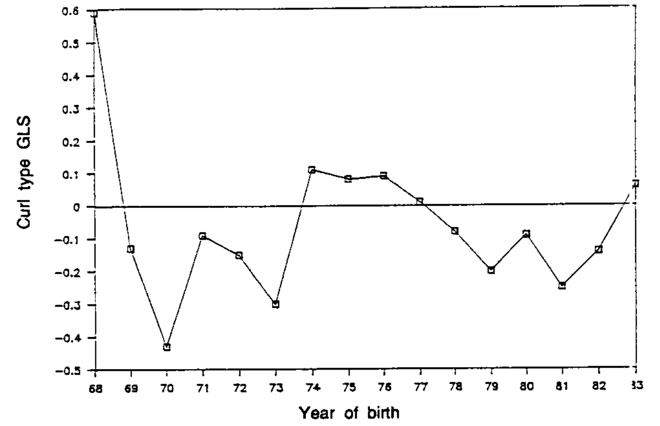

Figure 1 Generalized least squares by year of birth for curl type.

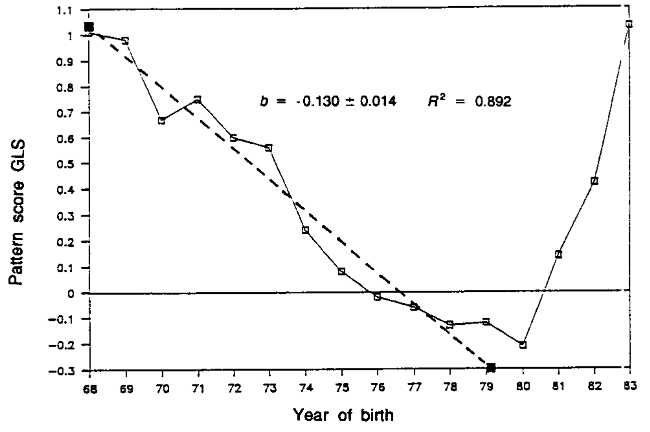

Figure 2 Generalized least squares by year of birth for pattern score.

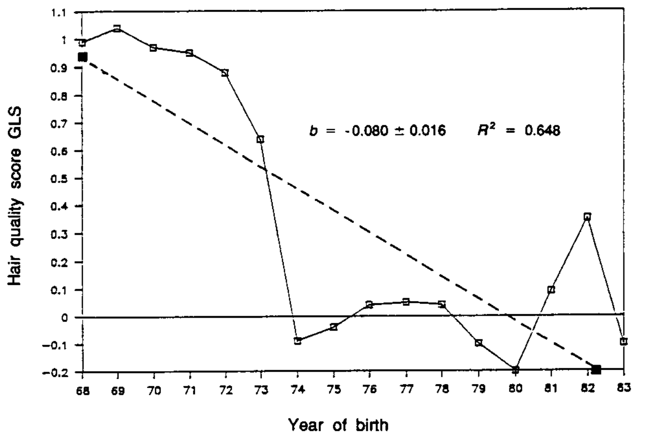

Figure 3 Generalized least squares by year of birth for hair quality score.

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.

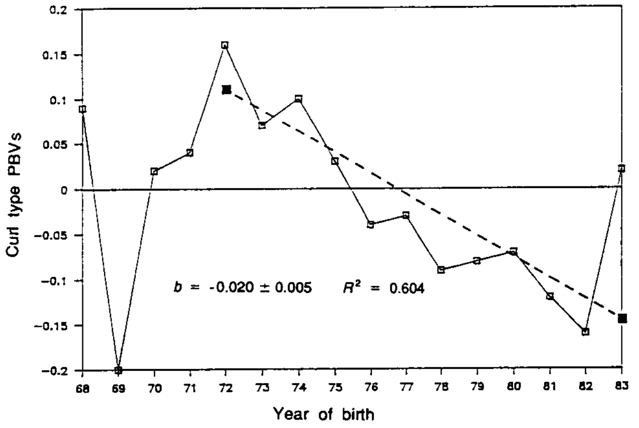

Figure 4 Genetic trend for curl type.

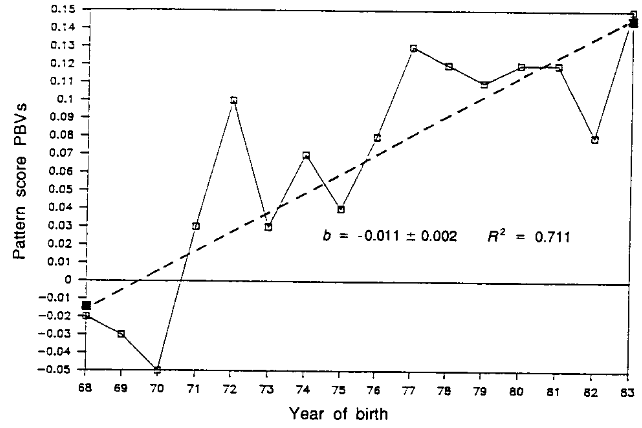

Figure 5 Genetic trend for pattern score.

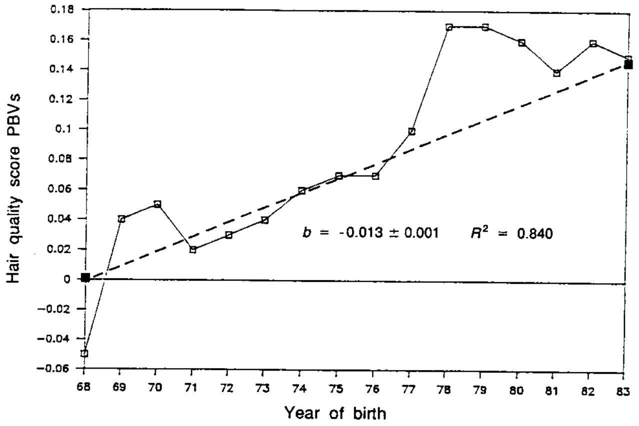

Figure 6 Genetic trend for hair quality score.

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 ($r = -0.22$) 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.

Mixed model methodology provides accurate solutions for fixed effects. In this study the influence of the inconsistency of subjective evaluation and changes in the score allocation procedure was illustrated. The full implications of subjective assessment of quantitative traits on genetic parameters as well as genetic trend is not quite clear. The consequences may even vary between flocks. However, irrespective of the above-mentioned, a low heritability for hair quality score and an undesirable correlation between pattern score and hair quality score, substantial genetic progress was made in this flock. The contribution of a single outstanding sire to genetic improvement in a relatively small flock, illustrates the effect a single outstanding sire can have on an entire flock.

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