

Genetic trends of selection for pelt traits in Karakul sheep

II. Correlated responses

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Correlated responses of curl development, hair quality, hair thickness, hair stiffness, hair length, lustre and pattern to selection for an increase in pattern and hair quality and a decrease in hair length and curl development were determined with mixed model methodology in a single trait selection experiment with Karakul sheep. No unfavourable genetic associations between pelt traits were found. The genetic relationship between pattern and hair quality was small and insignificant, which implies that pattern and hair quality can be improved together. A decrease in curl development resulted in an accompanying decrease in pattern. Selection for shorter hair resulted in an increase in pattern and *vice versa*. In most cases the correlations between relative breeding values were in the same direction and did not differ greatly from the estimated genetic correlations. The correlation of hair quality and its components, i.e. hair stiffness and hair thickness with some of the other pelt traits, differed from the estimated parameters. Mixed model methodology made it possible to detect more subtle correlated responses that would otherwise not have been possible.

Gekorreleerde responsies van krulontwikkeling, haarkwaliteit, haardikte, haarstyfte, haarlengte, glans en patroon vir seleksie vir 'n toename in patroon en haarkwaliteit en 'n afname in haarlengte en krulontwikkeling is met behulp van gemengde model metodologie in 'n enkelkenmerk seleksie-eksperiment by Karakoelskape bepaal. Geen ongunstige genetiese verwantskappe is tussen pelskenmerke gevind nie. Die genetiese verwantskap tussen patroon en haarkwaliteit is klein en onbelangrik, wat impliseer dat patroon en haarkwaliteit gelyktydig verbeter kan word. 'n Afname in krulontwikkeling het tot 'n afname in patroon gelei. Seleksie vir korter haar het patroon laat afneem en omgekeerd. Die korrelasies tussen relatiewe teelwaardes was in die meerderheid gevalle in dieselfde rigting en het nie veel van die beraamde genetiese korrelasies verskil nie. Die korrelasie van haarkwaliteit en sy komponente, haarstyfte en haardikte met die ander pelskenmerke het van die beraamde genetiese korrelasies verskil. Gemengde model metodologie het dit moontlik gemaak om klein gekorreleerde responsies te bepaal waar dit andersins nie moontlik sou gewees het nie.

Keywords: Correlated responses, pelt traits, selection, Karakul sheep.

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Introduction

Knowledge of the direction and degree of genetic correlations is important in formulating efficient breeding plans. Genetic correlations between pelt traits in Karakul sheep have been estimated by Malan (1959), Nel (1967), Van Niekerk *et al.* (1968), Van Niekerk (1972), Botma (1981) and Greeff *et al.* (1991a). Apart from Botma (1981) and Greeff *et al.* (1991a), each of these researchers worked with a Karakul population which had been subjected to selection for certain pelt traits. As selection changes the gene frequencies of characteristics in a population, the published results may not represent generally acceptable estimates (Falconer, 1989).

The two most important pelt traits affecting pelt price are pattern and hair quality. Schoeman (1984) stated that one of the most surprising features of genetic and phenotypic parameters of pelt traits is the discrepancy in the estimates reported in the literature concerning the association between these two traits. Schoeman & Albertyn (1991) indicated that published genetic correlation estimates between hair quality and pattern vary between -0.32 to 0.61, with the majority of

the estimates close to zero. In an attempt to clarify the genetic association between pelt traits, a single trait selection experiment for hair quality, pattern, hair length and curl development was initiated in 1970. The direct responses to selection were published by Greeff *et al.* (1993). This paper reports on the correlated responses in pelt traits.

Material and Methods

The management and selection procedures employed during the experiment have been described by Greeff *et al.* (1993). Subjective scores for pelt traits were allocated by one person only during the whole experiment according to the methods of Nel (1967), as described by Greeff *et al.* (1991b).

Statistical analysis

The statistical analysis was similar to that applied by Greeff *et al.* (1993). Genetic trend for each trait was calculated as the average breeding values for that trait within years. The product-moment correlation between predicted breeding values

(PBV) of two traits, which approximates a genetic correlation, was calculated. The correlated response was estimated as the regression of the cumulative correlated response of a trait not under selection on the cumulative selection differential of the selected trait (Falconer, 1989).

Results and Discussion

The observed correlated responses in pelt traits with selection for a decrease in hair length, an increase in pattern, an increase in hair quality and a decrease in curl development are illustrated in Figures 1 to 4. The direct responses are also shown for comparison. Table 1 indicates correlated responses and Table 2 the correlations between the PBVs for the different selection lines.

Hair length

Figure 1 indicates that selection for a decrease in hair length resulted in a highly significant ($P < 0.001$) correlated decrease in curl development which was in the same direction and of the same degree as the direct response. This agrees with the results of Botma (1981) and Nel (1967) that a decrease in hair

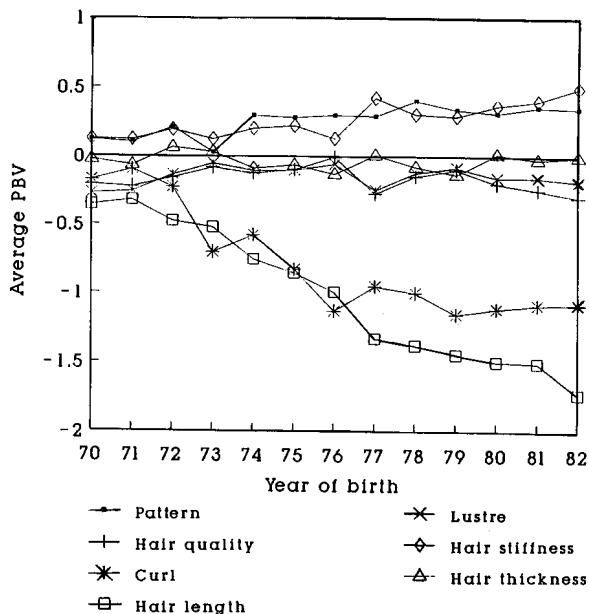


Figure 1 Correlated responses in pelt traits with selection for shorter hair.

length reduces curl development. This positive association between these two traits is reflected by a positive correlation of 0.38 (Table 2) between their PBVs, which resulted in a correlated decrease of 0.49 ± 0.08 units in curl development per unit selection pressure applied. This large correlated response is probably due to the high realized heritability of 0.56 for curl development (Greeff *et al.*, 1993).

Pattern showed a significant ($P < 0.01$), but slight improvement of -0.12 ± 0.03 units. This confirms the negative correlation of -0.32 between PBVs and the genetic correlations reported by Nel (1967) and Van Niekerk (1972), who stated that selection for shorter hair would lead to an improvement in pattern. This improvement will, however, only be temporary as a further reduction in hair length will probably cause pattern to deteriorate.

Hair stiffness also showed a small, but significant ($P < 0.01$) correlated response of -0.144 ± 0.036 units (Table 1) which resulted in an increase in hair stiffness (Figure 1). As hair quality was closely associated with hair stiffness ($r = -0.72$; Table 2) in this selection line, one would have expected a correlated response in hair quality. However, no trend could be noticed in any of the other pelt traits. This is contrary to the results of Nel (1967), Van Niekerk (1972) and Botma (1981), who stated that hair quality should decline with a shortening in hair length. This study showed a non-significant correlated response of only 0.007 units, which implies that hair quality can be improved without changing hair length. The 'realized' correlation between the PBV of hair length and hair quality was, in all the selection lines, lower than the genetic correlation of 0.45 estimated in the control flock. This is an indication that the genetic association between these two traits is not very strong and that good hair quality can be obtained with short hair.

Pattern

Figure 2 indicates that selection for an improvement in pattern resulted in hair length initially showing a sharp decrease from 1971 until 1973, after which it stabilized. In 1979 a small increase in hair length coincided with a similar decrease in the genetic trend for pattern. It would thus appear that the optimum hair length was reached in 1973 for the type of pattern which was desired. If hair length had decreased any further, pattern would probably have deteriorated. The observed negative correlations between the PBVs of pattern with hair length

Table 1 Correlated responses (\pm SE) for single trait selection for pelt traits

Pelt traits	Selection line			
	Hair length (-)	Pattern (+)	Hair quality (+)	Curl development (-)
Hair length	-	$-0.05 \pm 0.019^*$	0.06 ± 0.036	-0.02 ± 0.022
Pattern	$-0.12 \pm 0.033^{**}$	-	$0.10 \pm 0.019^{***}$	$0.33 \pm 0.034^{***}$
Hair quality	0.01 ± 0.037	-0.03 ± 0.014	-	$-0.06 \pm 0.021^{**}$
Curl development	$0.49 \pm 0.081^{***}$	0.03 ± 0.019	$-0.31 \pm 0.088^{**}$	-
Lustre	-0.05 ± 0.028	-0.03 ± 0.016	$0.28 \pm 0.023^{**}$	-0.03 ± 0.024
Hair stiffness	$-0.14 \pm 0.036^{**}$	$0.08 \pm 0.010^{***}$	$-0.11 \pm 0.019^{***}$	$0.15 \pm 0.018^{***}$
Hair thickness	-0.01 ± 0.026	$0.04 \pm 0.008^{***}$	$-0.08 \pm 0.024^{**}$	$0.07 \pm 0.013^{***}$

* Significant at $P < 0.05$; ** significant at $P < 0.01$; *** significant at $P < 0.001$.

Table 2 Correlation between PBVs of pelt traits within selection lines

Correlated traits	Selection line					
	Control ¹		Hair length	Pattern	Hair quality	Curl development
	1	2	(-)	(+)	(+)	(-)
Pattern with						
Hair quality	0.146	0.20	0.038	-0.109	0.116	-0.088
Curl development	-0.184	-0.39	0.070	0.057	0.147	0.694
Hair length	-0.348	-0.42	-0.321	-0.358	-0.209	-0.260
Lustre	0.169	0.32	0.101	-0.104	0.043	-0.035
Hair stiffness	0.075	0.01	0.143	0.377	0.229	0.684
Hair thickness	-0.035	0.22	-0.083	0.191	0.052	0.332
Hair quality with						
Curl development	-0.314	-0.22	-0.266	-0.338	-0.351	-0.215
Hair length	0.255	0.45	0.231	0.239	0.244	0.188
Lustre	0.898	0.91	0.884	0.902	0.893	0.885
Hair stiffness	-0.659	-0.64	-0.718	-0.664	-0.439	-0.327
Hair thickness	-0.324	-0.58	-0.461	-0.434	-0.265	-0.302
Curl development with						
Hair length	0.129	0.11	0.375	0.201	0.165	0.026
Lustre	-0.288	-0.23	-0.231	-0.289	-0.368	-0.158
Hair stiffness	0.248	0.31	0.201	0.321	0.444	0.600
Hair thickness	-0.037	-0.20	0.124	0.204	0.177	0.215
Hair length with						
Lustre	0.237	0.36	0.142	0.214	0.279	0.204
Hair stiffness	-0.374	-0.49	-0.462	-0.286	-0.149	-0.351
Hair thickness	0.168	-0.25	0.074	0.183	0.290	0.095
Lustre with						
Hair stiffness	-0.636	-0.48	-0.632	-0.640	-0.546	-0.296
Hair thickness	-0.328	-0.48	-0.459	-0.432	-0.301	-0.309
Hair stiffness with						
Hair thickness	0.455	0.35	0.492	0.545	0.440	0.491

¹ Control 1 signifies the correlations between PBVs; Control 2 signifies the estimated genetic correlations with a HS analysis (Greff *et al.*, 1991a).

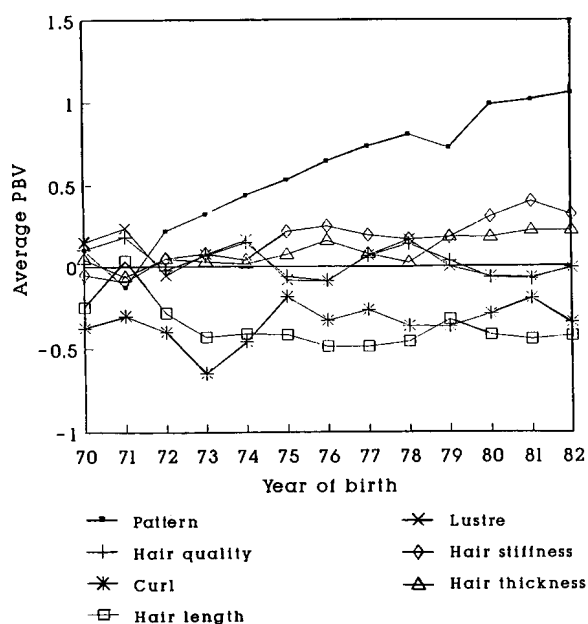


Figure 2 Correlated responses in pelt traits with selection for an increase in pattern.

in all the selection lines (Table 2), confirm the negative genetic association between them. These values are, however, slightly lower than those reported by Nel (1967), Van Niekerk (1972) and Botma (1981).

Highly significant ($P < 0.001$) correlated responses were recorded for hair stiffness and hair thickness while selecting for an increase in pattern. These changes were, however, very small, as illustrated in Figure 2. Hair stiffness showed a slightly larger response of 0.08 units compared to 0.04 units for hair thickness per unit selection pressure applied for pattern. These results imply a positive genetic correlation between these two traits and pattern which was confirmed by the correlations of 0.38 and 0.19, respectively, between their PBVs (Table 2).

The increase in hair stiffness and hair thickness would suggest a possible deterioration in hair quality in this selection line. Van Niekerk (1972) thought that an increase in pattern would lead to a decrease in curl size which would result in a decrease in hair quality. Botma (1981) reported a definite decrease in hair quality in both ram and ewe lambs from 1970 until 1977 in this selection line. This study indicated (Table 1) a small decrease of -0.03 ± 0.014 units in hair quality per

unit selection pressure applied for pattern. This trend was only significant at the 9% level which was probably caused by the low correlation of -0.11 between their PBVs. Figure 2 illustrates this trend very clearly by showing that hair quality oscillated around the zero line. This also confirms the conclusion of Schoeman & Albertyn (1991) that the genetic correlation between hair quality and pattern is low and not important. Lustre showed the same trend as hair quality, while curl type and hair length stayed reasonably the same over the whole period.

Hair quality

Selection for an increase in hair quality resulted in highly significant ($P < 0.01$) correlated responses in pattern, curl development, lustre, hair stiffness and hair thickness (see Table 1). Only hair length did not change significantly.

As in Figure 2, the close association between lustre and hair quality is again illustrated in Figure 3. This association was noticed in all selection lines as indicated by the high correlation between their PBVs of approximately 0.89 in all selection lines (Table 2). As hair quality had already reached a high level, it might not have been possible to distinguish between the different lustre types because of the subjective nature of the evaluation process.

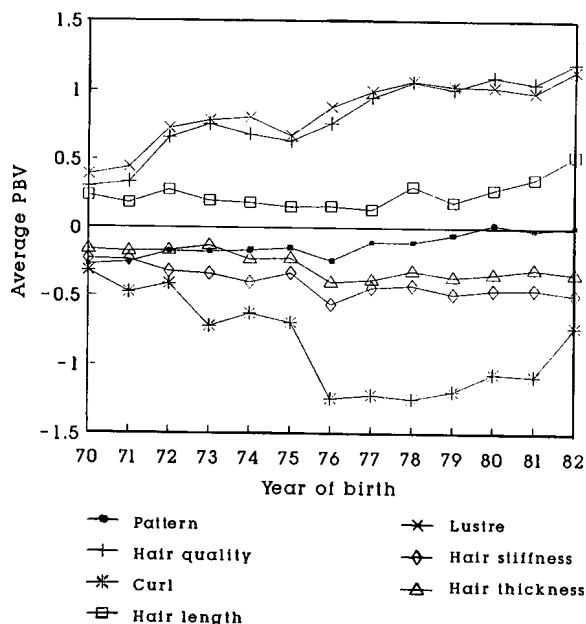


Figure 3 Correlated responses in pelt traits with selection for an increase in hair quality.

Figure 3 indicates that curl development decreased sharply until 1976 as a correlated response to selection for an improvement of hair quality. Although significant correlated responses were observed over the whole experimental period, as indicated by the correlated responses shown in Table 1, Figure 3 also indicates that the observed correlated responses changed from 1977. From 1970 up to 1976, pattern, hair length, hair stiffness and hair thickness remained virtually constant, but from 1976 to 1982, these traits showed an increased correlated response from 0.05 ± 0.02 to 0.25 ± 0.07 for pattern, -0.01 ± 0.03 to 0.50 ± 0.12 for hair length, -0.12 ± 0.04 to 0.06 ± 0.08 for hair stiffness and $-0.06 \pm$

0.05 to 0.09 ± 0.05 for hair thickness per unit selection pressure applied. Curl development showed the largest increase from -0.27 ± 0.13 during the first seven years to 0.69 ± 0.15 for the last six years.

The simultaneous changes in correlated response of pelt traits to selection for an increase in hair quality in 1977, indicate that these trends are not only a simple correlated response and that other factors may have been involved. An explanation could lie in the selection of breeding animals. From 1970 until 1976 one manager (A) was in charge of the experiment, whereas from 1977 another manager (B) took responsibility. The change in management coincided with the change in direction in the correlated traits. It would thus appear that manager A or manager B, knowingly or unknowingly, took some of the other pelt traits into consideration in the selection of breeding animals. This incident agrees with a similar incident described by Olivier (1989) in Merino sheep. This trend also shows that an improvement of hair quality does not necessarily imply a deterioration in curl development.

Curl development

Selection for a decrease in curl development resulted in a significant ($P < 0.01$) correlated response in pattern, hair quality, hair stiffness and hair thickness. Relative to the other selection lines, the correlated responses in pelt traits in this line were much greater. Only lustre and hair length did not show a significantly correlated response. As in the other selection lines, lustre followed the same trend as hair quality. Because of the higher and lower means in the first and last two years, its correlated response was, however, not significant. In the case of hair length, it showed a sharp initial decrease after which it increased again until 1981, causing this trend to be insignificant over the whole experimental period. This is contradictory to the response obtained for selection for shorter hair. A possible explanation might be that estimating hair length from a smooth pelt is probably easier and more accurate than estimating hair length from a curly pelt, which could have resulted in a concurrent decrease in curl development. In the case of selecting for a decrease in curl development, hair length should not play any part in scoring the smoothness of the pelt.

Pattern showed the largest correlated response which was in the same direction as curl development and it agrees with the findings of Botma (1981). This is, however, contrary to what was expected from the estimated genetic correlation of -0.39 between pattern and curl development (Greeff *et al.*, 1991a) and the negative correlation of -0.18 between their PBVs in the control flock. However, with a smoother pelt such as the galliac and watersilk types, it is to be expected that pattern would eventually decrease. This conclusion is supported by the high observed correlation of 0.69 between the PBVs of pattern and curl development in this selection line which is also much higher than that in the other selection lines. Selection for a decrease in curl development led to a change in correlation between the PBVs of curl development with pattern from a negative value to a highly positive value. This is not uncommon, as theory predicts that selection will change the gene frequencies (Falconer, 1989). Brown & Turner (1968) also reported a change in genetic correlation between

fibre density and clean wool weight in Merino sheep selected for clean wool weight.

Selection for less curl development resulted in a small, but significant correlated increase in hair quality over the whole experimental period. However, Figure 4 shows that as curl development decreased, hair quality steadily increased but only until 1977. After 1977 hair quality decreased slightly. This change in correlated response for hair quality coincided with a decrease in hair stiffness and hair thickness as curl development decreased. Hair stiffness exhibited a response twice as great as that of hair thickness, i.e. 0.15 ± 0.02 compared to a response of only 0.07 ± 0.01 for hair thickness. As the genetic correlation of hair quality with hair stiffness and hair thickness was negative (Table 2), a decrease in hair stiffness and hair thickness would result in softer hair with a consequent increase in hair quality. Figure 4 indicates that hair stiffness and hair thickness decreased from 1977 with a relative sharp decrease in hair stiffness, while hair quality, contrary to expectation, showed a slight decline during the same period. These changes in correlated response might also have been caused by the change in management in 1977.

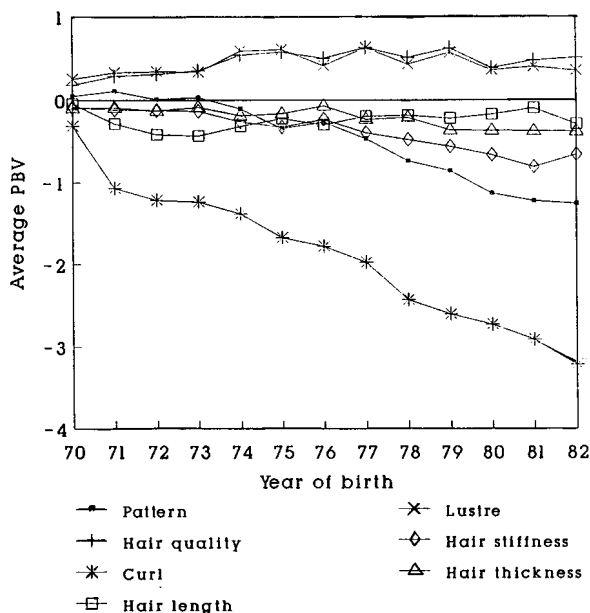


Figure 4 Correlated responses in pelt traits with selection for a reduction in curl development.

Conclusion

This study indicated that unfavourable genetic associations between pelt traits are relatively unimportant. The most important association, i.e. between pattern and hair quality, was small and insignificant, and implies that pattern and hair quality can be improved together. A decrease in curl development would result in an accompanying decrease in pattern but, as curl development would in practice never be reduced to the same extent as in the selection line for a decrease in curl development, this will not be a serious problem. Selection should rather be directed to an increase in pattern and to eradicate the undesirable types which may influence hair quality. This agrees with the conclusion of Le Roux (1979) who suggested that selection should be directed towards a certain curl type with the emphasis on hair quality and lustre

in particular. Traits such as curl size and hair length should be allowed to find their own intermediate optimum.

Selection for shorter hair resulted in an increase in pattern and *vice versa*. However, as progress is made for shorter hair, and curl development decreases as a correlated response, it can be expected that pattern will eventually decrease because of the strong decrease in pattern with selection against curl development.

The changes in correlated responses in curl development, while selecting for hair quality, indicate the risk of selecting for subjectively evaluated traits. Erasmus (1988) stated that in subjective selection with Merino sheep, the trait in question is not necessarily directly evaluated, but rather components thereof. Furthermore, various authors have shown that slower genetic progress is made through subjective scoring than objectively measured traits, as the increased environmental variance of subjectively scored traits reduces the accuracy of selection. With Karakul sheep, however, there is no alternative but to evaluate pelt traits subjectively. The high responses obtained in this study especially for curl development, do not support the general contention that genetic progress in subjective traits is slower than in other production traits.

Although selection resulted in changes in genetic parameters of pelt traits, the 'realized genetic correlations' between relative breeding values were, in most cases, in the same direction and did not differ much from the estimated genetic correlations of Greeff *et al.* (1991a). Only in the case of the correlation of hair quality and its components, i.e. hair stiffness and hair thickness with some of the other pelt traits, were large differences recorded. This supports the theory that selection can change the gene frequencies of these traits with a resulting change in genetic correlation (Falconer, 1989).

The discrepancies found between this study and that of Botma (1981) are most probably due to the differences in statistical techniques used. In general, however, his conclusions on the large correlated responses agree with the results of this study, but mixed methodology has made it possible to detect more subtle correlated responses than would otherwise have been noticed.

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