

Genetic trends of selection for pelt traits in Karakul sheep

I. Direct responses

J.C. Greeff* and A.S. Faure

Irene Animal Production Institute, Private Bag X2, Irene, 1675 Republic of South Africa

G.J. Minnaar

Karakul Research Station, P.O. Box 37, Upington, 8800 Republic of South Africa

S.J. Schoeman

Department of Animal Science, University of Pretoria, Pretoria, 0001 Republic of South Africa

Received 10 December 1991; revised 24 August 1992; accepted 13 April 1993

Genetic trends owing to selection for an increase in pattern and hair quality and a decrease in hair length and curl development in the Karakul were estimated with the Animal Model in four selection lines and in a control flock over 12 years (3.6 generations). The objective was, firstly, to determine whether the control flock remained genetically stable during the course of the experiment and, secondly, to determine the size of the additive genetic component of the phenotypic variance for pattern, hair quality, hair length and curl development. Results indicated that the control flock did not remain genetically stable as pattern and hair quality showed a small positive change, whereas curl development and hair length showed a small negative change. A mean annual response of 2.52%, 1.31%, 2.96% and 7.1% were obtained for selection for pattern, hair quality, hair length and curl development, respectively. Realized heritabilities were 0.20, 0.34, 0.63 and 0.56, respectively.

Genetiese tendense as gevolg van seleksie vir 'n toename in patroon- en haarkwaliteitswaardes en 'n afname in haarlengte en krulontwikkeling is met behulp van die Dieremodel in vier seleksielyne en in 'n kontrolekudde oor 12 jaar (3.6 generasies) beraam. Die doel van die studie was eerstens om te bepaal of die kontrolekudde geneties stabiel gedurende die eksperiment gebly het, en tweedens om die grootte van die additiewe genetiese komponent van die fenotipiese variasie vir patroon, haarkwaliteit, haarlengte en krulontwikkeling te bepaal. Resultate dui aan dat die kontrolekudde nie geneties stabiel gebly het nie aangesien patroon en haarkwaliteit 'n klein positiewe verandering, en krulontwikkeling en haarlengte 'n klein negatiewe verandering ondergaan het. Die gemiddelde jaarlikse responsie vir seleksie vir patroon, haarkwaliteit, haarlengte en krulontwikkeling was onderskeidelik 2.52%, 1.31%, 2.96% en 7.1%. Verhaalde oorerflikhede was onderskeidelik 0.20, 0.34, 0.63 en 0.56.

Keywords: Control flock, genetic trends, Karakul, pelt traits, selection.

* To whom correspondence should be addressed.

Introduction

In the Karakul industry, selection is based solely on subjective scores for pelt traits as no other method exists whereby pelt traits can be measured objectively. The effectiveness of selection based on traits measured subjectively in Merino sheep was questioned by Laubser (1961), Roux (1961) and Nel (1970) because of the generally low correlation between subjective scores and objective measurements. Therefore a selection experiment on economically important pelt traits in the Karakul was initiated to evaluate the genetic response to selection for subjectively evaluated pelt traits. Botma (1981) analysed the data up to 1977. He expressed genetic response to selection as deviations from a control flock. As he was unable to determine whether the control flock remained genetically stable, the responses may be misleading. It was therefore decided to re-analyse Botma's data along with a substantial amount of data collected since 1977, with mixed model methodology. This technique separates the total phenotypic variance into its genetic and environmental components to yield estimates of genetic variance and of selection response (Henderson, 1984; Sorensen & Kennedy, 1986). The non-

genetic factors which affect these traits have been discussed by Greeff *et al.* (1991a).

Materials and Methods

Experimental material

The experimental flock originated in 1962 from the purchase of 1200 Karakul ewes from 29 different breeders and was managed as discussed by Greeff *et al.* (1991a; 1991b).

In 1970 the animals were randomly divided into five different groups, i.e. a control group and four selection groups of about 200 ewes each, in such a way that the age structure of each group was approximately the same. Selection was applied for an increase in hair quality and pattern scores, and a decrease in hair length and curl development. These traits are considered by Nel (1967), Schoeman & Nel (1969) and Van Niekerk (1972) to be, economically, the most important pelt traits in the Karakul. Selection was largely concentrated on males. Approximately 40 ewes and four of the eight rams per selection line were replaced annually.

The fifth flock was kept as a control group on which no selection was applied. A random replacement procedure was

followed as discussed by Greeff *et al.* (1991b). In 1975 a large number of the rams which were kept for replacement purposes died owing to Pulpary kidney, and consequently only seven new rams were available for mating in the control flock. Some rams were used twice in consecutive years which resulted in a slight increase in the generation length. Although random mating was practised, care was taken to ensure that no matings occurred between closely related individuals in the control flock.

The dataset comprised a total of 12 511 records which were made up of 2 787 records of the hair length selection line, 2 406 records of the pattern selection line, 2 531 records of the hair quality selection line, 2 283 records of the curl development selection line and 2 504 records for the control flock.

Description of pelt traits

Lambs were evaluated for hair quality, pattern, hair length and curl development, as described by Greeff *et al.* (1991a), according to the methods described by Nel (1967). The subjective measurements consisted of scores between 1 and 10 for the different pelt traits.

Statistical analysis

For the prediction of genetic changes with BLUP technology, precise, unbiased estimates of genetic parameters in the base population are necessary. A Restricted Maximum Likelihood (REML) procedure was used to estimate genetic variance and covariance components for setting up the mixed model equations for best linear unbiased predictions (BLUP). This technique makes the best use of all the data, including information of the relatives, and takes selection or culling into account (Hill & Meyer, 1988).

For the estimation of variance components of curl development, hair quality, hair thickness, hair length, lustre, pattern and hair stiffness, data of the control flock were analysed with an Individual Animal Model (IAM) with the derivative-free, univariate REML computer program of Meyer (1989).

The number of levels of the factor age was reduced to three only, according to the results of Greeff *et al.* (1991a). The following model was used to obtain estimates of genetic variances:

$$Y_{ijklmn} = \mu + a_i + c_j + d_k + f_l + g_m + u_n + e_{ijklmn}$$

where Y_{ijklmn} = the observed value of a given dependent variable,

μ = the overall mean,

a_i = the fixed effect of the i^{th} year of birth, and $i = 1$ to 13,

c_j = the fixed effect of the j^{th} age of the dam, and $j = 1, 2$ or 3 where 1 represents ewes two years and younger, 2 = ewes 3 to 8 years of age, and 3 = ewes older than 8 years of age,

d_k = the fixed effect of the k^{th} sex of the lamb,

f_l = the fixed effect of the l^{th} season of measurement (birth), and $l = 1, 2$, or 3 where 1 represents January and February, 2 = March to August and 3 = September to December,

g_m = the fixed effect of the m^{th} type of birth,

u_n = the random effect of the n^{th} individual, and
 e_{ijklmn} = the random error.

The estimates of genetic variances were used as starting values for the estimation of breeding values by BLUP.

Breeding values were estimated using the PEST computer program of Groeneveld & Kovac (1990) and Groeneveld *et al.* (1990). All the groups were analysed together to obtain estimates of fixed and random effects with smaller sampling variances. The solutions were considered to be converged when a criterion of 0.0001 was reached. The model for the BLUP analysis was similar to the previous model used for the estimation of genetic variances.

Cumulative selection differentials

Cumulative selection differentials were calculated according to the method of Newman *et al.* (1973). Animals in the base population were given a zero value. Realized heritability was estimated as the regression of cumulative response on cumulative selection differential (Hill, 1972b).

Inbreeding

Inbreeding coefficients were calculated with the algorithm of Quaas (1976) with the derivative-free, univariate REML computer program of Meyer (1989).

Results and Discussion

Genetic stability of the control flock

Hill (1972a) indicated that a properly managed control flock is one where the number of animals which enter the flock each year and the age distribution of individuals in the flock should remain constant, or at least show little variation. Table 1 indicates the number of ewes, the number of rams used and the number of new rams brought into the control flock each year. It is clear that a large proportion of rams was replaced each year. In 1976 and 1978 all rams were replaced. The lowest replacement rate was in 1971 when only 23.9% of rams were replaced.

Table 1 Number of ewes which lambed and the number of rams used in the control flock per year

Year	No. of ewes	No. of rams	No. of new rams
1970	124	53	53
1971	174	46	11
1972	198	39	31
1973	163	37	15
1974	191	23	19
1975	218	14	6
1976	212	32	32
1977	249	20	17
1978	231	27	27
1979	243	41	27
1980	273	46	26
1981	222	45	30
1982	6	5	-
Total	2504	428	294

Figures 1 to 4 indicate the genetic trends for the selected traits in the control flock. The R^2 values give an indication of the accuracy of fit. Hill (1976) indicated that tests of significance on these R^2 values are not valid, as the values of the different generations are not independent. Such tests of significance may be too lenient. However, as no other suitable procedure exists, it was decided to use R^2 merely as an indication of which correlated responses deserve attention. With 13 values, a R^2 of 59% is needed for significance at the 10% level.

On the assumption that the initial heritabilities (Table 3) are correct it is clear that, although relatively small, significant ($P < 0.10$) genetic changes occurred in the control flock during the experiment for all the important pelt traits except for curl development. Hair quality and pattern exhibited a slight improvement, whereas hair length and curl development showed a decreasing trend. As the main functions of a control population are to ensure genetic stability over time, to measure

the effect of the environment on populations subjected to selection, and to serve as a gene pool with known parameters for use as base material in selection experiments (Gowe *et al.*, 1959), these changes will have an effect if the genetic response of selection lines is expressed as a deviation from the control flock. It is strange, however, that the changes were all in an advantageous direction. One would rather have expected these traits to deteriorate, following a period of selection similar to that which occurred in most stud flocks. One explanation might be found in the subjective method of evaluation. As genetic progress was made in the selection lines, a slight change in the scale of evaluation might have occurred, which resulted in the positive trends.

In an attempt to elucidate these changes, the cumulative selection differentials of hair quality, pattern, curl development and hair length of the control flock were also estimated. The cumulative selection differentials of these traits were also regressed on the year of birth and are given in Table 2. On the

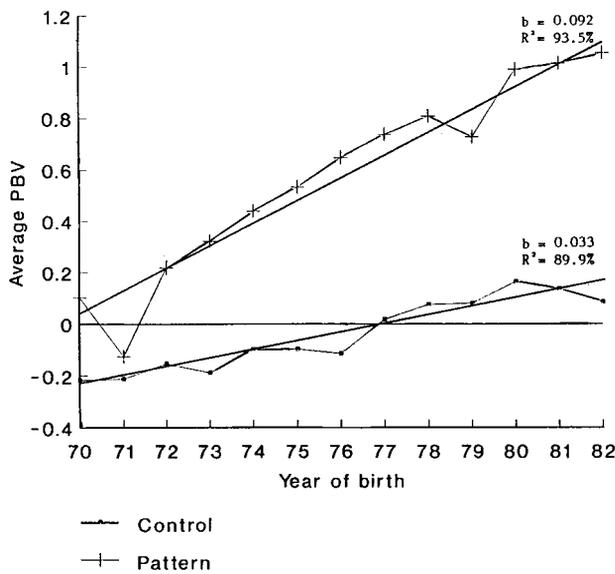


Figure 1 Genetic trend in pattern.

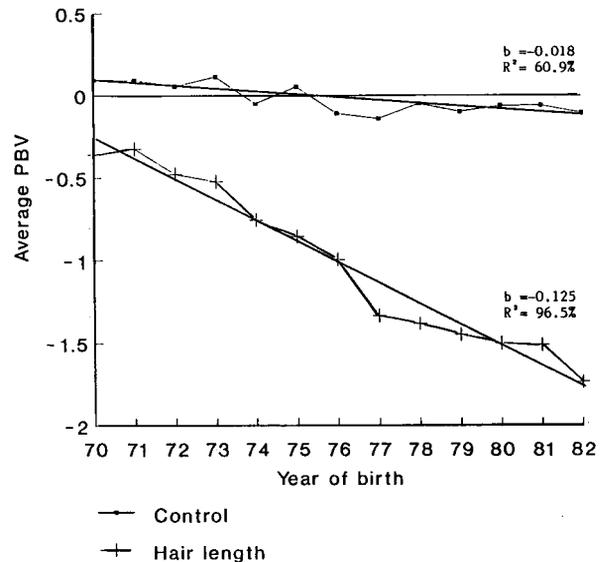


Figure 3 Genetic trend in hair length.

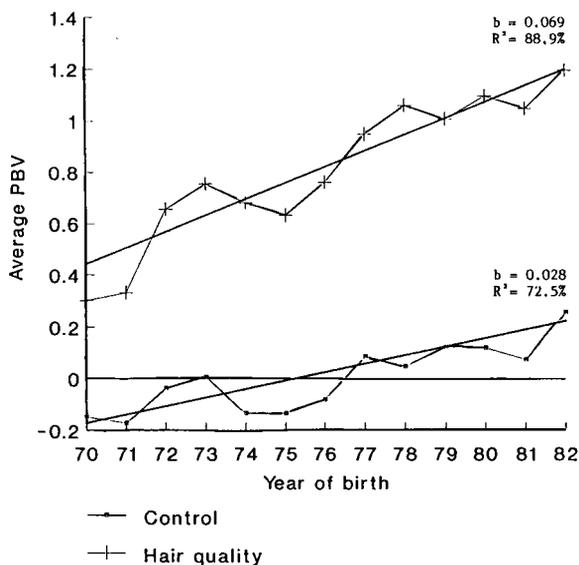


Figure 2 Genetic trend in hair quality.

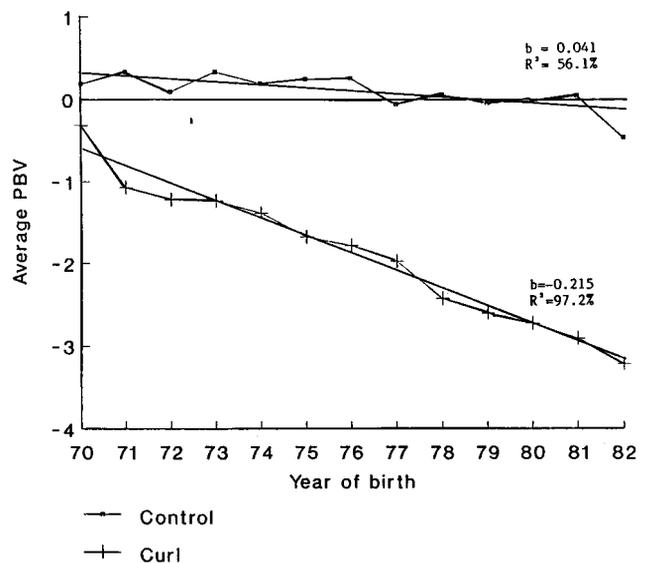


Figure 4 Genetic trend in curl development.

Table 2 Slopes of cumulative selection differentials of the selected traits in the control flock regressed against birth year

Trait	Slope \pm SE	R ² (%)
Pattern	-0.004 \pm 0.007	3.1
Hair quality	0.003 \pm 0.016	0.4
Curl development	-0.020 \pm 0.015	14.3
Hair length	-0.020 \pm 0.011	23.9

same basis as above, it is clear that none of the slopes differs significantly ($P < 0.10$) from zero, which implies that no selection pressure was applied on these traits.

Genetic trends in the selection lines

The heritability estimates obtained with the REML analysis of the control flock, which were used for the initial value for the estimation of predicted breeding values, are shown in Table 3.

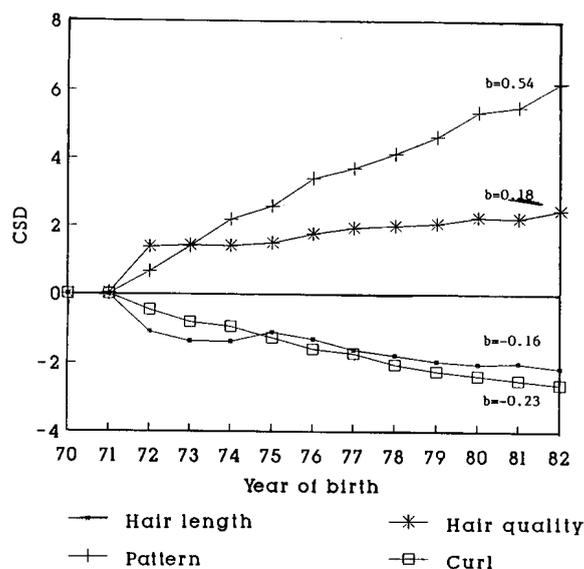
Table 3 Heritabilities estimated with REML in the control flock and the realized heritabilities (h^2_r) of pelt traits

Trait	h^2	h^2_r
Pattern	0.3271	0.207
Hair quality	0.3689	0.342
Curl development	0.6606	0.561
Hair length	0.3839	0.631

The genetic trends of pattern, hair quality, hair length and curl development of the selection lines and the control flock, expressed as the mean breeding value predicted per year of birth, are indicated in Figures 1 to 4.

It is clear that selection for pelt traits was effective. The relatively good fits are an indication of the linear trend observed and the consistency in visual evaluation of pelt traits. Curl development showed the highest annual response (7.11%), followed by hair length (2.96%), pattern (2.52%) and hair quality (1.31%). The responses obtained for curl development and hair length compare favourably with the results of Botma (1981). He reported an annual response of *ca.* 5% for curl development and *ca.* 2.8% for hair length. However, he reported a very weak response for pattern and hair quality. This may have resulted from the fact that he expressed response as a deviation from the control line. As the control line did not remain genetically stable and pattern and hair quality increased in the same direction as the selection line, this may account for the low responses that he obtained. The responses obtained in this study also compare well with the published result of between one and two per cent obtained in single trait selection experiments for objectively measured characteristics in the Merino (Turner, 1977; McGuirk, 1979; Heydenrych *et al.*, 1984a). The high response of 7.1% per annum for a decrease in curl development confirms the fast response that Nel (1967) obtained in developing a shallow curl type flock from a predominantly pipe curl type flock.

Differences in genetic response are also a function of differences in the amount of selection applied. As pelt traits were subjectively evaluated, it could be expected that the accuracy of selection would differ between traits. To compare the amount of selection applied to the different traits, the cumulative selection differential of each trait was divided by its phenotypic standard deviation. Figure 5 illustrates the standardized selection differentials and the slopes of the regression coefficients of the different selection lines.

**Figure 5** Standardized selection differentials of the different selection lines.

The largest amount of selection pressure applied was for pattern, followed by curl development, hair quality and hair length. This indicates that pattern and curl development may be evaluated fairly consistently. A sharp increase in response in hair quality and hair length was observed at the beginning, after which a steady linear response was followed. Intensity of selection for hair length decreased slightly in 1975, whereafter it increased again, probably owing to a large number of rams which died from Pulpy kidney during this year. It appears that only the selection line for hair length was affected by this incident.

Realized heritabilities

Realized heritabilities give an indication of the amount of additive genetic variance that traits exhibit. With mixed model methodology this heritability is, however, dependent upon the initial heritability needed by the BLUP techniques for the prediction of breeding values. Table 3 gives the realized heritabilities obtained by regressing the cumulative response of each trait against its cumulative selection differential.

Relatively accurate realized heritabilities were estimated as indicated by their respective small standard errors. Apart from hair quality and, to a certain extent, curl development, the realized heritabilities differed from the estimated heritabilities (Table 3). The realized heritability of pattern was 36% smaller, that of curl development 15% greater, and that of hair length, a massive 64% greater than their initial values. The phenotypic coefficient of variation for pattern of the base

population (control flock) and the selection line was exactly the same, viz. 29%. Between the other selection lines and the control flock, changes in the phenotypic coefficients of variation took place. The phenotypic coefficient of variation of the hair quality line was slightly less than that of the base population (24 to 21%), while that of the hair length line increased slightly (19 to 24%). The curl development line showed a large increase in the phenotypic coefficient of variation, from 33% in the base population to 49% in the selection line. This increased variation rendered selection more effective as a large component is due to genetic variation. The reasons for these discrepancies between the realized and estimated heritabilities, especially in the case of pattern and hair length, are unclear but again highlight the problems associated with estimating genetic parameters.

Inbreeding

Inbreeding may have had a significant effect on selection response. Figure 6 indicates the mean annual inbreeding coefficient of the different selection lines.

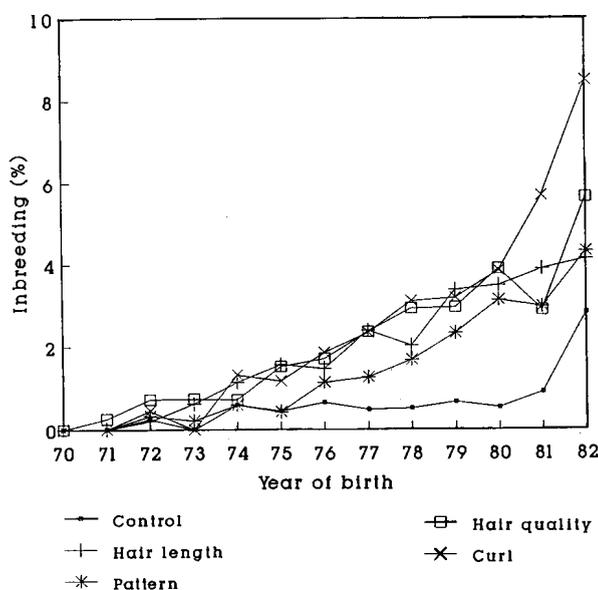


Figure 6 Mean annual inbreeding coefficient of the control flock and selection lines.

It is clear that the mean inbreeding coefficient of the selection lines increased faster than that of the control flock. This was to be expected because of the smaller effective population sizes of the selection lines owing to the smaller number of rams used when compared to the control flock.

Until 1981 the selection line for pattern had a slightly lower rate of inbreeding than the other three selection lines. From 1980, the mean inbreeding coefficient of the curl development line showed a sharp increase. The following year the same trend occurred in the hair quality line, the pattern line and in the control flock. However, the control flock produced only six offspring in 1982. Except for the curl development line in 1981 and 1982, and the hair quality line in 1982, the mean inbreeding coefficient of the selection lines was relatively low. It was doubtful whether such a low inbreeding coefficient would have a significant effect on pelt traits and it was therefore ignored.

Conclusions

Results from this study indicate that small genetic changes have occurred in the control flock during its 12 years of existence. These genetic trends were not observed by Botma (1981), but were clearly identified with mixed model methodology. This made it possible to make valid conclusions regarding genetic changes in pelt traits under selection.

If the process of the replacement of rams and ewes can be improved, this flock is ideally suited to evaluate the genetic status of flocks subjected to selection for pelt traits in a similar manner as the Tygerhoek Merino Control Flock is currently being used (Poggenpoel & Van der Merwe, 1987). Heydenrych *et al.* (1984b) are of the opinion that a central genetic control flock, used in this way, has its limitations especially with regard to genotype \times environmental interactions. Van Niekerk (1972) is also of the opinion that genotype \times environmental interaction may be important, but Turner & Young (1969) are of the opinion that such interactions may not be large, depending on the localities in which the flocks under comparison are located. As the Karakul is normally kept under extensive arid conditions and since the unborn lamb is largely buffered against unfavourable environmental conditions, this may not be a serious handicap in determining genetic differences between flocks.

The genetic trends observed indicate that selection for pelt traits can be relatively effective. Responses to selection compare favourably with objectively measured characteristics in other sheep breeds. Annual responses of between 1 and 3% were obtained for hair quality, hair length and pattern. A response of more than 7% per year was observed for selection for a decrease in curl development. It would have been interesting to establish whether selection for an increase in curl development would have yielded the same response. The relatively high responses obtained indicate that pelt traits can be evaluated fairly accurately.

Mixed model methodology can successfully be applied for subjectively evaluated pelt traits and offers large benefits to the Karakul industry. Karakul breeders have, in general, always concentrated on economically important pelt traits in their selection programmes. As the Karakul lamb is evaluated at birth, its breeding value, estimated from its own phenotypic value and from information of its relatives, can be available before the animal has reached sexual maturity. Prerequisites for the implementation of these techniques are performance records on pelt traits and accurate pedigrees. The higher accuracy of selection as well as the shorter generation interval will allow breeders to adapt quickly to changes in breeding objectives.

Acknowledgements

The authors thank the Director of the Orange Free State Region for making the data available. Mr. A. Thorne of the Bureau of Computer Service at the University of Pretoria is also thanked for his help in running the computer programs.

References

- BOTMA, W.D., 1981. Selection response in four pelt traits in the Karakul. M.Sc. Agric. treatise, Univ. of the Orange Free State, Bloemfontein.

- GOWE, R.S., ROBERTSON, A. & LATTEER, B.D.H., 1959. Environment and poultry breeding problems. 5. The design of poultry control strains. *Poult. Sci.* 38, 462.
- GREEFF, J.C., FAURE, A., MINNAAR, G.J. & SCHOEMAN, S.J., 1991a. Non-genetic factors affecting pelt traits in Karakul sheep. *S. Afr. J. Anim. Sci.* 21, 173.
- GREEFF, J.C., FAURE, A., MINNAAR, G.J. & SCHOEMAN, S.J., 1991b. Genetic and phenotypic parameters of pelt traits in a Karakul control flock. *S. Afr. J. Anim. Sci.* 21, 156.
- GROENEVELD, E. & KOVAC, M., 1990. A generalized computing procedure for setting up and solving mixed linear models. *J. Dairy Sci.* 73, 513.
- GROENEVELD, E., KOVAC, M. & WANG, T., 1990. Pest, a general purpose BLUP package for multivariate prediction and estimation. Vol. XIII. *Proc. 4th Wld Congr. Genet. Appl. Livest. Prod.*, Edinburgh, 23-27 July 1990.
- HENDERSON, C.R., 1984. Applications of linear models in animal breeding. Univ. Guelph, Italy.
- HEYDENRYCH, H.J., DU PLESSIS, J.J. & CLOETE, S.W.P., 1984a. Increasing the wool production of Merino sheep by direct and indirect selection. *Proc. 2nd Wld Congr. Sheep and Beef Cattle Breed.* Eds. Hofmeyr, J.H. & Meyer, E.H.H., Pretoria, 16-19 April.
- HEYDENRYCH, H.J., VOSLOO, L.P., DU PLESSIS, J.J. & MEISSENHEIMER, D.J.B., 1984b. Maintaining genetic stability in a control flock of South African Merino sheep. *S. Afr. J. Anim. Sci.* 14, 34.
- HILL, W.G., 1972a. Estimation of genetic change. I. General theory and design of control populations. *Anim. Breed. Abstr.* 40, 1.
- HILL, W.G., 1972b. Estimation of realised heritabilities from selection experiments. II. Selection in one direction. *Biometrics* 28, 767.
- HILL, W.G., 1976. Variation in response to selection. *Proc. Int. Conf. Quantit. Genet.* Ames, Iowa. p. 343.
- HILL, W.G. & MEYER, K., 1988. Developments in methods for breeding value and parameter estimation in livestock. In: Animal breeding opportunities. Proc. of a symposium organized jointly by the British Society of Animal Production and The British Poultry Breeders Roundtable. Durham, Sept. 1988.
- LAUBSER, F.X., 1961. Breeding improvement of SA Merino flocks. *Wool Grow.* April 1961, 7 (Afrikaans).
- MCGUIRK, B.J., 1979. Selection experiments in laboratory and domestic animals. Proc. of a Symposium held at Harrogate, UK. 21-22 July, 1979.
- MEYER, K., 1989. Restricted maximum likelihood to estimate variance components for animal models with several random effects using a derivative-free algorithm. *Genet. Sel. Evol.* 21, 317.
- NEL, J.A., 1967. Genetic studies in Karakul sheep. DSc.(Agric) thesis, Univ. of Stellenbosch, Stellenbosch.
- NEL, J.E., 1970. Subjective judging and the prediction of breeding value in Merino sheep. *Agroanimalia* 2, 145.
- NEWMAN, J.A., RAHNEFELD, G.W. & FREDEEN, H.T., 1973. Selection intensity and response to selection for yearling weight in beef cattle. *Can. J. Anim. Sci.* 53, 1.
- POGGENPOEL, D.G. & VAN DER MERWE, C.A., 1987. Selection response with index selection in three commercial Merino flocks. *S. Afr. J. Anim. Sci.* 17, 70.
- QUAAS, R.L., 1976. Computation of the diagonal elements and inverse of a large numerator relationship matrix. *Biometrics* 32, 949.
- ROUX, C.Z., 1961. Considerations for planning and execution of breeding plans suitable for woolled sheep. M.Sc.(Agric.) treatise, Univ. Stellenbosch, Stellenbosch (Afrikaans).
- SCHOEMAN, S.J. & NEL, J.A., 1969. The relative economic importance of Karakul pelt traits. *Agroanimalia* 1, 189.
- SORENSEN, D.A. & KENNEDY, B.W., 1986. Analysis of selection experiments using mixed model methodology. *J. Anim. Sci.* 68, 245.
- TURNER, H.N. & YOUNG, S.S.Y., 1969. Quantitative genetics in sheep breeding. Ithaca, New York, USA.
- TURNER, H.N., 1977. Australian sheep breeding research. *Anim. Breed. Abstr.* 45, 9.
- VAN NIEKERK, A.J.A., 1972. A study of breeding problems in the Karakul with special reference to the Niemöller flock. D.Sc.(Agric.) treatise, Univ. of the Orange Free State, Bloemfontein.