Maintaining genetic stability in a control flock of South African Merino sheep

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A genetic control flock of Merino sheep consisting of 160 ewes and 16 rams, was established in 1969 at the Tygerhoek Experimental Farm near Riviersonderend in the South Western Districts of South Africa. In 1976 it was extended to 200 ewes and 20 rams. Ewes are replaced by their second ewe lamb when it reaches joining age and rams are replaced yearly, by a randomly chosen son. Four body-mass and six wool traits of the offspring are measured every year. Random discrepancies between the means of whole progeny and replacement groups for the measured characters varied from 0 to 6,2 % over a period of 11 years, but was on average, roughly zero for individual traits over all years. Regression equations for trait means on time showed the following total changes from 1971 to 1981: Birth mass −23,4 %, 42-day body mass −8,9 %, 120-day body mass +4,7 %, 18-month body mass −1,7 %, greasy fleece mass −11,1 %, percentage clean yield +1,5 %, clean fleece mass −9,8 %, staple length +1,0 %, crimp frequency −1,5 % and fibre diameter −0,7 %. Only the regression for birth mass (−0,096 ± 0,01 kg/year) was significant. That the changes with regard to 42-day body mass and greasy and clean fleece mass were not caused by genetic drift, is indicated by the low increase in inbreeding of only 1,2 % over the 11 years covered in this report. It is concluded that genetic stability can be maintained in a Merino control flock of this size under practical conditions.
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'n Genetiese kontrolekudde van Merinoskape is in 1969 op die Tygerhoekproefplaas by Riviersonderend gestig met 160 ooie en 16 ramme. Dit is in 1976 uitgebrei tot 200 ooie en 20 ramme. Ooie word deur hulle tweede ooilam vervang wat teelouderdom bereik en ramme word jaarliks deur 'n lukraakverkose seun verplaas. Vier liggaamsmassa en ses wolkenmerke is jaarliks op die nageslag gemeet. Toevallig verkreë verskille tussen hele nageslag- en verplasingsgroep gemiddeldes t.o.v. die gemete kenmerke, het oor 'n 11 jaar periode gevarieer van 0 tot 6,2 %, maar was oor jare gemiddeld bykans 0 vir individuele kenmerke. Regressievergelykings vir gemiddeldes van kenmerke oor tyd toon die volgende totale veranderinge van 1971 tot 1981: Geboortemassa −23,4 %, 42-dae-massa −8,9 %, 120-dae-massa +4,7 %, 18-maande-massa −1,7 %, ruvagmassa −11,1 %, persentasie skoonopbrengs +1,5 %, skoonvagmassa −9,8 %, stapellengte +1,0 %, kartelfrekwensie −1,5 % en veseldikte −0,7 %. Slegs die regressie t.o.v. geboortemassa (−0,096 ± 0,01 kg/jaar) was betekenisvol. Dat die veranderinge t.o.v. 42-dae-massa, ruvagmassa en skoonvagmassa nie deur genetiese drywing veroorsaak is nie, word aangedui deur die feit dat die beraamde toename aan inteelt oor die proefperiode slegs 1,2 % bedra. Die gevolgtrekking word gemaak dat handhawing van genetiese stabiliteit in 'n kontrolekudde van hierdie grootte met Merinoskape prakties moontlik is.
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Introduction

Genetic control populations have three main functions: (1) to remain genetically stable over an extended period; (2) to measure fluctuations in the environment; and (3) to serve as a gene pool with known parameters for use as base material in selection experiments (Gowe, Robertson & Latter, 1959). The whole problem of the estimation of genetic change was extensively reviewed by Hill (1972a, 1972b). Hill (1972a) stated that a genetic control flock is a segregating population in which special efforts are made to minimize genetic changes due to selection or random genetic drift.

Genetically stable control popuplations are very useful to measure environmental variations in selection experiments and to evaluate the relative genetic differences between farm animal populations. In South Africa, rams from a control flock of Merino sheep have been used to measure genetic progress in, and the relative difference between the flocks of members of the Breed Society for Performance Tested Merinos (Erasmus, 1976, 1977; Van der Merwe & Poggenpoel, 1977). Also the Döhne Merino Breeder's Association has since expressed their urgent need for a genetic control flock of their own breed (J.C. MacMaster, 1982, personal communication), which is presently being established at the Döhne Experimental Station, Stutterheim.

Apart from flock size being sufficient to minimize inbreeding and consequently genetic drift, the replacement of breeding animals must also be carefully planned to prevent unintentional selection. One possibility is to use as replacements, only those young animals which phenotypically best resemble the average of the contemporary group with regard to the selected character (Edwards, Omtvedt & Whatley, 1971). It has also been suggested that the male progeny of the control population be ranked according to the selected character, the list divided into deciles and an equal number of animals be drawn at random from each decile as required, so that the average of the chosen animals corresponds to that of the whole group prior to selection (Turner, Dolling & Kennedy, 1968). Both these methods have the serious disadvantage that such control flocks can only be used with regard to character for which a zero selection differential is maintained. A more random replacement procedure was practised in the present study as the control flock was intended to evaluate genetic deviations in several traits.

The main objective of this paper is to evaluate the genetic stability of the Tygerhoek Merino Control Flock of the South African Department of Agriculture.

Procedure

The Tygerhoek Merino Control Flock was established at the Tygerhoek Experimental Farm, Riviersonderend, in the South Western Cape, in 1969. The background of the Control Flock is briefly, as follows: During 1960, 218 Merino ewes made up of groups varying from 4 to 40 in number, were obtained from breeders in the Caledon-Swellendam area. Two significant additions from outside were made in 1962 and 1967 when 120 and 98 ewes, respectively, were acquired from the Grootfontein College of Agriculture at Middelburg, Cape. Rams used for breeding from 1960 to 1969 were bought from different neighbouring breeders.

On account of the composition of the flock, it is reasonable to assume that the average inbreeding coefficient was roughly zero in 1960. Furthermore, it may be assumed that considerable genetic variance must have existed in the flock for most economic traits. As the flock was allowed to increase from the original 436 ewes to 800 in 1969, selection was limited to the culling of individuals with serious congenital body and/or wool defects. The Tygerhoek Merino Flock was therefore exceptionally well suited for breeding experiments.

In 1969 the available 800 ewes, ranging in age from 1,5 to 5,5 years, were divided into five equal groups by stratified sampling within age groups according to their wool production at 18 months. Four groups of 160 ewes each were subjected to different selection procedures (Heydenrych, 1975; Heydenrych, Vosloo & Meissenheimer, 1977), while the fifth group, consisting of 160 ewes, formed the basis of the Control Flock. The ewe flock of the control group was enlarged to 200 animals in 1976.

Twenty-one rams, obtained from different sources, were mated to the 160 ewes in 1969. Sixteen two-tooth rams were selected at random from the 1969 lamb crop and mated to the control ewes in 1970. These young rams were the progeny of 13 of the 21 rams used in 1969, thus ensuring a broad genetic base. From 1971 until 1975 the 16 Control Flock rams were replaced yearly, each by a son selected at random. From 1976 onwards, 20 rams were mated yearly; the 4 rams added in 1976 were chosen such that no sire contributed more than two sons.

Normally Control Flock ewes were replaced by a second daughter reaching joining age. Ewes failing to produce a substitute as a result of death, infertility or for any other reason, were replaced by a young ewe randomly selected from the progeny of the other parents. No breeding ewe, however, was allowed to contribute more than two members to the next generation. No individual with a body defect or serious wool fault was used as a parent. This ewe replacement procedure made it possible to maintain a balanced five-age-group ewe flock structure.

Each mating season, ten breeding ewes were randomly allocated to each sire, but with the restriction that no offspring – parent, full, or half-sib. matings were made.

The data for this investigation consisted of four body-mass and six wool characters, measured on each Control Flock lamb born each year. Body mass was measured at birth, at 42 days, 120 days and 18 months; the latter after shearing. Greasy fleece mass (12 month's wool growth) was measured at 18 months but, for practical reasons, mid-rib wool samples for the determination of wool quality traits (percentage clean yield, staple length, crimp frequency and fibre diameter) were taken three months earlier. Clean fleece mass was determined from the values for greasy fleece mass and the percentage clean yield of the wool sample.

The incidental discrepancies between the progeny group and the replacement group means for individual traits were calculated each year to evaluate the reliability of the replacement procedure. Genetic trends in selected animal populations are normally investigated by regressing total response on accumulated selection differentials or by regressing population means on generation numbers. Since no selection took place in the present flock and it was not designed to distinguish separate generations, neither of the above procedures could be followed. However, to gain some insight into possible genetic trends in the measured characteristics, the regressions of progeny group averages for individual traits on time were calculated. Furthermore, 95 %-confidence limits were fitted to progeny group means for the different traits in each year.

Although complete pedigrees could be drawn up for each lamb born in this flock, the calculation of individual inbreeding coefficients was not deemed necessary. Since handmating was practised, with restrictions on closely related matings, it was reasoned that the average inbreeding coefficient of the flock would be lower rather than equal to the value estimated for a flock of this effective size on the assumption of random mating.

Results and Discussion

Replacement procedure

The calculation of the selection differential is of course only valid in truncation selection. Even in indirect selection, only the selection differential of the selected character is determined and used in predictions of expected genetic change in the correlated trait. Nevertheless, when several traits are measured in a genetic control population, scrutiny of the discrepancies in the means of the whole progeny group and the replacement group, may at least serve as an indication of the suitability of the applied replacement procedure.

Absolute differences between progeny groups and replacement groups for lambs born in the Tygerhoek Merino Control Flock from 1969 to 1979, are shown in Table 1 (body-mass traits) and Table 2 (wool traits). It is clear that these differences are rather small, the largest being the positive difference of 1,19 μ (6,17 %) in fibre diameter in 1974. The average relative differences for individual traits (expressed as a percentage) also indicate that the replacement groups were, at least phenotypically, very similar to the whole progeny group from which they were drawn. However, these results do not necessarily imply that natural selection has not taken place. It must be remembered that in the present study, replacement animals were not drawn before the age of 18 months, while most deaths in lambs normally occur between birth and ten days. However, Gowe *et al.* (1959) indicated that the effects of natural selection for viability could be greatly reduced if every effort is made to reduce mortality before breeding age, as much as possible. In the present study special care was taken to improve the survival rate of lambs and Heydenrych (1975) found the death rate of lambs, although rather high at 18 % from birth to weaning, to be very similar in the Control Flock and in four selection groups from the same base population run on the same farm. High death rates of lambs are not unfamiliar in the South Western Districts as lambs are born under cold and wet conditions during April and May.

Differences in the reproduction rates of individual members of a population is of course also of concern in a control flock (Gowe *et al.*, 1959). In the present study, however, handmating was practised and family groups were very similar in size (six to ten lambs per sire). A few instances occurred where rams

Table 1 Progeny group means ± SE and discrepancies with replacement group means for four body mass traits from 1969 to 1981. (All values calculated over both sexes)

Year	Birth mass (kg)			42-day body mass (kg)			120-day body mass (kg)			18-month body mass (kg)		
	$\bar{X}$	± SE	Discr.	$\bar{X}$	± SE	Discr.	$\bar{X}$	± SE	Discr.	$\bar{X}$	± SE	Discr.
1969	4,00	–	0,00	–	–	–	–	–	–	–	–	–
1970	3,76	–	0,22	10,78	–	0,33	24,23	–	0,92	–	–	–
1971*	4,19	0,06	−0,12	13,40	0,21	−0,15	21,55	0,33	−0,01	51,00	0,84	0,34
1972	3,91	0,07	0,20	12,82	0,23	0,72	22,40	0,38	1,10	47,12	0,09	−0,17
1973	3,96	0,07	0,09	12,14	0,22	−0,02	21,07	0,31	−0,26	49,20	0,65	−0,31
1974	3,86	0,08	−0,08	13,33	0,69	−0,72	–	–	–	46,72	0,76	−0,24
1975	3,47	0,06	−0,03	12,36	0,22	−0,18	21,53	0,37	−0,42	49,51	0,79	0,88
1976	3,64	0,07	0,00	14,02	0,23	0,19	22,68	0,37	0,84	53,14	0,64	0,83
1977	3,56	0,07	0,10	13,40	0,25	0,60	22,78	0,38	0,41	48,67	0,74	0,68
1978	3,47	0,06	0,02	13,46	0,22	0,04	21,68	0,31	0,03	50,79	0,90	−0,37
1979**	3,32	0,04	0,02	11,00	0,17	0,08	19,77	0,26	0,14	45,32	0,53	0,12
1980	3,15	0,05	–	11,75	0,19	–	24,57	0,32	–	51,57	0,76	–
1981	3,21	0,06	–	–	–	–	–	–	–	46,50	0,58	–
Average			1,04 %			0,74 %			1,31 %			0,38 %

* First lambs born from own ram replacements.

** Last group of replacements from which lambs were born (1981).

Table 2 Progeny group means ± SE and discrepancies with replacement group means for six wool traits from 1969 to 1981. (All values calculated over both sexes)

Year	Greasy fleece mass (kg)			Clean yield (%)			Clean fleece mass (kg)			Staple length (cm)			Crimp frequency (/25mm)			Fibre diameter (μ)		
	$\bar{X}$	± SE	Discr.	$\bar{X}$	± SE	Discr.	$\bar{X}$	± SE	Discr.	$\bar{X}$	± SE	Discr.	$\bar{X}$	± SE	Discr.	$\bar{X}$	± SE	Discr.
1969	5,90	–	0,02	60,36	–	0,18	3,55	–	0,01	8,29	–	0,07	11,00	–	0,00	19,50	–	0,02
1970	5,46	–	0,13	66,17	–	−0,03	3,60	–	0,09	6,38	–	−0,02	11,86	–	−0,02	19,73	–	0,19
1971*	6,67	0,08	−0,15	68,66	0,42	−0,35	4,57	0,06	−0,13	7,24	0,06	−0,11	9,62	0,13	0,00	21,16	0,14	0,26
1972	5,32	0,09	0,10	69,22	0,42	−0,21	3,67	0,06	0,05	7,38	0,09	−0,06	9,82	0,16	−0,08	18,53	0,14	0,06
1973	6,58	0,12	0,02	68,39	0,44	0,15	4,50	0,09	0,01	6,92	0,07	−0,16	9,80	0,13	0,13	20,83	0,17	−0,33
1974	4,69	0,09	0,09	68,80	0,44	0,10	3,22	0,06	0,07	5,97	0,07	0,04	10,15	0,15	−0,18	19,30	0,12	1,19
1975	5,82	0,11	0,10	68,71	0,40	0,34	3,98	0,08	0,09	6,76	0,07	0,01	10,66	0,13	−0,09	19,82	0,11	0,30
1976	6,64	0,08	−0,10	70,15	0,41	−0,18	4,66	0,06	−0,02	7,40	0,07	−0,01	10,05	0,13	0,15	20,32	0,11	0,28
1977	5,58	0,10	0,17	67,52	0,37	0,63	3,76	0,06	0,16	7,70	0,07	0,07	9,91	0,12	0,20	19,80	0,12	0,14
1978	6,66	0,10	0,07	69,31	0,31	−0,65	4,61	0,07	−0,01	7,35	0,07	−0,33	9,32	0,14	0,35	20,38	0,11	0,10
1979**	4,82	0,06	−0,02	69,46	0,32	−0,45	3,33	0,04	−0,03	6,84	0,05	−0,06	9,04	0,12	0,14	19,54	0,12	0,41
1980	6,32	0,11	–	69,21	0,39	–	4,36	0,07	–	7,60	0,07	–	9,53	0,13	–	20,91	0,11	–
1981	4,69	0,07	–	70,33	0,33	–	3,30	0,05	–	6,53	0,06	–	10,46	0,11	–	19,30	0,11	–
Average			0,77 %			−0,06 %			0,79 %			−0,72 %			0,59 %			1,22 %

* First lambs born from own ram replacements.

** Last group of replacements from which lambs were born (1981).

refused to mate. Such rams were replaced by a paternal half-sib.

Gowe *et al.* (1959) as well as Hill (1972b) pointed out that natural selection may have greater effects on control groups founded on artificially selected populations, especially in the first one or two generations after the relaxation of selection. As stated however, no directional selection was practised in the Tygerhoek Merino Flock for several years prior to the formation of the present control flock. Therefore it appears from the foregoing discussion that, although the absence of natural selection cannot be proved in the present study, it is unlikely to have had any significant effects.

Genetic change

Apart from unintentional selection, natural selection and sampling variance, genetic change in a control population may also be caused by genetic drift. Foster & Thompson (1980) stated that 'as control strains usually consist of a single line, direct evidence of the existence of genetic drift is not readily available'. In the present control flock, consisting of only one line, evidence of genetic change or stability, was investigated by determining the regression equations of progeny group means on time for the 11-year period from 1971 to 1981. (The first lambs sired by own-ram replacements were born in 1971). This period covers approximately 3,7 generations. These regressions are plotted in Figure 1 along with the original values. Also shown are 95 %-confidence limits of the respective means; estimated as an interval of two standard errors above and below each mean. Although the reliability of the regression of progeny group means on time as a measure of genetic change is seriously hampered by environmental effects, such regressions serve a useful purpose, especially if they are discussed in relation to known environmental circumstances.

It is clear from Figure 1 that considerable environmental

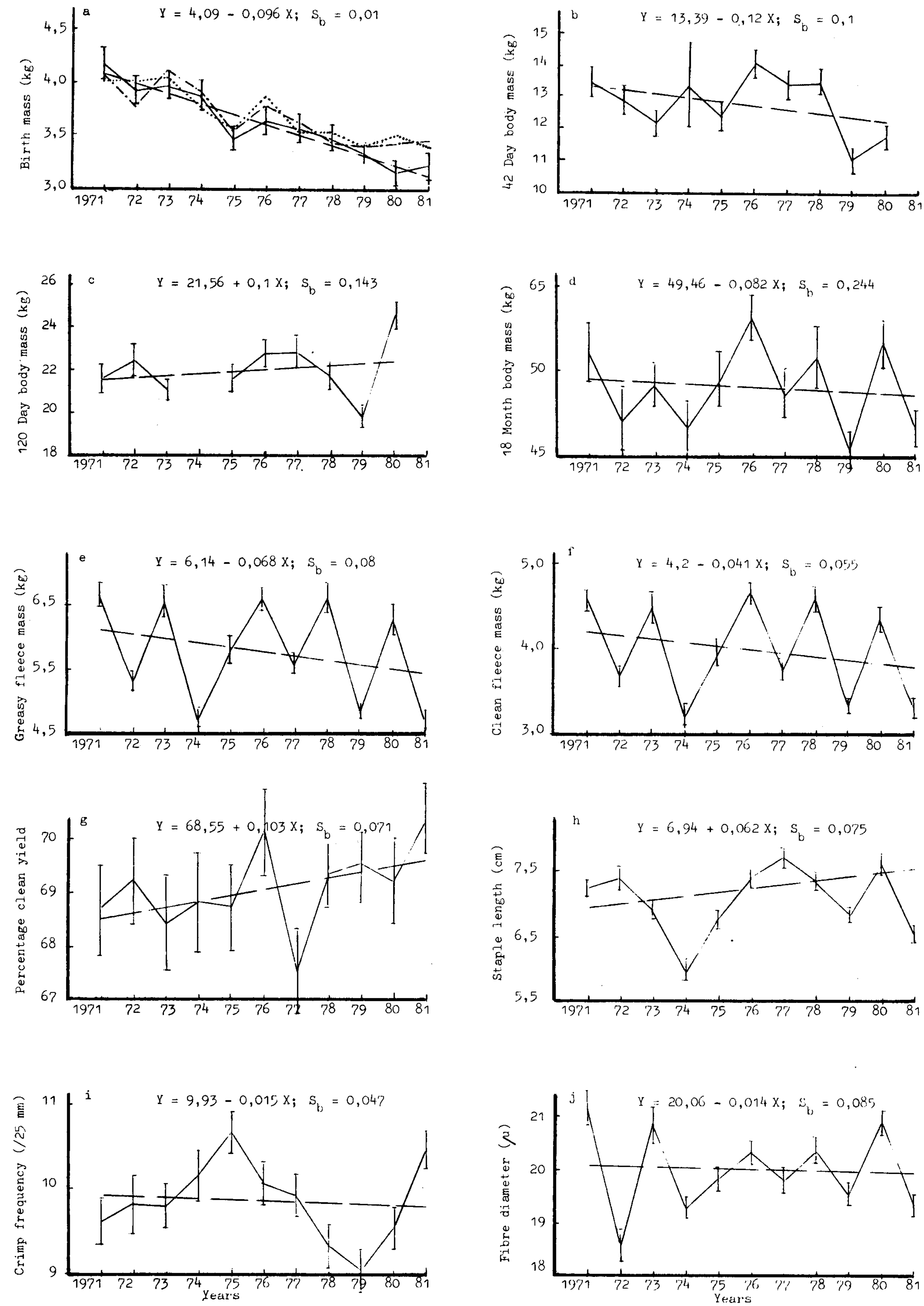

Figure 1 Regressions (— —) of progeny group means on years in four body-mass and six wool traits, shown with original values and confidence intervals. In 1 a —·—·— denotes Selection Group 1 and · · · · Selection Group 2; see text.

fluctuations occurred from year to year. Also Turner & Young (1969), summarizing the work of Dunlop (1962) and of Brown, Turner, Young & Dolling (1966) pointed out that yearly variations on the same property in Australia can have effects on the performance of sheep as large as those of vastly different environments. Therefore it is obvious that only long-term observations can give any clear picture with regard to genetic change in farm animals.

Except for birth mass, none of the measured traits showed any significant change with time. The apparent downward trends in 42-day body mass (–8,9 %), greasy fleece mass (–11,1 %) and clean fleece mass (–9,8 %) over the 11-year period (3,7 generations), were most probably caused by the extremely adverse environmental conditions experienced in 1974, 1979 and 1981. In 1974 for example, all lambs were severely infected with clamydioses *(Clamydia psittaci)*, nutritional conditions were bad and considerable losses occurred. As described by Heydenrych *et al.* (1977) these conditions even reduced the previously discernible differences between the Control Flock and the four selection groups for 18-month body mass and fleece mass, to almost zero. Although the lambs were not disease infected in 1979 and 1981, similar conditions occurred in these years and in 1981 all lambs produced a tender wool. Turner *et al.* (1968) also ascribed an apparent reduction in body mass (over a 15-year period) in their Cunnamula Merino Control Flock to a lower rainfall in the later years.

Edwards, Omtvedt & Whatley (1971) successfully applied 95 %-confidence limits to yearly population means to prove genetic stability in a control population of pigs kept in a fairly constant environment from year to year. In the present study, however, Figure 1 shows that very few confidence intervals overlap; even in adjacent years. This phenomenon not only indicates the unsuitability of this technique for the evaluation of control groups under more variable natural environmental conditions, but once more stresses the problem of large environmental effects when comparing genetic groups.

The highly significant negative trend ($Y = 4{,}09 - 0{,}096\,X$; –23,44 %) in birth mass (Figure 1) is of special interest. In the absence of measurements on other characters in the same population, such a trend may easily be mistaken for a genetic change. Plotting of the yearly birth-mass means of two selection groups (selected directly and indirectly for increased wool production) revealed similar regular downward trends, and clearly pointed to some important environmental factor. As stated earlier, the lambing season takes place from April to May under rather adverse climatic conditions and ewes reach their term of pregnancy when the nutritional plane is at its lowest. This called for supplementary feeding in late pregnancy. Owing to the expansion of other experiments, however, the amount of grazing available to the sheep-breeding experiment was gradually reduced. The plane of supplementary feeding was simultaneously lowered for economic reasons. The other traits being measured at, or shortly after, times of abundant grazing, naturally did not reflect the same trend.

Inbreeding

The dispersive process causing genetic drift, may be quantified either in terms of the variance of gene frequencies or in terms of inbreeding. The latter, however, is more useful as it applies equally to any mean or initial gene frequency (Falconer, 1981). Used for this purpose ΔF expresses the rate of dispersion and F the cumulated effect of random drift. In situations of overlapping generations the effective population size which dictates the rate of inbreeding, can according to Hill (1972a) be estimated as $N_y = 4mfL^2/(m+f)$. The number of males and females entering the breeding flock yearly are denoted by m and f, respectively, and the generation interval by L. For the present Control Flock the effective number was $4 \times 16 \times 38 \times 3^2/(16 + 38) = 405$ from 1969 to 1975 and $4 \times 20 \times 44 \times 9/64 = 495$ from 1976 onwards. These effective sizes are large compared to the 'rough guide' of 300 suggested by Gowe *et al.* (1959) for long-term studies that are expected to proceed for 20 generations or more. Turner & Young (1969), however, suggested a minimum of 50 ewes and 10 rams for a practical control group. Assuming the same replacement rate as in the present study, this gives an effective population size of 188.

The yearly rate of inbreeding, measured as the inverse of double the effective population size, was 0,12 % for the first period (1969 to 1975) of this study and 0,1 % for the second (1976 to 1981). This gives a mean estimated inbreeding coefficient of roughly 1,22 % after 3,7 generations, assuming zero inbreeding in 1969. Therefore it is unlikely that genetic drift has had any significant influence on the Tygerhoek Merino Control Flock over the first 11 years of its history.

Foster & Thompson (1981) used three White Leghorn control lines of approximately equal size from the same base population and found discernible genetic drift in several traits after nine generations of closed breeding. The average effective population size of their control lines was 38 and they reached an eventual inbreeding coefficient of 10 %. With the present population size, however, an inbreeding coefficient of 10 % should not be reached before the completion of approximately 33 generations (99 years) of closed breeding. In addition, Hill (1972a) pointed out that the effective population size could be doubled by ensuring that each male was replaced by a son, as was done in the present case. Furthermore, quoting several workers (Kimura & Crow, 1963; Robertson, 1964; Wright, 1965 and Cockerham, 1967, 1970), Hill (1972a) indicated that genetic drift may be reduced by practising non-random mating of individuals on the basis of their relationship to each other. However, Hill (1972a) warned that 'maximum avoidance' of mating relatives will increase heterozygosity over random mating and consequently increase drift. This effect, however, is not serious. For example, if family sizes are equal, the avoidance of all full-sib. matings will reduce the effective population size by only 1 (Robinson & Bray, 1965).

Conclusions

From the available evidence it appears that the Tygerhoek Merino Control Flock has remained fairly stable over the first 3,7 generations of its existence. There is also litte danger of serious inbreeding and perhaps also of natural selection in future generations. Furthermore, being controlled by the Department of Agriculture, continuity of experimental procedures and management is guaranteed. Since the Control Flock and the selection groups at Tygerhoek were drawn from the same base population, this Control Flock is most suitable for its original intended purpose.

Starting in 1973, rams from the Tygerhoek Merino Control Flock have also been used to evaluate genetic gain in and differences between the flocks of members of the Performance Section of the South African Merino Studbreeder's Association. The practical procedures for these comparisons were described by Van der Merwe & Poggenpoel (1977), while Roux (1982) discussed the theoretical aspects. Using a central genetic control flock in this way has its limitations, especially with regard to genotype × environment interactions and errors of measurement when assertaining the progeny group means of lambs sired by farm-bred and by control flock rams. With regard to the first problem, Turner (1977, personal communication to C.A. van der Merwe) indicated that both control flock and central testing station tests will be hampered by genotype × environment interactions, but she was of the opinion that 'hopefully such interactions may not be large, depending on the localities in which the flocks under comparison are located'.

Since most South African Merino Stud flocks are of reasonable size, progeny groups of 90 to 200 can be tested and therefore group means can be assertained with a satisfactory degree of accuracy. Another point of importance is that the testing capacity of the on-farm control ram system is much larger than when the same number of animals as the control flock are accommodated at a central testing station. Thus it may be concluded that the Tygerhoek Merino Control Flock is also well suited to this secondary purpose of between-flock testing of breeding values and to measuring genetic gains made through selection in individual flocks.

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