Genetic parameters for reproduction rate in the Tygerhoek Merino flock. 1. Heritability

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Data of the Tygerhoek Merino flock were used to obtain halfsib heritability estimates for the components of reproduction rate within age groups as well as averaged over a number of lambing opportunities. Two separate sets of data were considered. The first set of data included progeny of all the selection group rams retained for two breedings seasons, while the second set of data included progeny of all the available rams. Reproduction traits investigated were ewes conceived/ewe mated (Ec/Em), lambs born/ewe conceived (Lb/Ec), lambs born/ewe mated (Lb/Em), the maternal component of pre-weaning mortalities/lamb born (Ld/Lb), and lambs weaned/ewe mated (Lw/Em). The obtained heritability estimates suggested that selection for Ec/Em is unlikely to yield substantial genetic progress in the Tygerhoek Merino flock. Multiple birth rate, on the other hand, was heritable and it was contended that Lb/Ec would respond to selection, a finding which is in agreement with literature cited. The heritability estimates obtained for the maternal component of Ld/Lb were discouragingly low. Based on literature cited, however, it was concluded that the rearing ability of ewes should also be considered in a selection programme for Lb/Ec, if the objective is to markedly improve the composite trait of Lw/Em. Methods for the acceleration of the genetic progress in Lb/Ec and Lw/Em by the use of modern technology are proposed.

Data van die Tygerhoek-Merinokudde is gebruik om halfsib-oorerflikheidsberamings vir die komponente van reproduksietempo binne ooi-ouderdomsgroepe en van die gemiddelde reproduksie oor 'n aantal lamgeleenthede te ondersoek. Twee afsonderlike datastelle is geanaliseer. Die eerste datastel het nageslag van alle seleksiegroepramme wat vir twee paarseisoene behou is, ingesluit, terwyl nageslag van alle beskikbare ramme opgeneem is in die tweede datastel. Reproduksie-eienskappe wat geanaliseer is, was ooie beset/ooi gepaar (Ec/Em), lammers gebore/ooi beset (Lb/Ec), lammers gebore/ooi gepaar (Lb/Em), die maternale komponent van voorspeense vrektes (Ld/Lb) en lammers gespeen/ooi gepaar (Lw/Em). Die verkreë oorerflikheidsberamings dui daarop dat seleksie vir Ec/Em waarskynlik nie noemenswaardige genetiese vordering in die Tygerhoek-kudde sal veroorsaak nie. Meerlinggeboortes, aan die ander kant, was tot 'n mate oorerflik, en Lb/Ec sal waarskynlik reageer op seleksie. Hierdie bevinding is in ooreenstemming met aangehaalde literatuur. Die oorerflikheidsberamings vir die maternale komponent van Ld/Lb was ontmoedigend laag. Volgens aangehaalde literatuur, blyk dit nogtans dat die vermoë van ooie om hulle nageslag groot te maak in 'n seleksieprogram vir Lb/Ec oorweeg behoort te word, indien noemenswaardige verhoging in die saamgestelde eienskap van Lw/Em ten doel gestel word. Metodes waarvolgens genetiese vordering in Lb/Ec en Lw/Em deur die gebruik van moderne tegnologie versnel kan word, word voorgestel.

Keywords: Paternal halfsib heritability, reproduction rate, Merino sheep

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Introduction

Reproduction rate markedly affect selection intensity and therefore also the genetic progress and the number of surplus lambs available in sheep production systems, whereas a minimum level of reproduction is required for the maintenance of the breeding flock. Reproduction is therefore generally considered to be one of the most important production traits in practical sheep husbandry. According to de Klerk, Düval & Terblanche (1983), the reproduction rate of woolled and dual-purpose sheep is disturbingly low in South Africa, despite its importance. The purpose of this article is to discuss genetic aspects related to reproduction rate which should be considered in the formulation of breeding plans.

In the late sixties and early seventies, reproduction rate was considered to be of a low heritability, and not worth selecting for (de Lange, 1984). During the last 15 years, however, evidence of substantial genetic progress via selection for reproductive performance accumulated (Clarke, 1972; Turner, 1978; Hanrahan, 1984). Selection for increased reproduction reported by the authors cited was based on selection for multiple births. Ovulation rate was also extensively used as an indicator of multiple birth rate (Hanrahan, 1980; 1984; Piper & Bindon, 1984). This characteristic has a few important advantages as a selection criterion for reproduction rate, as it leads to a shorter generation interval and is independent of the male for expression (Piper & Bindon, 1984). In less prolific breeds with an average litter size of less than 1,40 a strong relationship exists between ovulation rate and litter size (Hanrahan, 1980). In these breeds the comparative advantage of selection for ovulation rate instead of litter size is relatively small (Piper & Bindon, 1984). Recent research findings also emphasize the possibility of selection against lamb mortalities (Piper, Hanrahan, Evans & Bindon, 1982; Haughey, 1983; 1984).

The results cited above suggest strong possibilities of selection for components of reproductive performance in sheep. Data from the Tygerhoek flock were therefore used to obtain heritability estimates for reproduction traits in South African Merino sheep.

Material and Methods

The data included in this investigation are part of the data previously discussed by Cloete & Heydenrych (1986). The data were considered fit for this purpose, as no intentional selection for reproduction was applied within the flock. Genetic parameters were obtained by halfsib analysis of variance procedures (Turner & Young, 1969) using the LSML76 computer program (Harvey, 1977) to calculate variance components and obtain heritability estimates by mixed-model methods in an unbalanced experiment (Harvey, 1970).

It should be noted that the Tygerhoek data had a few shortcomings with regard to the estimation of genetic parameters. All the control group rams and almost half of the selection group rams were used for one mating season only. The fact that some rams were available for two mating seasons and the majority for one only, complicated the choice of a suitable statistical model. It was therefore decided to analyse two sets of data using slightly different models. For the first set of data, only progeny of selection group rams used in two breeding years was considered. This constraint limited the number of observations available in the original set of data. The second set of data involved data for all the available rams used at least once in the breeding flock. Seeing that the majority of rams were used for only one season and that the birth years of these rams were confounded with those of the ewes to which they were mated, rams used for more than one breeding season were treated as separate individuals during each breeding season, an approach also followed by Shelton & Menzies (1970). This method of analysis, together with the high proportion of rams per breeding ewe in the control group (8 - 10%) to minimize inbreeding (Heydenrych, 1975), resulted in the average number of progeny per sire being low.

Variance components within and between sires were calculated for reproduction traits within ewe age groups, as well as for average reproduction over two, three, four or five lambing opportunities. The reproduction traits considered were ewes conceived/ewe mated (Ec/Em), lambs born/ewe conceived (Lb/Ec), lambs born/ewe mated (Lb/Em), pre-weaning mortalities/lamb born (Ld/Lb) and lambs weaned/ewe mated (Lw/Em). Pre-weaning mortalities were not included as a dependent variable in analyses within ewe age groups, but only in the analyses on average lifetime reproduction. Both sets of data were analysed by the LSML76 computer program according to Model 03 described by Harvey (1977; 1982). The general model applied was:

$$y_{ijkl} = \mu + A_i + s_{ij} + F_k + e_{ijkl}$$

with y_{ijkl} = the $ijkl$'th observation for a specific dependent variable; μ = the overall mean; A_i = the fixed i'th contemporary group, inherent to a specific sire in the first data set, or the progeny of a specific sire in the second data set; s_{ij} = the random effect of the j'th sire nested within the i'th contemporary group; F_k = the other fixed effects included in the model; and e_{ijkl} = the sum of squares for the remaining variance, used as the error term to test the s_{ij} and F_k effects for significance.

The analyses involved two runs in a mixed model. During the first run constants were fitted for all the effects in the model except for the random s_{ij} effects. Variance components for s_{ij} and heritability estimates were calculated in the subsequent run (Harvey, 1977). In the first set of data, the effect of the i'th contemporary group consisted of a combination of the birth year and selection group for a specific sire. Sire birth years commenced in 1969 and ended in 1979 when ewes available for one, two and three lambing opportunities were considered; in 1978 when ewes available for four lambing opportunities were considered; and in 1977 when ewes available for five lambing opportunities were considered. Selection groups were Group 1 (selected on clean fleece mass) and Group 2 (selected on S/P ratio), as was previously defined (Cloete & Heydenrych, 1986). In the second set of data the i'th contemporary group consisted of the birth year and selection group for the ewes included in the analyses. Ewe birth years commenced in 1971 and ended in 1979, 1980, 1981, 1982 and 1983 when ewes available for one to five lambing opportunities were considered. Other fixed effects included in the model were the age of the sire and dam of individual halfsisters at birth in the first data set, with only age of dam retained in the analyses on the second data set. Birth type was excluded as an independent variable in all these analyses, as the effect of birth type on reproductive performance was assumed to be partly genetic in origin (Ch'ang & Rae 1970). Variance components obtained from the model specified above were used to calculate heritability estimates according to standard procedures (Harvey, 1977). Appropriate standard errors were calculated by the modified formula given by Swiger, Harvey, Everson & Gregory (1964).

The analyses on the respective dependent variables involved a comparatively large number of analyses. Individual analysis of variance tables will not be presented, but details such as the number of observations, degrees of freedom for sires within contemporary groups and for error, and the weighted average number of offspring per sire (k) are given in Table 1. The information is presented on a per-ewe-mated basis for the analyses conducted on Ec/Em, Lb/Em and Lw/Em, as well as on a per-ewe-conceived basis for the analyses regarding Lb/Ec and Ld/Lb.

Results and Discussion

Ewes conceived/ewe mated

Heritability estimates for ewes conceived/ewe mated were low — less than 0,10 in many cases — with obtained estimates rarely exceeding their standard

Table 1 The number of observations (n), degrees of freedom for sires within contemporary groups ($df_{s/cg}$) and error (df_e) and k values for the analyses within ewe age groups and averaged over a number of lambing opportunities

	Ewe age group (number of lambing opportunities)				
Item	2 years (1)	3 years (2)	4 years (3)	5 years (4)	6 years (5)
First set of data					
per ewe mated					
n	825	724	561	437	364
$df_{s/cg}$	41	41	38	35	35
df_e	757	656	498	379	306
k	12,4	10,7	8,9	7,5	6,3
per ewe conceived[a]					
n	614	627(691)	485(551)	374(432)	307(360)
$df_{s/cg}$	41	41	38	35	35
df_e	546	559(623)	422(488)	316(374)	249(302)
k	9,1	9,2(10,2)	7,7(8,7)	6,3(7,4)	5,3(6,3)
Second set of data					
per ewe mated					
n	1703	1429	1162	917	747
$df_{s/cg}$	364	328	300	269	236
df_e	1296	1060	825	614	480
k	4,0	3,7	3,3	2,9	2,7
per ewe conceived[a]					
n	1207	1209(1344)	1001(1137)	766(908)	628(739)
$df_{s/cg}$	325	311(320)	289(298)	260(268)	220(235)
df_e	839	858(984)	675(802)	472(606)	377(473)
k	3,1	3,3(3,6)	2,9(3,3)	2,5(2,9)	2,4(2,7)

[a] Values in brackets indicate corresponding numbers for the analyses on ewes available for a number of lambing opportunities, where only ewes not conceiving at least once were excluded.

errors. Negative between-sire variance components furthermore prevented the estimation of heritability in five analyses. Individual estimates are therefore not presented, but the general trend is in agreement with obtained heritability estimates of -0,03 to 0,03 (Purser, 1965, for British hill breeds), 0,067 (Shelton & Menzies, 1970, for the McGregor Rambouillet flock), -0,07 to 0,16 (Forrest & Bichard, 1974, for Clun Forest ewes belonging to different age groups), 0,06 and 0,09 (Fogarty, Dickerson & Young, 1985, for crossbred ewes), 0,02 (Clarke & Hohenboken, 1983, for crossbred ewes), and -0,15 to 0,06 (Lewer,Rae & Wickham, 1983, for Perendale ewes of different age groups). Estimates from the present investigation tend to be smaller than those obtained by Shelton & Menzies (1970) for the Sonora Rambouillet flock (0,268) and by van der Merwe (1976) for the Elsenburg Dormer flock (0,45 for 2-year olds, 0,34 for 3-year olds and 0,10 for 4-year olds). It should be mentioned that both authors cited reported a relatively high frequency of barrenness in the flocks under consideration. Shelton & Menzies (1970) stated that their relatively high heritability estimate may be related to adaptability under the conditions of nutritional stress occurring in the Sonora flock. Fogarty, *et al.* (1985) also contended that selection for fertility may prove to be of value under regimes of accelerated lambing, where fertility tends to be low, and where genetic variance may be expressed. The present results, and most of the other sources in the literature, appear to suggest that genetic progress in selection against barrenness is likely to be slow in most flocks where normal conception rates prevail.

Lambs born/ewe conceived

Heritability estimates for lambs born/ewe conceived are also presented within age groups and for average performance over a number of lambing opportunities (Table 2). The mean square for sires tended to be significant ($P \leq 0,05$) in most of the analyses regarding this trait, and this resulted in estimates that could be considered useful (11 estimates were larger than twice their standard errors). In general, heritability estimates obtained from both sets of data tended to be higher than 0,2, whereas estimates as high as 0,3 - 0,6 were obtained. Comparable heritability estimates in the literature are -0,05 to 0,17 for Merino ewes (Mann,Taplin & Brady, 1978), 0,07 - 0,18 for Targhee ewes (Thapan, Bell &

Table 2 Heritability estimates (h^2) and appropriate standard errors (*SE*) for lambs born/ewe conceived within ewe age groups and averaged across a number of lambing opportunities for the first and second sets of data

	First set of data		Second set of data	
Item	h^2	*SE*	h^2	*SE*
Age of ewe				
2 years	-	-	0,153	0,115
3 years	0,246[a]	0,113	0,366[a]	0,117
4 years	0,282[a]	0,137	0,189	0,132
5 years	0,105	0,142	0,081	0,167
6 years	0,467[a]	0,209	0,278	0,198
Lambing opportunities				
2	0,071	0,082	0,262[a]	0,104
3	0,332[a]	0,132	0,386[a]	0,122
4	0,383[a]	0,159	0,461[a]	0,146
5	0,554[a]	0,196	0,653[a]	0,170

[a] Denotes estimates larger than twice their standard errors.

\- Estimate could not be made because of negative between-sire variance components.

Parker, 1970; Basuthakur, Burfening, van Horn & Blackwell, 1973), 0 - 0,48 for Clun Forest ewes (Forrest & Bichard, 1974), 0,14 - 0,16 for British hill breeds (Purser, 1965), 0,10 - 0,14 for Rambouillet ewes (Shelton & Menzies, 1970), 0,09 - 0,40 for SA Mutton Merino ewes (Vosloo, 1967; Kritzinger, Stindt & van der Westhuysen, 1984), 0,01 - 0,15 for Perendale ewes (Lewer, *et al.*, 1983), - 0,20 to 0,42 for Dormer ewes (van der Merwe, 1976; Kritzinger, *et al.*, 1984), 0,11 - 0,16 for crossbred ewes (Fogarty, *et al.*, 1985) and 0,21 for ewes of mixed breeds (Vakil, Botkin & Roehrkasse, 1968). The heritability estimates reported in Table 2 tend to be amongst the higher values presented above. It thus appears that, in agreement with previous conclusions (Turner, 1969), moderate genetic gains owing to selection for multiple births may be expected.

In the past, successful selection for multiple births was based on selection for maternal performance (e.g. birth type) and the screening of large populations for highly prolific individuals (Clarke, 1972; Turner, 1978; Hanrahan, 1984), whilst ovulation rate was also successfully implemented as an indirect selection criterion (Hanrahan, 1980; 1984). The screening of large populations for prolific individuals has led to the establishment of the high-fecundity Booroola Merino breed in Australia (Turner, 1978) in which the increased twinning rate appears to be related to a single-gene effect (Davis, Montgomery, Allison, Kelly & Bray, 1982). Homozygous carriers of this gene can be used to transfer some of the genetic potential for fecundity from this breed to less prolific breeds (Davis, Armstrong & Allison, 1984). Modern techniques like superovulation and embryo transfer can also be applied to establish prolific flocks from carriers of the high-fecundity gene, or from individuals with a known record for prolificacy (Hanrahan & Quirke, 1982; Kelly, Lewer, Allison, Paterson & Howarth, 1983). The possibility of manipulating the threshold for multiple birth rate by means of immunization against steroid hormones (Scaramuzzi, Geldard, Beels, Hoskinson & Cox, 1983) for selection purposes, could also be considered as a means of improving litter size by selection (de Lange, 1984). Selection could also be based on ranking tables where more than one maternal record can be taken in consideration (Turner, 1977). The prospects of selection for this component of reproduction rate thus appears to be favourable, especially if modern technology could be used for the acceleration of response.

Lambs born/ewe mated

Heritability estimates for lambs born/ewe mated are presented on a within age group basis and as an average over a number of lambing opportunities (Table 3). Estimates obtained from the second set of data tended to be more accurate, yielding five estimates that were larger than twice their standard errors and one estimate approaching this level, whilst only the estimate for 5-year old ewes could be considered to be significant in the first set of data. In general, the estimates ranged between 0,10 and 0,30, with only a few estimates not within these bounds. Comparable heritability estimates in the literature are 0,0 - 0,54 for Merino ewes (Young, Turner & Dolling, 1963; Kennedy,1967; Mann, *et al.*, 1978), 0,07 - 0,13 for Targhee ewes (Thapan, *et al.*, 1970, Basuthakur, *et al.*, 1973), 0,03 - 0,21 for Romney ewes (Ch'ang & Rae, 1970), 0,01 - 0,15 for Scandinavian ewes (Gjedrem, 1966; Eikje, 1975), 0,0 - 0,39 for Clun Forest ewes (Forrest & Bichard, 1974), 0,19 for Ice-

Table 3 Heritability estimates (h^2) and appropriate standard errors (*SE*) for lambs born/ewe mated within ewe age groups and averaged across a number of lambing opportunities for the first and second sets of data

	First set of data		Second set of data	
Item	h^2	*SE*	h^2	*SE*
Age of ewe				
2 years	-	-	0,201[a]	0,086
3 years	0,104	0,083	0,231[a]	0,098
4 years	0,104	0,101	-	-
5 years	0,349[a]	0,154	0,267	0,141
6 years	0,172	0,153	0,262	0,164
Lambing opportunities				
2	0,136	0,088	0,305[a]	0,101
3	0,103	0,101	0,252[a]	0,116
4	0,112	0,124	0,361[a]	0,143
5	0,057	0,138	0,326	0,165

[a] Denotes estimates larger than twice their standard errors.

\- Estimates could not be made because of negative between-sire variance components.

landic ewes (Jónmundsson, 1977), 0,07 - 0,18 for Galway ewes (More O'Ferrall, 1976), 0,0 - 0,07 for British hill breeds (Purser, 1965) and 0,18 - 0,28 for Rambouillet ewes (Shelton & Menzies, 1968). The present estimates fit in the range of values from the literature summarized above. Lb/Em is a composite trait with conception rate and multiple births as components. Some genetic variance appears to exist for this trait, but some of the heritability estimates were associated with relatively large standard errors, making these estimates less accurate than those obtained for Lb/Ec. Methods to improve this characteristic by selection have been discussed together with the component traits, and Lb/Em as such is therefore not discussed in detail.

Pre-weaning mortalities/lamb born

The next component trait to be considered is pre-weaning mortalities/lamb born, which can be considered either as a trait of the offspring or as a trait of the dam. Cundiff, Gregory & Koch (1982) concluded that the heritability of the maternal component of pre-weaning survival (0,08) was about double that of the offspring component (0,04). Therefore selection can possibly be directed towards the improvement of the maternal component of lamb survival, the heritability of which was investigated with the present data. Only the average reproductive performance of ewes was considered in this respect. The obtained heritability estimates were low — less than 0,10 in all the analyses, with the obtained estimates consistently lower than their standard errors. In general, these values were somewhat lower than corresponding estimates of 0,13 and 0,19 (Shelton & Menzies, 1970), 0,10 (Piper, *et al.*, 1982); 0,08 (Cundiff, *et al.*, 1982) and 0,15 (Fogarty, *et al.*, 1985). It thus appears that selection against the maternal effect of lamb mortalities is unlikely to yield any worthwhile genetic progress in the Tygerhoek flock. It should, however, be pointed out that Fogarty, *et al.* (1985) concluded that fertility and pre-weaning survival are the most important components of reproduction rate to be selected for in accelerated lambing regimes. The authors cited contended that the low conception and survival rates under such systems favour the expression of genetic superiority in these traits, and are worth selecting for.

Lambs weaned/ewe mated

The final trait to be considered is the composite trait of Lw/Em , which consists of conception rate, multiple births and pre-weaning survival. Heritability estimates within ewe age groups and for the average lifetime rearing performance of ewes after two to five lambing opportunities are presented in Table 4. The obtained estimates ranged from slightly below 0,1 to 0,2 in most runs. Judged by their standard errors, these estimates cannot be considered very accurate, with only one estimate reaching a magnitude twice as large as its standard error and two more approaching this level. Comparable heritability estimates in the literature are 0,0 - 0,29 for Merino sheep (Young, *et al.*, 1963; Kennedy, 1967), 0,06 - 0,13 for Targhee ewes (Basuthakur, *et al.*,1973), -0,01 to 0,09 for Scandinavian breeds (Gjedrem, 1966; Eikje, 1975), 0,13 for Icelandic sheep (Jónmundsson, 1977), -0,02 to 0,24 for Perendale ewes (Lewer, *et al.*, 1983), 0,16 - 0,24 for Galway ewes (More O'Ferrall, 1976), 0,0 - 0,03 for British hill breeds (Purser, 1965), 0,22 - 0,28 for Rambouillet ewes (Shelton & Menzies, 1968) and 0,01 - 0,10 for ewes of mixed breeds (Fogarty, *et al.*, 1985). The obtained heritability estimates in Table 4 are in general agreement with those summarized above. Although not necessarily statistically different from zero, most estimates in the present investigation and in the literature were positive. There thus appears to be some genetic variation in the composite trait of Lw/Em in most flocks.

Table 4 Heritability estimates (h^2) and appropriate standard errors (*SE*) for lambs weaned/ewe mated within ewe age groups and averaged across a number of lambing opportunities for the first and second sets of data

	First set of data		Second set of data	
Item	h^2	*SE*	h^2	*SE*
Age of ewe				
2 years	-	-	0,096	0,082
3 years	0,164	0,091	0,169	0,096
4 years	0,074	0,097	0,207	0,115
5 years	0,063	0,117	0,173	0,139
6 years	0,088	0,142	-	-
Lambing opportunities				
2	0,059	0,077	0,147	0,095
3	0,133	0,105	0,206	0,115
4	0,040	0,113	0,289[a]	0,142
5	-	-	0,183	0,162

[a] Denotes estimates larger than twice their standard errors.
- Estimates could not be made because of negative between-sire variance components.

Selection for multiple births was considered to be the most likely avenue of improving the composite trait of Lw/Em in sheep (Turner, 1969). Unfortunately selection response in multiple birth rate tends to be associated with an increase in pre-weaning mortality, which cancels some of the progress made (McGuirk, 1976; Hall, 1984). De Lange (1984) quoted results indicating a marked advantage in the pre-weaning survival rate of quadruplets in Romanov crosses in comparison with Booroola Merinos. These results led him to propose the possibility of the loss of a major gene or genes controlling lamb mortalities during the formation of the latter breed. This possibility must also be considered for optimal genetic improvement of the composite trait of Lw/Em, unless intensive managerial practices are implemented. Although recent research confirms realized genetic improvement of pre-weaning survival in Merinos (Haughey, 1983; 1984), it should be noted that the initial selection in the selection trial reported by Haughey (1983; 1984) was for rearing performance of maternal ancestors over a number of lambing seasons, or lambs weaned/lambing opportunity. Selection for Lw/Em by taking multiple birth rate as well as pre-weaning mortalities into consideration thus appears to be feasible in practice, as was also advocated by Piper, *et al.* (1982). Genetic gains in the composite trait can be accelerated by the techniques proposed earlier with regard to multiple birth rate.

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