

Genetic analysis of faecal worm egg count in South African Merinos under natural challenge

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Abstract

Sheep from a Merino selection experiment at the Tygerhoek research farm in the Southern Cape provided material for this study. The selection lines involved included a line selected for clean fleece weight, a “Wet and Dry” line, a fine wool line and an unselected Control line. Rectal faeces samples were obtained from individual animals at 13 to 16 months of age, after drenching was withheld for at least 10 weeks. Nematode eggs in these samples were counted. Fitting the appropriate fixed effects, the heritability of untransformed, cube root transformed and log transformed faecal nematode egg count (FEC) was obtained from single-trait analyses. The effects of sex and birth year were involved in a significant interaction. Means for FEC were generally higher in ram progeny than in ewes, but the magnitude of the sex difference was not consistent. Multiple lambs had a slightly lower mean for FEC than singles, while FEC was unaffected by dam age. The heritability of FEC was estimated at between 0.14 for untransformed data and 0.18 for log transformed FEC. Genetic correlations of log transformed FEC with two-tooth staple strength (-0.49) and coefficient of variation of fibre diameter (0.30) were favourable. Clean fleece weight was unfavourably related to FEC on a genetic level (0.19). Selection for resistance to parasitic nematodes after natural challenge should thus be feasible in the Merino lines studied.

Keywords: Fleece weight, genetic correlation, heritability, live weight, resistance

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Introduction

The usage of chemicals to control external and internal parasites of livestock is being challenged on a global scale. Resistance of gastro-intestinal nematodes to the present generation drugs is commonly experienced (Bath, 2006), while indications are that no new drenches are in the process of being developed. Existing strategies for the control of these pathogens are thus challenged (Bath, 2006), and alternative strategies need to be formulated (Vatta *et al.*, 2000).

A possible avenue for dealing with the challenge of gastro-intestinal helminths is to select livestock for resistance and/or tolerance to infestation (Vatta *et al.*, 2000). Research in other countries demonstrated genetic variation in resistance of sheep to nematode infestations (Greeff *et al.*, 1995; Morris *et al.*, 1996; Greeff & Karlsson, 1999; Khusro *et al.*, 2004), and successful breeding programs for resistance/tolerance have been reported (Woolaston & Piper, 1996; Greeff *et al.*, 1999; Morris *et al.*, 2005). Farming with resistant strains of sheep will result in a reduced reliance on anthelmintics to control parasitic nematodes, and associated economic advantages (McEwan *et al.*, 1995). The economic output of a resistant Merino strain was markedly higher than that of a control strain when no drenching was administered (Greeff *et al.*, 2006). The strains assessed were of equal genetic merit for production traits, and they grazed separate pastures where cross-contamination was impossible.

South African research on genetic parameters for resistance to gastro-intestinal nematodes of sheep is limited to a few studies (Cloete *et al.*, 2000; Bisset *et al.*, 2001; Nieuwoudt *et al.*, 2002; Snyman, 2007). No studies on genetic correlations of faecal worm egg counts (FEC) with other traits of economic interest have been published, apart from a preliminary study on the Tygerhoek Merino flock (Cloete *et al.*, 2000). International studies on these correlations are accordingly scarce, with fewer than five estimates for genetic

correlations of wool traits with FEC listed in the comprehensive review of Safari *et al.* (2005) on genetic parameters for sheep. The need for further studies on this topic is evident from these comments.

Against this background, the present study reports environmental factors impacting on FEC, estimates of the heritability of FEC before and after transformation as well as genetic correlations of FEC with live weight and wool traits. Based on previously derived selection line differences for FEC (Cloete *et al.*, 2000), breeding values for animals belonging to four single trait selection lines were also compared.

Material and Methods

Merino sheep from different selection lines on the Tygerhoek research farm in the Southern Cape area of South Africa provided material for the study. The climate at the site is Mediterranean, with a total annual precipitation of 425 mm, of which ~ 60% is recorded from April to September. The following selection lines were involved:

- Fleece weight – This line was selected since 1970 for an increase in clean fleece weight with a check on fibre diameter (Cloete *et al.*, 1998).
- Wet and Dry – Ewes in this line have been culled since 1993 on failure to lamb or to rear at least one lamb per lambing opportunity. During this period, rams were selected as was described by Cloete & Scholtz (1998). This line was discontinued in 2002, and data are only available up to the 2002 drop.
- Fine wool – This line was descended from a similar line maintained at Cradock (Olivier *et al.*, 1999), of which ewes were introduced to Tygerhoek during 1997. During the formation of this line, ewes were screened from their flocks of origin on the basis of a low fibre diameter and an above average live weight.
- Control – no directed selection was applied to this line since 1970, although a measure of random genetic drift was measured in some traits (Cloete *et al.*, 1998). It is maintained as a control for the other lines.

No directed selection for resistance to gastro-intestinal nematodes was applied in any of the lines. Progeny were maintained in single flocks (separated on sex) throughout the trial. Rectal faeces samples were obtained from individual animals at 13 to 16 months of age, after drenching was withheld for at least 10 weeks. Sampling took place during the years from 1995 to 2005. The exception was the progeny group of 2004, of which no samples were taken. Sampling generally took place in the winter-spring months of July-September. The heritability of FEC after natural infection was shown to be highest during the period from June to September under Mediterranean conditions in Western Australia (Greeff *et al.*, 1995). Experience of the pathogen species present at the experimental site during this time of the year suggest that the animals were likely to be subjected to a mixed challenge by *Ostertagia* and *Trychostrongylus* spp. The number of nematode eggs per sample was counted at the Western Cape Provincial Veterinary Laboratory, using the McMaster technique, with a sensitivity of 100 eggs per gram of wet faeces (Van Schalkwyk *et al.*, 1994). During the same period FEC was recorded, two-tooth data were also recorded. The traits under consideration included two-tooth live weight, clean fleece weight, fibre diameter, staple strength, coefficient of variation (CV) of fibre diameter and total fold score. These recordings were made on 2127 to 3470 individuals, born during the period from 1995 to 2005.

Untransformed FEC data were skew and leptokurtic (Table 1). These data were thus subjected to a cube root or log transformation. Both these transformations are commonly used to normalise FEC data (Eady, 1995; Woolaston & Piper, 1996; Khusro *et al.*, 2004; Morris *et al.*, 2005). The natural logarithm of FEC was computed, after 100 were added to FEC to account for zero counts. Both transformations markedly improved the distribution of the data, as depicted in Table 1. The ASREML program (Gilmour *et al.*, 1999) was used for the analysis of the fixed effects, and also subsequently to estimate variance components in single-trait animal model analyses. The first analysis involved fitting various combinations of fixed effects to obtain an operational model, including the effects of birth year (1995-2003; 2005), sex (male and female), age of dam (2 – 7 years) and birth type (singles and pooled multiples). All two-factor interactions were considered initially, but only the birth year x sex interaction was significant and was retained. Effects found to be significant ($P < 0.05$) in these preliminary analyses were included in an operational model for subsequent analyses. Random terms were added to the operational model, resulting in the following models for analyses (in matrix notation):

$$y = Xb + Z_1a + e \quad (1)$$

$$y = Xb + Z_1a + Z_2c + e \quad (2)$$

$$y = Xb + Z_1a + Z_3m + e \quad (3)$$

$$[\text{Covariance (a,m)}=0]$$

$$y = Xb + Z_1a + Z_3m + Z_2c + e \quad (4)$$

$$[\text{Covariance (a,m)}=0]$$

$$y = Xb + Z_3a + Z_3m + Z_2c + e \quad (5)$$

$$[\text{Covariance (a,m)}= A\sigma_{am}]$$

In these analyses, y was a vector of observations for untransformed FEC, cube root transformed FEC or log transformed FEC, and b , a , m and c vectors of fixed effects, direct genetic variances, maternal genetic variances and maternal permanent environmental variances respectively. X , Z_1 , Z_2 and Z_3 were the corresponding incidence matrices relating the respective effects to y , while e was the vector of residuals. A was the numerator relationship matrix, and σ_{am} the covariance between direct genetic and maternal genetic effects.

It was assumed that:

$$V(a) = A\sigma_a^2; V(m) = A\sigma_m^2; V(c) = I\sigma_c^2; V(e) = I\sigma_e^2,$$

With I being identity matrixes; σ_a^2 , σ_m^2 , σ_c^2 and σ_e^2 the direct genetic variance, maternal genetic variance and the maternal permanent environmental variance and environmental (residual) variance, respectively. These analyses yielded estimates of genetic and permanent environmental variances. Ratios for direct additive genetic and maternal permanent environmental variances were computed from these estimates. These variances were expressed relative to the total phenotypic variance. Likelihood Ratio tests (LRT) were performed to assess the significance of the contribution of each random term to improvements in the model for analysis. The LRT is based on testing twice the increase in Log-likelihood resulting from adding a random term to the model of analysis as a χ^2 statistic. Alternatively, for two models with the same number of random terms, and assuming identical fixed effect modelling, the model with the higher value for the Log-likelihood fits the data better. All analyses included the full pedigree file of animals from 1969 to 2005, consisting of 10850 individuals, the progeny of 949 sires and 3603 dams. Subsequently, two-trait animal models were fitted to calculate all relevant direct and maternal correlations of log transformed FEC with two-tooth live weight and wool traits. The wool traits under consideration were clean fleece weight, fibre diameter, staple strength, CV of fibre diameter and total fold score. Details of the single-trait and two-trait analyses on these two-tooth traits were omitted as it was recently reported by Matebesi *et al.* (2007), and the present analysis did not add any new information on the (co)variances among them.

Direct breeding values for log transformed FEC were obtained from the single-trait analysis with the best log likelihood, and averaged for the respective selection lines within birth years. Genetic trends derived in this way were inspected for differences between lines, using standard errors of the means to inspect line differences within birth years for significance. These breeding values were obtained from an analysis where selection line and its interactions with other traits were excluded from the operational model.

Results

Descriptive statistics for untransformed FEC indicated extreme variation and a non-normal distribution (Table 1). The properties of the data were markedly improved by the transformations applied, which validate the usage of these transformations. The log transformation improved the extreme variance in particular, resulting in a coefficient of variation of below 20%.

The type of transformation that was applied resulted in minimal changes in conclusions derived from the data as pertaining to the fixed effects analysed. Only the results obtained from the analysis involving log transformed FEC will thus be presented. Fixed effects that influenced the data significantly were sex, birth year the sex x birth year interaction (all $P < 0.01$) as well as birth type ($P < 0.05$). The effect of selection line approached significance ($P = 0.06$), while FEC was independent of dam age. In general, ewes excreted fewer worm eggs in their faeces than rams (Figure 1). However, the magnitude of the difference between

Table 1 Descriptive statistics for the faecal worm egg counts (FEC in eggs per gram wet faeces) of 3560 Merino two-tooth sheep from the Tygerhoek Merino flock during the period from 1995 to 2005

Trait	Mean ± s.d.	Range	CV (%)	Skewness	Kurtosis
FEC	799 ± 1204	0 – 13700	151	3.451	19.051
Cube root of FEC	6.93 ± 4.67	0 – 23.85	67	0.081	-0.464
Log of (FEC + 100)	6.15 ± 1.15	4.61 – 9.53	19	0.199	-0.917

rams and ewes differed between years, resulting in the observed interaction. During the earliest (1995 and 1996) and the most recent production years (2003 and 2005) the differences in FEC between ewes and rams were particularly large.

Multiple lambs had slightly lower means for log transformed FEC's than singles (6.11 ± 0.04 vs. 6.19 ± 0.04 , respectively; $P < 0.05$). Respective geometric means obtained by back transformation amounted to 354 for multiples compared to 388 for singles. Least squares means for log transformed FEC ranged from 6.09 ± 0.08 for the progeny of 7-year-old dams to 6.20 ± 0.05 for the progeny of 4-year-old dams ($P > 0.10$). Since detailed attention is given to the averaged breeding values of animals in the respective selection lines, no results for the phenotypic selection line differences will be presented here.

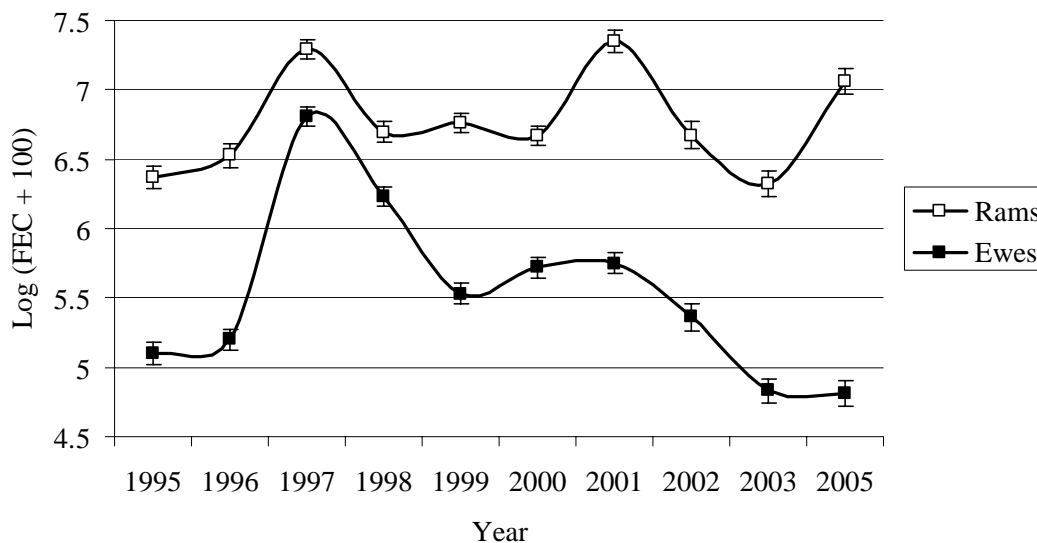


Figure 1 Least squares means depicting the interaction between birth year and sex for FEC in two-tooth animals from the Tygerhoek flock. Vertical bars about the means depict appropriate standard errors. (FEC - faecal worm egg count)

The single-trait animal model fitting the data best included direct additive effects as the only significant random source of variation in the case of untransformed FEC (Table 2). The “best” model for both cube root and log transformed FEC included direct additive and dam permanent environmental effects as random.

Heritability estimates derived from the variance components amounted between 0.14 for untransformed data to 0.18 for log transformed data, the estimate for cube root transformed data being intermediate (Table 3). Although the derived h^2 estimates did not differ from each other (when the s.e.'s

provided were considered), there is some evidence that the transformation of the data to ensure a better distribution resulted in a slightly higher estimate of the direct additive variation. Maternal variance components were of smaller magnitude for the transformed data sets, and accounted for ~ 5% of the overall phenotypic variation.

Table 2 Log Likelihood ratios for the respective random effects models fitted to the FEC data of two-tooth animals from the Tygerhoek flock. The model of choice is depicted in bold figures

Effects	FEC	Cube root of FEC	Log of (FEC + 100)
Fixed effects only	-6454.38	-6327.83	-1377.53
Fixed + h ²	-6427.58	-6282.64	-1329.13
Fixed + h ² + c ²	-6427.31	-6279.04	-1325.76
Fixed + h ² + m ²	-6426.14	-6280.80	-1327.58
Fixed + h ² + m ² + c ²	-6426.14	-6279.02	-1325.75
Fixed + h ² + m ² + r _{am} + c ²	-6426.26	-6277.33	-1324.49

FEC - faecal worm egg count

Table 3 Variance components and ratios (\pm s.e.) for FEC data of two-tooth animals from the Tygerhoek Merino flock

Component or ratio	FEC	Cube root of FEC	Log of (FEC + 100)
Variance components:			
Direct additive	163228	2.1641	0.14208
Maternal PE	-	0.65573	0.03754
Residual	964399	9.93791	0.59589
Variance ratios:			
h ²	0.144 \pm 0.029	0.170 \pm 0.032	0.183 \pm 0.033
c ²	-	0.051 \pm 0.019	0.048 \pm 0.019

FEC - faecal worm egg count

Pearson's correlations among the predicted breeding values derived from the respective data sets were computed. The correlation of untransformed FEC data with cube root transformed data amounted to 0.869. The corresponding correlation was 0.870 for the analysis involving log transformed FEC data. Breeding values derived from cube root transformed FEC data were highly correlated to log transformed FEC, the applicable correlation being 0.991.

It was hypothesised that the lower means for FEC in female animals may have resulted in these animals not being able to express their genetic superiority in terms of resistance to gastro-intestinal nematodes because of an inadequate natural challenge. Separate analyses were therefore conducted within gender groups to test this hypothesis. The overall mean for FEC in 1899 females was markedly lower than that of 1661 males. Respective mean values (\pm s.d.) were 385 \pm 748 vs. 1273 \pm 1431 for untransformed data, 4.83 \pm 4.10 vs. 9.32 \pm 4.10 for cube root transformed data and 5.62 \pm 0.98 vs. 6.75 \pm 1.08 for log transformed data. Despite these marked gender differences in FEC, no difference was found in the derived h² estimates from the respective gender groups. As a matter of fact, the h² estimate for log transformed FEC obtained

from females (0.226 ± 0.048) was slightly larger in absolute terms than the estimate of 0.203 ± 0.056 derived for males. Part of the phenotypic variation was partitioned to a dam permanent environmental variance ratio of 0.081 ± 0.039 in rams, while no such effect was found in ewes. However, owing to larger standard errors because of the smaller data sets, the gender difference in the derived h^2 estimates for rams and ewes did not approach significance ($P < 0.10$).

No clear genetic trends in log transformed FEC were discernable over the interval for which data were available (Figure 2), and it is obvious that none of the lines were subjected to directed selection to reduce FEC. Up to 2001, annual predicted breeding values for the line selected for clean fleece weight were generally higher than particularly the Wet and Dry line, with a few exceptions. The Control line was intermediate in most instances. The differences between lines were smaller since the year 2002, when only the Fleece weight selected line and the Control line were depicted. Overall means for breeding values of log transformed FEC were 0.124 ± 0.007 for the line selected for clean fleece weight, 0.054 ± 0.006 for the Control line, -0.036 ± 0.007 for the Fine wool line and -0.045 ± 0.006 for the Wet and Dry line. These comparisons are complicated by the fact that the Wet and Dry line and the Fine wool line were present for only part of the study period (1995 to 2002 for the Wet and Dry line and 1998 to 2005 for the Fine wool line). However, the overall means suggested that the line selected for clean fleece weight was the most susceptible to internal parasites, with the Wet and Dry and Fine wool lines being the most resistant ($P < 0.05$). The Control line was intermediate and significantly different from all the other lines ($P < 0.05$).

Further analyses involving the genetic correlations of FEC with two-tooth live weight and wool traits were based on a log transformation of FEC. A favourable (i.e. negative) genetic correlation of log transformed FEC with staple strength approached -0.50 (Table 4). The negative correlation with live weight did not differ from zero, although it exceeded -0.10 . The favourable genetic correlation (positive in this case because low values are desired for both traits) of log transformed FEC with CV of fibre diameter amounted to 0.30 . Clean fleece weight was unfavourably related to log transformed FEC, but the correlation was still low at ~ 0.20 . For practical purposes, fibre diameter and total fold score were unrelated to FEC on a genetic level, the absolute value of both correlations being lower than 0.03 .

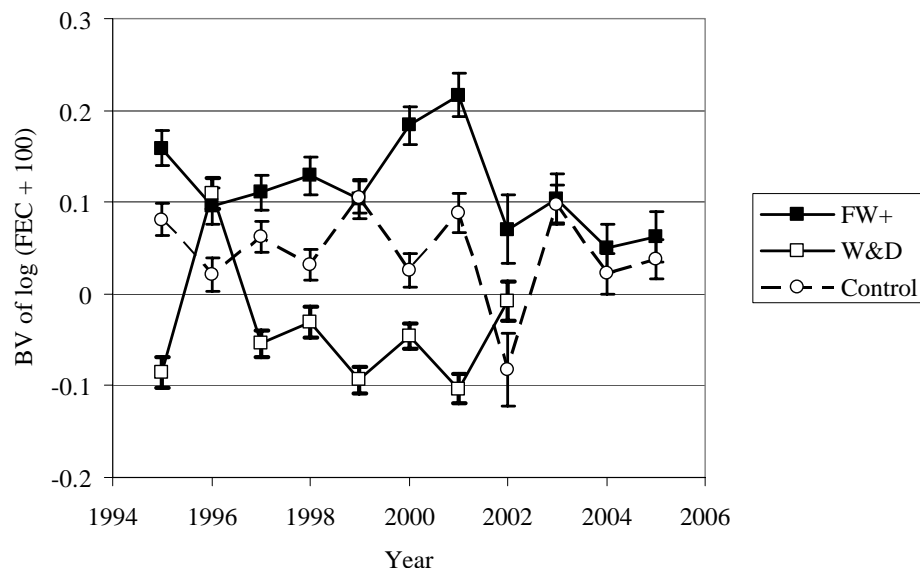


Figure 2 Averaged annual predicted breeding values for log transformed FEC according to selection line (FW+ – line selected for clean fleece weight; W&D – Wet and Dry line; Control – unselected control line). Vertical bars on graph represent standard errors. (FEC - faecal worm egg count)

Table 4 Genetic, environmental and phenotypic correlations (\pm s.e.) of log transformed FEC with two-tooth live weight and wool traits

Correlated trait	Type of correlation		
	Genetic	Environmental	Phenotypic
Live weight (kg)	-0.119 \pm 0.098	-0.074 \pm 0.034	-0.078 \pm 0.018
Clean fleece weight (kg)	0.190 \pm 0.089	-0.025 \pm 0.035	0.039 \pm 0.018
Fibre diameter (μ m)	-0.026 \pm 0.082	-0.036 \pm 0.048	-0.025 \pm 0.019
Staple strength (N/ktex)	-0.493 \pm 0.126	0.054 \pm 0.038	-0.066 \pm 0.023
CV of fibre diameter (%)	0.298 \pm 0.089	-0.030 \pm 0.040	0.081 \pm 0.020
Total fold score (n)	0.003 \pm 0.104	0.008 \pm 0.032	0.006 \pm 0.019

FEC - faecal worm egg count

Phenotypic and environmental correlations of log transformed FEC with two-tooth live weight were in the same direction as the genetic correlation, but of a somewhat smaller magnitude (Table 4). Environmental correlations for the wool traits with log transformed FEC were not significant. The favourable phenotypic correlations of log transformed FEC with live weight, staple strength and CV of fibre diameter were significant ($P < 0.05$), but below 0.10.

Discussion

Marked variation is commonly reported for FEC data. Means for FEC in three contemporary groups ranged from 612 to 7010 (Eady, 1995). Snyman (2007) reported individual FEC values ranging from 0 to 87800 in the Klerefontein Afrino flock. Khusro *et al.* (2004) reported respective means of 779 and 736 eggs per gram of faeces for yearling and hogget Merino sheep in the Australian National evaluation. Individual FEC values ranged from 0 to >50000 in both age groups. The transformations applied to the present data are commonly used in the literature. In their documentation involving genetic parameters for sheep, Safari & Fogarty (2003) list 26 h^2 estimates for FEC, of which a cube root transformation has been applied in 12 cases, and a log transformation in 14 cases. Means in these studies ranged from 2.75 to 22.6 for cube root transformed FEC and from 6.88 to 7.49 for log transformed FEC. In New Zealand Perendale sheep, log transformed FEC averaged 5.98 at 22 weeks of age and 6.20 at 30 weeks of age (Morris *et al.*, 2005). Results from the present investigation are consistent with these literature reports.

Results pertaining to the sex effect on FEC were variable in the study of Khusro *et al.* (2004). In yearling animals, rams had a lower mean for FEC than ewes, while the opposite was true in hoggets. The latter authors suggest that care should be taken in the interpretation of these results, as the experimental animals are always separated on gender. The same reasoning applies to the present investigation, where gender effects differed between years. In the study of Khusro *et al.* (2004) sex was completely confounded with contemporary group, and sex effects were removed by fitting contemporary group, much like the sex x year interaction constituted contemporary groups in this study. The lower FEC of multiples compared to singles is supported by a corresponding birth type difference in the study of Khusro *et al.* (2004). The latter study found no effects of dam age (fitted as a regression) on hogget FEC, as was also found in the present study.

Genetic parameters for FEC were included in the comprehensive review of genetic parameters for sheep (Safari *et al.*, 2005). Earlier estimates included in this review will therefore not be cited, unless pertinent to this study. The present h^2 estimates of 0.14 to 0.18 (depending on the transformation) are somewhat lower than the averaged estimate of 0.27 derived from 16 literature sources (Safari *et al.*, 2005). At least some of these estimates were derived from studies where artificial challenge was used, and where more control can be exercised upon the challenge delivered to the animals. An h^2 of 0.15 was estimated for cube root transformed FEC in naturally challenged Merino sheep under Mediterranean conditions, under climatic conditions fairly similar to those experienced in the present study (Greeff *et al.*, 1999). Khusro

et al. (2004) reported an h^2 of 0.21 for cube root transformed yearling FEC, while hogget FEC exhibited substantially more genetic variation with an h^2 of 0.38. These records were obtained from commercial properties, and limited information is available on the method of challenge. Pollott *et al.* (2004) reported that the h^2 of FEC increased from 0.20 at weaning to 0.65 at 400 days of age, with an average of 0.28. An industry data set of ~ 39000 records yielded an h^2 estimate of 0.24 for FEC, while the sire x environment interaction accounted for 3% of the phenotypic variation (Pollot & Greeff, 2004). Estimates of h^2 of log transformed FEC amounted to 0.22 at 22 weeks of age and to 0.16 at 30 weeks of age in New Zealand Perendale sheep subjected to natural challenge (Morris *et al.*, 2005). The latter study reported divergence in FEC after selection from 1986 to 2002. The h^2 of untransformed FEC in South African Afrino sheep subjected to artificial challenge with 4000 to 6000 infective *Haemonchus contortus* larvae was estimated at 0.19 (Snyman, 2007). The significant genetic variation (linked to high levels of phenotypic variation) and good correspondence with parameter estimates in the literature suggest that genetic progress in FEC in the Mediterranean parts of South Africa is more than likely. Realised genetic gains were reported under similar conditions (Karlsson *et al.*, 1995; Woolaston & Piper, 1996; Morris *et al.*, 2005). Selection for a reduced FEC is assumed to lead to benefits in parasite resistance with associated economic advantages in the local sheep flock, as was reported for Australian sheep flocks (Greeff *et al.*, 2006).

Cube root transformed FEC and log transformed FEC were affected by a dam permanent environmental variance ratio amounting to ~ 5% of the phenotypic variation. Safari *et al.* (2005) did not report maternal variance ratios for FEC in their overview of genetic parameters for sheep. However, Khusro *et al.* (2004) reported a maternal genetic effect of 0.06 for yearling FEC in their study, while no effect of the dam was evident for hogget FEC. The estimate for yearling FEC was in good agreement with the results of the present study. No attempt was made by Khusro *et al.* (2004) to partition the maternal variance in its genetic and permanent environmental components.

The Pearson's correlation between predicted breeding values for cube root transformed FEC and breeding values for log transformed FEC approached unity in the present study. A similar conclusion was made by Eady (1995) who found correlations of between 0.97 and 1.00 between breeding values derived from analyses on FEC using the square root, cube root and log transformations. Depending on the nature and distribution of the FEC data, both transformations may be applicable to South African data sets.

Selection line means for log transformed breeding values for FEC suggest that the line selected for clean fleece weight was more susceptible to internal parasitism than the other lines, and particularly the Wet and Dry and Fine wool lines. These means support phenotypic means reported previously by Cloete *et al.* (2000). The literature is undecided with regard to the genetic association of clean fleece weight with FEC. Unfavourable correlated responses were reported in the New Zealand literature for non-Merino breeds (Williamson *et al.*, 1994; Morris *et al.*, 2000; 2005). These results are supported by a fairly high unfavourable genetic correlation of 0.56 reported recently by Morris *et al.* (2005). Results from the present study would support these results, although the genetic correlation between log transformed FEC and clean fleece weight reported in Table 4 was substantially lower at 0.19. The latter correlation is in fair agreement with corresponding values of 0.15 and 0.13 reported by respectively Eady *et al.* (1998) and Morris *et al.* (2000). Khusro *et al.* (2004) reported the genetic correlation of FEC with greasy fleece weight at 0.07 in both yearlings and hoggets. The corresponding genetic correlations between FEC and clean fleece weight were 0.11 in yearlings and -0.01 in hoggets. Another industry data set yielded an overall genetic correlation of 0.05 between FEC and greasy fleece weight (Pollot & Greeff, 2004). In contrast, the overall genetic correlation between FEC and clean fleece weight derived from four literature sources by Safari *et al.* (2005) amounted to 0. This low correlation is supported by no evidence of a correlated response in clean fleece weight to selection for a reduced FEC in the Rylington Merino flock (Greeff *et al.*, 1999). In fact, no unfavourable correlated responses in any other production trait to selection for a reduced FEC were found by Karlsson *et al.* (1995). Even though some literature sources suggest an unfavourable genetic correlation between fleece weight and FEC in sheep, this relationship may not be sufficiently strong to preclude genetic progress in both traits in Merinos.

The genetic correlation of live weight with FEC was favourable (i.e. negative) but not significant. Corresponding genetic correlations (number of references) derived by Safari *et al.* (2005) from literature estimates were -0.03 for weaning weight (5), -0.24 for post-weaning weight (4) and -0.12 for mature weight (3). It has to be conceded that the derived estimates were associated with wide confidence intervals,

including positive values in all instances. Estimates obtained from the Australian National Merino Evaluation were -0.14 for yearling weight and -0.02 for hogget weight (Khusro *et al.*, 2004). Favourable genetic correlations of respectively -0.09 and -0.32 between FEC and live weight of Merinos were reported by Pollott & Greeff (2004) and by Pollott *et al.* (2004). The genetic correlation obtained in the present study is consistent with these estimates pertaining to sign and magnitude. Conversely, the genetic correlation of FEC with live weight in New Zealand Perendales was positive and fairly high at 0.36 (Morris *et al.*, 2005).

Fibre diameter appeared to be fairly independent of FEC on the genetic level. Safari *et al.* (2005) used three literature values to derive an averaged value of 0.01, while Khusro *et al.* (2004) obtained estimates of -0.05 for both yearling and hogget FEC. The corresponding estimate derived by Pollott & Greeff (2004) amounted to -0.04. All these estimates accorded with the value of -0.03 reported in the present study. Previous estimates for the genetic correlation of FEC with staple strength were variable, and generally lower than the present estimate of -0.49. Literature values included positive (i.e. unfavourable) estimates of 0.15 and 0.21 (Greeff & Karlsson, 1998) and 0.13 (Greeff & Karlsson, 1999). At -0.20, the genetic correlation reported by Pollott & Greeff (2004) between FEC and staple strength were similar in sign but lower in magnitude compared to the present study. However, a random regression approach yielded smaller estimates. Pollott & Greeff (2004) attributed the discrepancy between the point estimate and results yielded by the random regression approach to a relatively low number of animals with staple strength records. Based on these differences between literature sources, further research on the genetic relationship of FEC with staple strength appears to be warranted.

The genetic correlation of FEC with CV of fibre diameter was positive (i.e. favourable) in the present study. Three comparable estimates reported by Greeff & Karlsson (1998; 1999) ranged from -0.05 to 0.10. Two of these estimates were in the same direction as the correlation reported in Table 4, but smaller in magnitude. The genetic correlation of FEC with total fold score was negligible. No comparable results were found in the literature.

Phenotypic correlations derived from the literature for FEC with the other two-tooth traits were -0.08 for post-weaning live weight, 0.00 for clean fleece weight, and -0.02 for fibre diameter (Safari *et al.*, 2005). Phenotypic correlations of FEC with traits assessed in the Australian National Merino database were -0.02 with yearling live weight, 0.02 with yearling clean fleece weight and 0.01 with yearling fibre diameter (Khusro *et al.*, 2004). Corresponding correlations at a hogget age were -0.06, 0.02 and -0.02. These estimates were broadly consistent with those obtained in the present study.

Conclusions

Directed selection for the reduction of FEC seems feasible under natural challenge conditions in the Mediterranean parts of South Africa. According to Morris *et al.* (2004), a sound strategy for selection against intestinal nematode infestation should include resistance to worm infestation (as reflected by a low FEC) as well as resilience, i.e. an ability to maintain production in the presence of a parasite burden. The net effect of such a strategy would be a minimum contamination of the pasture being utilised, as well as minimal anthelmintic intervention. Age at first drench was considered as a measure of resilience in the latter study. This trait had an h^2 of 0.14, and was shown to respond to selection.

Selection for FEC is unlikely to result in marked unfavourable correlated responses in wool traits and live weight. The exception to this rule is clean fleece weight which may respond unfavourably when selection is based on FEC. However, with a genetic correlation of below 0.20 it seems as if genetic progress in both traits should be attainable, should it be desired. Research on genetic parameters for FEC and other traits of economic importance should continue to ensure that internal nematode control is dealt with in a sustainable manner in South African sheep flocks.

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