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Genetic parameters and relationships of faecal worm egg count with objectively measured wool traits in the Tygerhoek Merino flock

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Abstract

The costs of internal parasite control and treatment are potentially very high in grazing sheep. Faecal worm egg count (FEC) has been suggested as a suitable criterion for selection for resistance to nematode infestation in livestock. Genetic parameter estimates for FEC and its relationship with wool traits were assessed in the current study, using data from Merino sheep from a selection experiment maintained at Tygerhoek Research Farm. Data consisted of ~7 100 animals born between 1989 and 2010. Rectal faecal samples were taken from individual sheep at 13 to 16 months of age, after drenching had been withheld for at least 10 weeks, generally in July to September. Nematode eggs were counted with the McMaster technique, with a sensitivity of 100 eggs per gram of wet faeces. The fixed effects of birth type, sex, birth year and sex x birth year interaction were included in the operational model for FEC. Only the effect of additive animal affected the data for FEC. Heritability estimates of FEC ranged from 0.10 for untransformed FEC to 0.16 for Log (FEC + 100). The genetic relationships of Log (FEC + 100) with staple strength (SS), staple length (SL), coefficient of variation of fibre diameter (CVFD) and standard deviation of fibre diameter (SDFD) were favourable. The genetic correlations of FEC with wool weight traits were unfavourable in absolute terms, but not significantly different from zero. Selection for FEC is unlikely to result in unfavourable correlated responses to wool traits in South African Merinos, with the exception of wool weights.

Keywords: Internal parasites, fleece weight, fibre traits, staple traits, correlations, resistance
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Introduction

Internal parasite infestations constitute a major disease problem for domestic livestock, which poses a threat to sustainable production worldwide (Karlsson *et al*., 1995; Zhang *et al*., 1997; Nieuwoudt *et al*., 2002; Perry *et al*., 2002; Chauhan *et al*., 2003). Grazing livestock is often at the highest risk from infection by gastro-intestinal nematode parasites (Bisset *et al*., 1992; Chauhan *et al*., 2003). Internal parasites cost sheep producers hundreds of millions of dollars each year (Brown & Tier, 2003; Khusro *et al*., 2004) because of expense of treatment, increased level of management and vigilance, loss of production and even mortality in severe cases (Nieuwoudt *et al*., 2002; Brown & Tier, 2003; Khusro *et al*., 2004; Snyman, 2007).

Resistance of gastro-intestinal parasites to anthelmintics has become more prevalent over the past years (Gray, 1991; Eady, 1995; Karlsson *et al*., 1995; Greeff & Karlsson, 1999; Nieuwoudt *et al*., 2002) and is now at a very high level that threatens sustainable control and treatment of internal parasites (Karlsson & Greeff, 2006; Snyman *et al*., 2007; Reynecke *et al*., 2011). In addition, there has been growing concern that consumers demand animal products that are free from contamination of chemicals (Khusro *et al*., 2004). Research suggested that selection for resistance to nematode infestation and its inclusion into the breeding objectives should receive attention (Gray, 1991; Eady, 1995; Amer *et al*., 1997; Vatta *et al*., 2000). Integrated parasite control measures (Karlsson, 1999; Nieuwoudt *et al*., 2002) may contribute towards reducing the parasite burden in a variety of small ruminants. Gary (1991) identified faecal worm egg count (FEC) as a valuable criterion for improving genetic resistance to gastro-intestinal nematodes.

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As a result, FEC has been widely used to estimate genetic variation in resistance to nematode infestation in sheep (Greeff *et al*., 1995; Morris *et al*., 1996; 1997; Cloete *et al*., 2000; Khusro *et al*., 2004; Yadav *et al*., 2006; Cloete *et al*., 2007; Snyman, 2007) and goats (Mandonnet *et al*., 2001; Olayemi *et al*., 2001; Chauhan *et al*., 2003; Mandal & Sharma, 2008). Several authors have reviewed genetic parameters for resistance to nematodes in sheep (Safari *et al*., 2005; Morris, 2011). The evidence of successful Australian (Pocock *et al.,* 1995; Woolaston & Piper, 1996; Greeff *et al*., 1999; Greeff *et al*., 2006) and New Zealand (Bisset & Morris, 1996; Morris *et al*., 2005) breeding programmes for resistance and resilience (Morris *et al*., 2010) to nematode infestation may guarantee economic advantages in South African Merino sheep.

In South Africa, published reports could not be found on breeding programmes for resistance to nematode infestation. However, a few studies estimated genetic parameters for nematode resistance in sheep, using FEC as an indicator trait (Cloete *et al*., 2000; Bisset *et al*., 2001; Nieuwoudt *et al*., 2002; Cloete *et al*., 2007; Snyman, 2007) with only two publications on genetic correlations of FEC with other traits of economic importance (Cloete *et al*., 2000; 2007). Other published reports on genetic parameters for nematode resistance used the clinical evaluation of anaemia and body condition score system (Famacha) in South African small ruminants (Van Wyk & Bath, 2002; Vattaa & Lindberg, 2006). Current South African published reports on genetic correlations of FEC and other traits do not include all traits of economic importance in wool sheep, such as staple length (SL), greasy fleece weight (GFW), clean yield (CY) and standard deviation of fibre diameter (SDFD). Relationships of FEC with wool traits are limited in the literature. The suggestions by Cloete *et al.* (2007) for further investigations on genetic parameters for FEC and other traits of economic importance in South African sheep flocks are heeded to owing to the paucity of analyses of FEC data in local sheep flocks.

The objectives of the present study were to estimate the (co)variance components and ratios as well as genetic, phenotypic and environmental correlations between FEC and objectively measured wool traits in South African Merino sheep.

Material and Methods

Performance records were obtained from four lines (a line selected for clean fleece weight, a fine wool line, an unselected control line, and a line selected against failure to lamb or to rear a lamb per lambing opportunity) of Merino sheep born on Tygerhoek Experimental Farm, Western Cape Department of Agriculture, near Riviersonderend in Western Cape, South Africa. The lines were not genetically linked, but the offspring were managed in the same contemporary group. The animals providing the data were the progeny born between 1989 and 2012. Pedigree records were collected from 1969 to 2012. The data included ~7 500 animals, the progeny of 567 sires and 2 605 dams. The origin and initial selection in the flock were first described by Heydenrych (1975) and Heydenrych *et al*. (1984). Subsequent analyses on animals from the flock involved studies on reproduction (Cloete, 1986), early liveweight, testicular size and reproduction (Duguma, 2002), objective wool traits, subjective wool traits and conformation traits, as well as liveweight at 16 months (Matebesi-Ranthimo, 2007).

There was no direct selection for FEC in any of the lines, as indicated by Cloete *et al*. (2007). The description of flock maintenance, husbandry, experimental design and sampling procedures for FEC was described by Cloete *et al*. (2007). The rectal faeces samples were obtained from 1995 to 2012 (with the exception of 2004) from individual animals between the ages of 13 and 16 months. The sampling was conducted after drenching had been withheld for at least 10 weeks, generally in July to September. During this time, animals are likely to be subjected to a mixture of *Ostertagia* and *Trychostrongylus* spp. (Cloete *et al*., 2007). Individual faecal samples were then assessed for FEC at 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).

Traits that were analysed were FEC, greasy fleece weight (GFW), clean fleece weight (CFW), clean yield (CY), fibre diameter (FD), staple length (SL) and staple strength (SS). Two measurements of the variability of FD were included in the analysis, namely standard deviation of FD (SDFD); and coefficient of variation of FD (CVFD). GFW was recorded at shearing in August–September each year, while the measures of quality were determined on a midrib wool sample taken from each animal at 14 - 16 months of age. Information on GFW was combined with CY data to derive CFW. Data for FEC were transformed to logarithms to the base of 10 (after a base number of 100 was added to each value to account for zero counts) or to cube roots to improve data distribution. These transformations have been used extensively by a number of researchers to normalize FEC data in Australia (Greeff *et al*., 1995; Karlsson *et al*., 1995; Doyle & Eady, 2001; Brown & Tier 2003; Pollott & Greeff, 2004), New Zealand (Morris *et al*., 1997), India (Yadav *et al*., 2006), South Africa (Cloete *et al*., 2007) and the United Kingdom (Matika *et al*., 2010). Untransformed data and data subjected to the transformations listed above resulted in three analyses on FEC.

The statistical analysis was done with the ASREML program (Gilmour *et al*., 2009). Initially the overview observation of the data structure was performed with the objective of identifying the abnormalities and biological feasibility of the records in the datasets. All animals without a sire or dam, birth status or sex were excluded from the analysis. Dams aged 7 years and beyond were pooled together. Triplets and twins were pooled as multiples. All animals without records were excluded from the analysis. Animals with a missing record for a particular trait were excluded from the analysis for that particular trait.

The significance of fixed effects was tested, leaving only significant effects in the final operational model. Fixed effects from the analyses were consistent with those reported in the literature, and thus were not presented and discussed further. The following fixed effects model was fitted for all traits:

$$Y_{ijklmnp} = \mu + s_j + bt_k + ad_l + y_m + g_n + sy_p + e_{ijklmnp}$$

where $Y_{ijklmnp}$ = an observation of a trait on the ith animal of the jth sex of the kth birth status from the lth age of the dam, mth birth year, nth line and pth sex by birth year interaction.

μ = the overall mean
s_j = the fixed effect of the jth sex (j = ram, ewe)
bt_k = the fixed effect of the kth birth status (k = singles, multiples)
ad_l = the fixed effect of the lth age of dam class (l = 2, 3, 4, 5, 6,7^{+} years)
y_m = the fixed effect of the mth birth year class (m = 89, 90, 91, …, 110)
g_n = the fixed effect of the nth line (n = 1, 2, 3, 4)
sy_p = the fixed effect of the pth sex by birth year interaction (n = 1, 2, 3, …, 42)
$e_{ijklmnp}$ = randomly distributed residual variance used as error term to test the other effects for significance.

The (co)variances components were estimated and obtained by fitting single-trait animal models initially. These models include a combination of direct additive, maternal additive and maternal permanent environmental effects, as well as the covariation between direct additive and maternal additive effects. Six forms of single-trait mixed animal models (in matrix notation) were fitted for all traits:

Model 1 $Y = X\beta + Z_1a + e$
Model 2 $Y = X\beta + Z_1a + Z_2m + e$ {with cov (a, m) = 0}
Model 3 $Y = X\beta + Z_1a + Z_2m + e$ {with cov (a, m) = $A\sigma_{am}$}
Model 4 $Y = X\beta + Z_1a + Z_2m + Z_3c + e$ {with cov (a, m) = 0}
Model 5 $Y = X\beta + Z_1a + Z_2m + Z_3c + e$ {with cov (a, m) = $A\sigma_{am}$}
Model 6 $Y = X\beta + Z_1a + Z_3c + e$

where Y is a vector of observations; β is a vector of fixed effects influencing traits; a, m, c are vectors of direct additive, maternal additive (dam) permanent maternal environmental and e is residual effects, respectively. X, Z_1, Z_2 and Z_3 are considered incidence matrices relating observations to their respective fixed and random effects. It was assumed that:

$$V(a) = A\sigma^2_a;\ V(m) = A\sigma^2_m;\ V(c) = Id\sigma^2_c;\ V(e) = I\sigma^2_e$$

where **A** is the numerator relationship matrix among animals in the pedigree file, and **I** is an identity matrix. The variances, σ^2_a, σ^2_m, σ^2_c, σ^2_e, were defined as the direct genetic variance, the maternal genetic variance, the permanent environmental variance due to the dam and the residual (error) variance, respectively. The phenotypic variance (σ^2_p) was defined as the sum of all variance components estimated in the model of analysis, and could be derived from all the above variances, as appropriate for the specific analysis. Heritability estimates were calculated as σ^2_a/σ^2_p and the maternal heritability as σ^2_m/σ^2_p.

The significance of the random effects was tested using log likelihood ratio tests after the inclusion of one additional random effect added to the model sequentially. A random effect was considered significant when its inclusion in the model caused a significant improvement in the log likelihood ratio. A chi-square distribution of $\alpha = 0.05$ at one degree of freedom was used as a test statistic (3.841). When −2 times the difference between the log likelihoods was greater than this critical value, the inclusion of the particular random effect was considered to significantly improve the fit of the model (Swalve, 1993). The objective of testing the significance of the various models was to identify the best and simplest models that could be used for subsequent runs. Therefore, the model with the least possible number of random effects was used when the inclusion of additional random effects did not significantly improve the observed log likelihood ratio.

The genetic, environmental and phenotypic correlations between FEC and objectively measured wool traits were estimated by fitting a series of two-trait and four-trait models. Starting values for the (co)variance components of two- and four-trait models were obtained from the single-trait models fitted initially.

Results and Discussion

The fixed effects of birth type (single/multiple, $P < 0.05$), sex (male/female), year of birth (1989 - 2003, 2005 - 2012) and the sex*birth year interaction had a significant ($P < 0.01$) effect on FEC. Transforming FEC data did not change the significance of the fixed effects. These results are consistent with those reported by Cloete *et al*. (2007) on the same Merino resource flock. A similar set of fixed effects for FEC, combined with selection line (1 - 4) and age of dam (2 - 7^+), significantly affected all objectively measured wool traits, and were included in the models used for subsequent analyses. The least square means depicting the influence of the fixed effects under consideration generally corresponded with those reported in the literature for wool and dual-purpose sheep (Safari *et al*., 2005). These effects are therefore not reported in detail, because it would duplicate results that have already been well described.

The descriptive statistics reported a considerable variation in the number of records used for the current study, ranging from 3 842 for SS to 7 274 for FD (Table 1). Untransformed FEC data suggested very high variation and a non-normal distribution, which were similar to findings reported by Pollott & Greeff (2004), Yadav *et al*. (2006) and Cloete *et al*. (2007). However, the application of transformations on data improved their properties to a point that the coefficient of variation was 19.77% in the log-transformed data. This indicated the need to transform data to improve the distribution. All objectively assessed wool traits were variable in the present study (Table 1). The wool quality traits CY and FD showed lower levels of variation (<11%) than the other objectively measured wool traits.

Table 1 Descriptive statistics of data used after editing from a Tygerhoek Merino resource flock (n = number of records, SD = standard deviation and CV = coefficient of variation)

Trait	N	Mean	SD	CV (%)	Minimum	Maximum
Faecal egg count traits (eggs per gram wet faeces)						
Faecal worm egg count (FEC)	5891	660.3	1203.0	182.27	0	32 700
FEC (Log+100)	5891	2.57	0.508	19.77	2.000	4.516
FEC (cube root)	5891	5.879	4.883	83.06	0	31.98
Objective wool traits						
Greasy fleece weight (kg)	7273	4.96	1.24	25.00	1.0	9.4
Clean fleece weight (kg)	7273	3.56	0.91	25.56	0.7	7.0
Clean yield (%)	7273	71.97	4.61	6.41	49.9	98.4
Staple length (mm)	7000	91.10	15.23	16.72	33.0	144.1
Staple strength (N/Ktex)	4294	34.81	12.25	35.19	2.0	77.0
Fibre diameter (µm)	7274	19.15	2.06	10.76	13.2	27.6
CV of fibre diameter (%)	6133	19.41	2.88	14.84	11.9	39.0
SD of fibre diameter (µm)	6133	3.69	0.74	20.05	2.1	6.8

FEC: untransformed faecal worm egg count data; FEC (Log+100): log-transformed data + 100 to cater for 0.
FEC (cube root): cube-root-transformed data.

An appropriate random effects model is important for the accurate estimation of genetic parameters in livestock (Van Wyk *et al*., 2003). The model with only the direct additive (σ^2_a) effect fitted the data best for all the FEC traits in the present study (Table 2). A similar random model was used in Australian Merinos (Pollott & Greeff, 2004). However, Cloete *et al*. (2007) fitted a different random model including both σ^2_a and dam permanent environmental effects (σ^2_{pe}) on the same Merino resource flock. In addition, Khusro *et al*. (2004) fitted different random effects models with σ^2_a and maternal additive (σ^2_m) effects on Australian Merinos, but did not partition the maternal variance into σ^2_m and σ^2_{pe}. The inclusion of only additive genetic variance fitted the data best for CY, SL, SS, CVFD and SDFD. A substantial number of these researchers did not find any maternal influence on the expression of corresponding traits on various sheep breeds. Maternal effects in addition to σ^2_a were present in the FD analysis, while the covariance between animal effects (σ_{am}) as well as σ^2_{pe} contributed to the variation of GFW and CFW. Several studies reported significant σ^2_m effects on wool weights in various sheep breeds. In contrast, Vaez Torshizi *et al.* (1996) reported no significant σ^2_m for any of the corresponding wool traits beyond 12 months of age. Some studies also reported the σ^2_{pe} having a significant effect on FD. However, Safari *et al.* (2007b) found a significant σ^2_m, σ_{am}, σ^2_{pe} as well as a litter effect on 14 - 17 months of age for GFW, CFW, FD, CY, SDFD and CVFD. The literature and the results from this investigation strongly indicate that more random effects should be considered during the analysis of models for FEC and also for some of the objectively measured wool traits.

Table 2 Log likelihood ratios for random effects model fitted to FEC and objectively measured wool traits data of Tygerhoek Merino resource flock with "best" model in bold

	Model 1	**Model 2**	**Model 3**	**Model 4**	**Model 5**	**Model 6**
Faecal egg count traits						
FEC	**−3630.44**	−3630.14	−3629.76	−3630.14	−3629.75	−3630.33
FEC(cube root)	**−5020.82**	−5020.53	−5020.51	−5020.53	−5020.51	−5020.74
FEC(Log+100)	**2578.45**	2579.74	2580.04	2580.35	2580.01	2579.20
Objective wool traits						
GFW	−2154.58	−2141.26	−2135.31	−2138.28	**−2132.35**	−2140.58
CFW	−267.346	−254.012	−246.262	−251.568	**−243.533**	−254.328
CY	**−3424.37**	−3423.76	3423.44	−3423.76	−3423.11	−3424.35
SL	**−8730.07**	−8730.07	−8729.02	−8730.03	N/C	−8730.03
SS	**−2450.77**	−2450.77	N/C	−2450.76	N/C	−2450.76
FD	−4926.91	−4924.16	**−4922.86**	−4924.16	−4922.86	−4926.27
CVFD	**−7813.53**	−7813.53	N/C	−7813.53	N/C	−7813.53
SDFD	**1689.40**	1689.40	N/C	1689.39	N/C	1689.40

FEC: faecal worm egg count; GFW: greasy fleece weight; CFW: clean fleece weight; CY: clean yield; SL: staple length; SS: staple strength; FD: fibre diameter; CVFD: coefficient of variation of fibre diameter; SDFD: standard deviation of fibre diameter; N/C: not significant.

Genetic parameters for FEC and wool traits are presented in Table 3. FEC was heritable regardless of the type of transformation applied to datasets (Table 3). The present heritability (h^2_a) estimates ranged from 0.10 for untransformed data to 0.16 for log-transformed data. The present range coincides with the corresponding range of 0.14 for untransformed FEC to 0.18 for log-transformed FEC reported earlier using data of the same Merino resource flock (Cloete *et al*., 2007). The h^2 estimates in this investigation for FEC are lower than the averaged value of 0.27 derived from a mixture of naturally and artificially challenged sheep datasets (Safari *et al*., 2005). The present h^2_a estimate for untransformed FEC data of 0.10 is lower than the estimate of 0.19 for South African Afrino sheep exposed to 4 000 - 6 000 artificial *Haemonchus contortus* infective larvae challenge (Snyman, 2007).

The cube-root-transformed FEC data yielded a h^2_a of 0.15, which is on the lower boundary of a range of 0.15 to 0.70 (all cube root transformed) from literature values (Greeff & Karlsson, 1998; Greeff *et al*., 1999; Woolaston & Windon, 2001; Khusro *et al*., 2004; Pollott *et al*., 2004; Huisman *et al*., 2008; Afolayan *et al*., 2009; Brown *et al*., 2010), the lowest being found in Merino flocks experiencing similar challenges and Mediterranean climatic conditions to those used in the current study (Greeff *et al*., 1999). Most of the comparable studies, however, did not indicate the method of challenge, and were conducted on industry datasets. Because FEC was counted at a relatively low accuracy of 100 eggs per gram of wet faeces, this could have contributed to the observed lower h^2_a estimates. The FEC (Log+100) data yielded an h^2_a estimate of 0.16 for FEC in the present study. This value is lower than the estimate of 0.24 reported in a South African Merino flock (Nieuwoudt *et al*., 2002). Morris *et al*. (2005) reported a higher h^2_a estimate of 0.22 at 22 weeks of age and a comparable value of 0.16 at 30 weeks of age in naturally challenged Perendale sheep in New Zealand. Yadav *et al*. (2006) also reported a higher value of 0.24 for Muzaffarnagari sheep. Raimundo *et al*. (2009) reported a range of 0.04 - 0.27 and 0.01 - 0.52 for Santa Ines lambs exposed to natural challenge on two separate occasions. The h^2_a estimate reported for Romney sheep selected for resilience/resistance under natural nematode parasite challenge was higher at 0.26 (Morris *et al.*, 2010). More recently, Pickering *et al.* (2012) reported marginally higher h^2_a estimates of 0.18 measured in summer and 0.19 measured in autumn for New Zealand dual-purpose sheep breeds. Genetic selection also reduced FEC substantially in an Australian Merino resource flock (Woolaston *et al.*, 1997). Phenotypic and genetic variation of FEC in the current study, as well as in the literature, suggests that worthwhile genetic progress in South African sheep breeds is feasible. Selection for reduced FEC resulted in increased profit in Australia (Greeff *et al.*, 2006), which could be achieved in South Africa if sound data collection procedures are followed, and the timing of sampling for FEC is optimized (Greeff & Pollott, 2004).

Table 3 (Co)variance components and ratios for faecal worm egg count and objectively measured wool traits in Tygerhoek Merino flock

	FEC	**Cube root FEC**	**Log of (FEC+ 100)**	**GFW**	**CFW**	**CY**	**SL**	**SS**	**FD**	**CVFD**	**SDFD**
(Co)variance components											
σ^2_a	113428	2.06	0.024	0.24	0.22	11.44	35.29	29.30	1.12	3.43	0.16
σ^2_m		-	-	0.06	0.04	-	-	-	0.06	-	-
σ^2_{pe}		-	-	0.03	0.02	-	-	-	-	-	-
σ_{am}		-	-	−0.06	−0.04	-	-	-	−0.06	-	-
σ^2_e	1004740	11.84	0.126	0.46	0.23	6.89	51.81	98.90	0.62	2.23	0.10
σ^2_p	1118200	13.91	0.15	0.76	0.45	18.33	87.10	128.20	1.74	5.70	0.26
Variance ratios											
h^2_a	0.10	0.15	0.16	0.46	0.49	0.62	0.40	0.23	0.65	0.60	0.62
SE	0.02	0.01	0.02	0.04	0.04	0.02	0.03	0.03	0.04	0.03	0.03
h^2_m	-	-	-	0.07	0.08	-	-	-	0.03	-	-
SE	-	-	-	0.02	0.03	-	-	-	0.01	-	-
c^2_{pe}	-	-	-	0.04	0.04	-	-	-	-	-	-
SE	-	-	-	0.02	0.02	-	-	-	-	-	-
r_{am}	-	-	-	−0.56	−0.52	-	-	-	−0.24	-	-
SE	-	-	-	0.09	0.08	-	-	-	0.11	-	-

FEC: faecal worm egg count; GFW: greasy fleece weight; CFW: clean fleece weight; CY: clean yield; SL: staple length; SS: staple strength; FD: fibre diameter; CVFD: coefficient of variation of fibre diameter; SDFD: standard deviation of fibre diameter.
σ^2_a: direct additive genetic variance; σ^2_m: maternal additive genetic variance; σ^2_{pe}: permanent environmental variance; σ^2_e: residual variance; σ^2_p: total phenotypic variance; σ_{am}: covariance between direct and maternal additive genetic effects; h^2_a: direct heritability; h^2_m: maternal heritability; r_{am}: genetic correlation between direct and maternal additive genetic effects.

Objective wool traits have been studied in the past and were reviewed recently by Safari *et al.* (2005). Studies included in that review and Matebesi *et al.* (2009) will be cited only if they are highly comparable with the current study. Wool weights were highly heritable at 0.46 for GFW and 0.49 for CFW in the current study, and were within the range of literature values. Current estimates accord well with those reported by Safari *et al.* (2007b; 0.46 for GFW and 0.42 for CFW), in which they emphasized a preciseness of their estimated values owing to the pooling of records from a number of Australian Merino resource flocks. Contrary to this study, Brown *et al.* (2010) reported a higher h^2_a range of 0.66 to 0.74 for GFW in Australian Merinos from a combination of two-trait analyses. CY was highly heritable at 0.65. The current h^2_a value is consistent with the previous estimates in the same Merino flock (Naidoo *et al.*, 2004; Matebesi *et al.*, 2009). Crossbred ewes had a lower h^2_a of 0.53 for CY when two-trait analyses were involved (Afolayan *et al.*, 2009). Studies on the major four representative strains of Australian Merino sheep yielded a lower h^2_a estimate of 0.54 for CY (Mortimer *et al.*, 2009).

Fibre diameter, the primary determinant of wool price (Purvis, 1995; Purvis & Swan, 1999), was highly heritable at 0.66 in the current study. The current h^2_a estimate is higher than the weighted mean value of 0.59 derived from a number of literature estimates (Safari *et al*., 2005). A very high h^2_a value of 0.92 was obtained from two-trait analyses involving crossbred ewes (Afolayan *et al*., 2009). Two measures of FD (CVFD and SDFD) were highly heritable at 0.60 and 0.62, respectively. The current h^2_a estimate of 0.23 for SS is lower than the weighted mean of 0.34 derived from literature values (Safari *et al*., 2005) and the range of values amounting to between 0.33 and 0.47 from recent studies on South African and Australian Merino sheep (Matebesi *et al*., 2009; Mortimer *et al*., 2009; Brown *et al*., 2010). SL seemed to be moderately heritable at 0.41. The current h^2_a estimate accords well with those estimated earlier on the same Merino resource flock, as well as the weighted mean estimated for wool sheep (Safari *et al*., 2005; Huisman *et al*., 2008; Matebesi *et al*., 2009; Mortimer *et al*., 2009; Brown *et al*., 2010).

The two wool weight traits were dependent on maternal genetic effects, amounting to 0.07 for GFW and 0.08 for CFW. These values are within the range of values obtained from the literature. The estimate of h^2_m accounted for 2% for FD in the present study, which is similar to the estimate reported for Australian Merinos (Huisman *et al*., 2008). Brown *et al*. (2005) did not find any maternal influence on FD. These results indicated that maternal effects are not that important as far as the expression of FD is concerned. Corresponding c^2_{pe} effects accounted for 4% of the total phenotypic variance for both fleece weight traits, which was slightly lower than the value of 0.05 estimated earlier (Matebesi *et al*., 2009). The results from the present study, those of Safari *et al.* (2007b), and those of Matebesi *et al*. (2009) suggest that h^2_m is generally more important than c^2_{pe} when wool traits of 16-month Merino sheep are considered.

The significant and negative correlations between direct and maternal genetic effects (r_{am}) were estimated at −0.30, −0.56 and −0.59 for FD, GFW and CFW, respectively (Table 3). Previous r_{am} estimates on the same Merino resource flock were higher at −0.65 for GFW and −0.70 for CFW (Matebesi *et al*., 2009). However, Huisman *et al*. (2008) reported lower values of −0.29 for GFW and −0.35 for CFW using a comparatively larger dataset. The differences between studies may be because the model reported on their analysis did not include c^2_{pe} effects, even though it was the best model according to the log likelihood ratio test. In their analysis, Huisman *et al*. (2008) indicated that the model that fitted fewer parameters and gave sensible results was preferred over other models based on the Bayesian information criterion value.

The relationships between FEC (Log+100) and objectively measured wool traits from two-trait analysis will be presented and discussed in the section on genetic correlations. The outcome of analyses involving cube root transformed FEC closely corresponded with those involving log transformed FEC, making the presentation of both sets of results superfluous. Therefore the estimates of genetic, phenotypic and environmental correlations between FEC (Log+100) and objectively measured wool traits are presented in Table 4. Wool weights were genetically unfavourable related to FEC. The magnitude of all genetic correlations, however, was lower than 20% in all cases, and did not reach significance (i.e. below double the corresponding standards error). An average r_g of 0.00 for wool weight with FEC was derived from four

Table 4 Correlations between faecal worm egg count and objectively measured wool traits in Tygerhoek Merino flock

Trait	Genetic (r_g)	Environment (r_e)	Phenotypic(r_p)
FEC(log+100) with:			
GFW	0.173 ± 0.095	0.011 ± 0.022	*0.040 ± 0.014
CFW	0.155 ± 0.095	0.027 ± 0.022	*0.051 ± 0.014
CY	0.053 ± 0.073	−0.016 ± 0.027	0.007 ± 0.015
SL	−0.006 ± 0.088	−0.014 ± 0.025	−0.009 ± 0.016
SS	*−0.540 ± 0.103	*0.079 ± 0.026	*−0.036 ± 0.014
FD	−0.091 ± 0.078	−0.003 ± 0.029	−0.029 ± 0.016
CVFD	*0.326 ± 0.072	−0.052 ± 0.027	*0.060 ± 0.015
SDFD	*0.253 ± 0.073	−0.057 ± 0.030	*0.043 ± 0.015

FEC (Log+100): log transformed data + 100 to cater for 0 GFW: greasy fleece weight; CFW: clean fleece weight;
CY: clean yield; SL: staple length; SS: staple strength; FD: fibre diameter; CVFD: coefficient of variation of fibre diameter
SDFD: standard deviation of fibre diameter.
* Significant correlation.

literature values in a review by Safari *et al*. (2005). A previous study on the same Merino resource flock yielded a r_g estimate of 0.19 between FEC and CFW (Cloete *et al*., 2007), which is slightly higher than the value of 0.16 derived in the current study. The results of genetic relationships of FEC with wool weights obtained from the current study are in line with those reported in Australian Merinos pertaining to sign and magnitude (Khusro *et al*., 2004), with the exception of the estimated r_g of −0.01 between CFW and FEC at the hogget stage in the study by Khusro *et al*. (2004). Similar values were estimated for the r_g of FEC with GFW (0.15) and CFW (0.13) in Australian Merinos (Pollott & Greeff, 2004). A recent study in New Zealand dual-purpose sheep breeds (Pickering *et al*., 2012) also reported unfavourable r_g estimates for fleece weight with FEC at 12 months in summer (0.11) and in autumn (0.17). CY was unfavourably related to FEC in absolute terms, but the estimate was smaller than the corresponding standard error. No comparable estimates were found in the literature.

The results from the present study suggested that FD was unfavourably genetically related to FEC – 0.09 ± 0.08 – but the estimate was not significant. Previous studies on Merino sheep reported the same inferences (Khusro *et al*., 2004; Pollott & Greeff, 2004; Safari *et al*., 2005; Cloete *et al*., 2007) following a very low range of r_g estimates (−0.05 to 0.01) derived from genetic studies involving FD and FEC. Two measures of variation in FD (CVFD and SDFD) were positively related to log transformed FEC at genetic level. A positive r_g is favourable in this instance, as lower values are striven for FEC, as well as in CVFD and SDFD. A similar result was obtained for the r_g of log transformed FEC with CVFD in a previous study on the same Merino resource flock (Cloete *et al*., 2007). The current r_g estimates of 0.33 for CVFD and 0.25 for SDFD are higher than those (0.09 and 0.10) reported by Greeff & Karlsson (1998), as well as the value of −0.05 reported by Greeff & Karlsson (1999) between FEC and CVFD. Favourable phenotypic relationships were observed between FEC and CVFD, as well as SDFD. These results suggested a reduced CVFD in animals with a lower FEC. It is evident from the current results that environmental effects affecting FEC do not affect measures of FD conclusively. Similar results were reported between FEC and CVFD in South African Merinos (Cloete *et al*., 2007). No comparable results were found for correlations of FEC with SDFD.

The r_g of FEC with SS was comparatively high and negative in sign in the current study at >−0.50 (Table 4). Studies in Australian Merinos yielded a lower r_g estimate of −0.20 where regression analysis was used (Greeff & Pollott, 2004). Cloete *et al*. (2007) reported a similar r_g estimate of –0.49 using the same Merino flock. However, these results suggested that SS may be improved when animals are selected for a reduced FEC. At genetic level, SL was favourably related to FEC in absolute terms, although the correlations were very small with high standard errors. Studies in Australian Merinos also yielded a favourable relationship that was below 10% in magnitude (Greeff & Karlsson, 1998). The results from the literature and obtained in the current study suggested that no detrimental effect is likely on SL if selection for FEC is included in Merino sheep breeding objectives when worm infestations may lower productivity.

Phenotypic and environmental correlations between wool weight and FEC (Log+100) were unfavourable but low. This is consistent with the values obtained from the literature (Khusro *et al*., 2004; Pollott & Greeff, 2004; Safari *et al*., 2005) with few exceptions. CY was unfavourable related to FEC at both r_p and r_e levels. Attempts to find comparable estimates from the literature were not successful. Therefore the results from the current study, as well as those reported in the literature, suggested that wool weights could be reduced if selection for reduced FEC were being practised.

Conclusions

Internal parasite infestations constitute a health problem to domestic livestock. The present study suggested that FEC is variable and heritable, and that selection should result in additive gains in the ability of animals to resist nematode infestation in South Africa. Significant additive genetic gains in FEC accrued in Australian Rylington Merinos (Karlsson & Greeff, 2006), resulting in a decline of nematode eggs from individual sheep. However, Karlsson & Greeff (2001) indicated that optimum procedures need to be followed for FEC to be included in breeding programmes. Selection for a reduced FEC is unlikely to result in unfavourable correlated responses in objectively measured wool traits in South African Merinos, as suggested by generally favourable genetic relationships of wool traits with FEC. Two important determinants of wool price, namely SS and FD, were generally favourably related to FEC in the present study. The exception to this trend was observed for wool weight traits, where FEC was unfavourably related to both GFW and CFW. This antagonistic relationship between wool weight and FEC was also observed in New Zealand (Bisset *et al*., 2011). However, the magnitude of these relationships in the current study is such that it ought to be feasible to simultaneously improve FEC and wool weights. Apart from being variable and heritable, FEC is practical to record in a well-equipped laboratory for counts, less expensive compared to losses due to nematode infestation, and simple to conceptualize. Identification of individuals that are resistant to nematode infestation is essential to conserve genotypes later that are adapted to various South African environments, which could be useful in future developments in small ruminant production.

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