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Resistance to nematode parasites in Merino sheep: correlation with production traits

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Abstract. Merino sheep representing a range of bloodlines in resource flocks located across Australia were tested for resistance to gastro-intestinal nematodes. These flocks included the JB Pye Flock (Camden, NSW), Katanning Base Flock (Katanning, WA), Turretfield Merino Resource Flock (Rosedale, SA), and the CSIRO Finewool Flock (Armidale, NSW) and included a total of 328 sire groups. Resistance to nematodes was measured by faecal egg count (FEC). Data were also available for greasy and clean fleece weight (GFW and CFW, respectively), fibre diameter (FD), and body weight (BW) at a range of ages from weaning to 21 months. Variance components were estimated by restricted maximum likelihood, fitting an animal model and estimating covariances in a series of bivariate analyses. Phenotypic correlations between $\mathrm{FEC}^{0\cdot33}$ and production traits were all close to zero (−0·09–0·02). Genetic correlations between $\mathrm{FEC}^{0\cdot33}$ and production traits were −0·20, −0·18, and −0·26 for weaning weight, 10-month BW, and 16-month BW, respectively; 0·21, −0·06, and 0·21 for 10-month GFW, 16-month GFW, and 21-month GFW; 0·21, −0·05, and 0·07 for 10-month CFW, 16-month CFW, and 21-month CFW; and −0·09, −0·12, and 0·04 for 10-month FD, 16-month FD, and 21-month FD. When estimates were pooled for all fleece traits and all BW traits, the genetic correlations between $\mathrm{FEC}^{0\cdot33}$ and GFW, CFW, FD, and BW were 0·15, 0·10, −0·06, and −0·21, respectively. Using pooled estimates for CFW, FD, and BW, selection for a breeding objective based on production traits alone would lead to an unfavourable correlated response in $\mathrm{FEC}^{0\cdot33}$ of approximately 1% per year.

Additional keywords: genetic covariance, faecal egg count, host resistance, correlated response.

Introduction

Once it has been demonstrated that a trait has sufficient additive genetic variance to respond to selection, the genetic and phenotypic relationships between that trait and others of importance need to be established. These estimates of phenotypic and genetic covariation provide some of the necessary information for a new trait to be included in a selection index, and also provide an estimate of the effect of its omission from the breeding plan.

Heritability estimates for a range of traits that are important in an Australian wool-producing enterprise are given in Table 1. Heritabilities for greasy and clean fleece weight (GFW and CFW, respectively) are moderate, whereas the heritability of fibre diameter (FD) and body weight (BW) tends to be higher. The most important genetic association between these traits is the unfavourable correlation of CFW with FD, as these 2 traits are the major contributors to economic gain in a Merino breeding program (Atkins 1987).

The heritability of resistance to helminth parasites has been estimated in a number of Merino flocks and is moderate in value: of the order of 20% (Eady *et al.* 1996). However, estimates of genetic correlations between the resistance trait of faecal egg count (FEC) and production traits, used so far to evaluate strategies for breeding for helminth resistance (Woolaston 1994), have been based on *Haemonchus contortus* challenge to sheep running on the Northern Tablelands (Woolaston *et al.* 1991). As the merit of breeding for improved helminth resistance is affected by assumed genetic

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Table 1. Heritability estimates (±s.e.) for hogget greasy fleece weight (GFW), clean fleece weight (CFW), fibre diameter (FD), and body weight (BW) and genetic correlation (±s.e.) between CFW and FD for a range of Merino flocks

To calculate the pooled estimate, each estimate was weighted in proportion to the reciprocal of its sampling variance

Reference	Strain	Heritability estimates GFW	CFW	FD	BWT	Genetic correlation CFW–FD
Morley (1955)	Peppin	0·40±0·06	0·47±0·07	n.a.	0·36±0·08	n.a.
Beattie (1962)	Peppin	0·35±0·18	0·34±0·18	0·57±0·17	0·54±0·20	0·16±0·27
Brown and Turner (1968)	Peppin	0·42±0·05	0·40±0·05	0·47±0·04	0·65±0·04	0·16±0·08
Mullaney *et al.* (1970)	Finewool	0·32±0·07	0·24±0·07	0·46±0·07	n.a.	0·39±0·11
Gregory (1982*a*, 1982*b*)	Bungaree	0·27±0·05	0·25±0·05	0·75±0·08	0·40±0·06	−0·06±0·11
Davis and Kinghorn (1986)	Peppin	0·55±0·12	0·49±0·13	0·78±0·19	0·68±0·16	0·46±0·15
Walkley *et al.* (1987)	Koonoona	0·30±0·09	0·37±0·10	0·45±0·10	n.a.	0·21±0·16
Mortimer and Atkins (1989)	Multiple	0·29±0·06	0·30±0·06	0·48±0·07	0·34±0·06	0·40±0·11
James *et al.* (1990)	Collinsville	0·34±0·12	0·39±0·13	0·42±0·13	n.a.	−0·12±0·26
Lewer *et al.* (1994)	Female	0·30±0·08	0·27±0·07	0·59±0·09	0·48±0·09	0·14±0·16
	Male	0·42±0·10	0·44±0·11	0·58±0·12	0·27±0·09	0·29±0·16
Gifford *et al.* (1994)	South Australian	n.a.	0·44±0·02	0·36±0·02	n.a.	n.a.
Swan *et al.* (1995)[A]	Finewool	0·32±0·06	0·28±0·06	0·67±0·09	n.a.	0·31±0·14
Vaez Torshizi *et al.* (1996)	Multiple	n.a.	n.a.	n.a.	0·33±0·06	n.a.
Pooled estimate		0·34±0·02	0·39±0·01	0·43±0·02	0·46±0·02	0·23±0·04

n.a., not available.

[A] Standard errors have been estimated from number of sires and mean sire group size.

parameters to a greater extent than by assumed costs associated with parasite infection, there is a critical need for more robust estimates to be made, to allow the development of a national breeding program.

Unfavourable genetic relationships between FEC and production have been suggested by several New Zealand studies. High fleece weight lines have higher FECs (McEwan *et al.* 1992; Watson *et al.* 1995), and studies with Romney sheep showed a consistent, but low, unfavourable genetic correlation (0·18–0·25) between FEC and body weight at 8 months of age and hogget fleece weight at 12 months of age (McEwan *et al.* 1995).

In breeding objectives for Merinos, the genetic correlations between FEC and the production traits of GFW, CFW, FD, hogget BW, and reproductive performance have been assumed to be close to zero or slightly favourable (Woolaston 1994). These values were based on estimates from the control line of the *H. contortus* selection flock and a CSIRO random bred flock (Woolaston *et al.* 1991) at Armidale, New South Wales. Helminth infections in these sheep were effectively controlled using the recommended strategic program based on paddock changes and anthelmintic treatment. Studies in Merino flocks selected for production traits in a relatively parasite-free environment (Eady *et al.* 1994) have shown no evidence of a correlated response in FEC, with the exception of the weaning weight lines where there was indication of a favourable association between FEC and weaning weight.

The present study investigates the genetic correlations between FEC and production traits in Merino sheep, when measured under conditions of routine helminth control, and considers the consequences of these correlations for genetic change in parasite resistance and productivity in a Merino breeding program.

Materials and methods

Generic resource flocks

Merino sheep representing a range of bloodlines, managed in resource flocks across Australia, were tested for resistance to helminth parasites. These flocks (JB Pye Flock, Camden, NSW; Katanning Base Flock, Katanning, Western Australia; Turretfield Merino Resource Flock, Rosedale, South Australia; CSIRO Finewool Flock, Armidale, NSW) and their management were previously described by Eady *et al.* (1996). All experimental groups as defined and tested for internal nematode resistance by Eady *et al.* (1996) were used in this study except for those groups where production data were unavailable (Turretfield 1993 and Katanning 1992 groups), sire information was limited (Trangie 1990 and 1991 groups), and age of FEC measurement (36 months) or reproductive status (pregnant) were not consistent with that of other experimental flocks (JB Pye 1990*b*). A summary of animal numbers and sire families for each flock is given in Table 2.

Parasite resistance was determined by the FEC of animals after exposure to either natural or artificial infection with strongyle nematodes as described by Eady *et al.* (1996). FEC after either natural challenge or artificial challenge with *H. contortus* or *Trichostrongylus colubriformis* was treated as the same trait. All FECs were transformed to their cube roots for analysis (Eady 1995; Woolaston and Piper 1996). Table 2 gives details of the FEC and production traits measured in the flocks. There was no planned culling of animals in any of the flocks.

Production data were limited to the drops where there was a FEC, because sampling variances for $\mathrm{FEC}^{0\cdot33}$ and wool traits and their covariance are more uniform with this use of data (James 1993). Number of animals measured for each pair of traits is given in Table 2. Body weights were measured at weaning (WW), 10 months of age (10BW), and/or 16 months of age (16BW). Depending on the experimental flock, GFW, CFW, and FD were measured at approximately 10 months (10GFW, 10CFW, 10FD, respectively), 16 months (16GFW, 16CFW, 16FD), and 21 months (21GFW, 21CFW, 21FD) of age with either 6–7 or 10–13 months wool growth (see Table 2). All ages are an average for the group, given an approximate spread in lambing dates over 5 weeks.

In the JB Pye flock, all sheep were first shorn as weaners at an average age of 4 months. Animals were allocated to a footrot experimental group or the breeding replacement group (see Vaez Torshizi *et al.* 1996 for detailed description of management groups) at 10 months of age, and those allocated to the footrot experimental group were shorn at this time (10 months). All sheep were shorn at 16 and 22 months of age. For the sheep born in 1990, only data from the footrot group (the JB Pye 1990*a* group) were used to estimate genetic correlations between $\mathrm{FEC}^{0\cdot33}$ and fleece traits at 10 and 16 months. For the 1991 drop, data from both the footrot and breeding groups were used to estimate genetic correlations between $\mathrm{FEC}^{0\cdot33}$ and fleece measurements. The 16-month and 22-month fleece data were used to maximise animals per sire group as only the footrot group was shorn at 10 months of age. To make the wool growth period equivalent for the 2 management groups, the 16-month fleece data for the footrot group were the sum of their 10- and 16-month measurements. Estimates of genetic correlations between $\mathrm{FEC}^{0\cdot33}$ and WW, 10BW, and 16BW were based on data from the footrot group (1990*a*) and both groups in 1991.

In the Katanning Base Flock, all sheep were first shorn as weaners at 4 months of age. The ewes were next shorn at 11 months of age and all sheep were shorn at 17 months of age. Genetic correlations were estimated between $\mathrm{FEC}^{0\cdot33}$ and 11-month fleece traits in the ewes and the 17-month fleece traits for all animals.

To make the wool growth period equivalent for the 2 sexes, the 17-month data for the ewes were the sum of their 11-month and 17-month measurements. Therefore, the 17-month fleece trait estimates for this flock are not entirely independent from those at 11 months, given that wool growth to 11 months is a component of the 17-month measurement. Genetic correlations between $\mathrm{FEC}^{0\cdot33}$ and WW, 10BW, and 16BW were estimated using data from both sexes.

In the CSIRO Finewool Flock, all sheep were first shorn at 10 months of age and again at 21 months of age. FD at 21 months was only measured on a portion of the group. Genetic correlations between $\mathrm{FEC}^{0\cdot33}$ and fleece traits at both shearings were estimated. Estimates of genetic correlations between $\mathrm{FEC}^{0\cdot33}$ and WW and 10BW were based on data from both sexes.

In the Turretfield Resource Flock, all sheep were first shorn as weaners at 4 months of age. The rams were next shorn at 10 months of age and all sheep were shorn at 16 months of age. Genetic correlations between $\mathrm{FEC}^{0\cdot33}$ and fleece traits were based on data from the 10- and 16-month shearing of rams as the only fleece measurement available for the ewes was GFW at 16 months. Estimates of the genetic correlation between $\mathrm{FEC}^{0\cdot33}$ and WW and $\mathrm{FEC}^{0\cdot33}$ and 16BW used data from both sexes, whereas for 10BW only data from rams were available.

Statistical analysis

No attempt was made to pool data from all flocks due to the complexity of management groups within each flock. The following linear model was fitted, using least squares, to determine the final model for each trait within each flock:

$$Y_{ijklmno} = \mu + \mathrm{BL}_i + \mathrm{Sire}_{j:i} + \mathrm{BRR}_k + \mathrm{DA}_l + \mathrm{Sex}_m + \mathrm{MG}_n + b(\bar{X} - X_0) + \text{interactions} + e_{ijklmno}$$

where Y is an observed trait, μ is the common mean, BL_i is the effect of the ith bloodline, Sire_j is the effect of the jth sire nested within bloodline, BRR_k is the effect of the kth birth rearing type (single born and reared, multiple born and single reared, multiple born and reared), DA_l is the effect of the lth dam age (maiden, mature), Sex_m is the effect of the mth sex (female, castrate male, entire male), MG_n is the effect of nth management group, b is the regression of phenotype on day of birth, $\bar{X}$ is the mean day of birth, X_o is the day of birth for animal_o, and $\mathrm{e}_{ijklmno}$ is the random error. First-order interactions of main effects were tested for significance and sequentially omitted from the model if non-significant (at $P = 0\cdot05$) or accounted for <2% of the variation. The final model used for each production trait is given in Table 3, with significant interactions reported in the text of the results. We analysed the cube root of $\mathrm{FEC}^{0\cdot33}$ and fitted models given by Eady *et al.* (1996).

Variance and covariance components were then estimated using a series of univariate (for heritability) and bivariate (for correlations) REML analyses (DFREML; Meyer 1989), using unequal design matrices according to the optimal model for each trait. Although an animal model was used it was effectively a sire model as maternal pedigrees were not included because of known maternal effects on some traits (Hickson *et al.* 1995; Mortimer and Atkins 1995). This was done in preference to fitting maternal effects as the number of lambs reared as multiples was relatively small, giving little power to estimate this effect directly. Where relationships between sires existed they were not included in the pedigree structure. Standard errors for heritability came from the DFREML analyses and for genetic correlations were calculated as suggested by Falconer (1989, p. 317). Pooled estimates for phenotypic correlations were calculated by transforming each r value to a Fisher's z value and weighting it by the reciprocal of its mean square (Snedecor and Cochran 1967, p. 187). Pooled estimates for genetic correlations were calculated by weighting each estimate by the reciprocal of its sampling variance. One set of pooled estimates came from grouping traits according to age at measurement, and a second set of pooled estimates came from grouping all CFW, FD, and BW estimates from different flocks.

Correlated response

The correlated response in FEC from selection for a breeding objective that included hogget (13–19 months of age) and adult (>19 months of age) CFW, FD, and BW and number of lambs weaned (NLW) was predicted using SELIND (Cunningham 1969). The relative economic value (REV) for each trait in the breeding objective is expressed per breeding ewe in the flock per year. REV for hogget CFW was \$0·87 per percentage unit change in CFW per breeding ewe per year, \$0·99 per percentage unit change in adult CFW, −\$4·56 per μm change in hogget FD, −\$4·56 per μm change in adult FD, \$0·32 per percentage unit change in hogget BW, \$0·06

Table 2. Number of sire families, worm infection type and species, and numbers of animals recorded for pairings of faecal egg count (FEC) and each production trait in each experimental flock

WW, weaning weight; BW, body weight; GFW, greasy fleece weight; CFW, clean fleece weight; FD, fibre diameter; Hc, *H. contortus*; Tc, *T. colubriformis*; 10, 16, and 21 refer to age in months at measurement

Flock	No of sire families	Infection type and species	Age at FEC testing (months)	WW	10 BW	16 BW	10 GFW	10 CFW	10 FD	Wool growth (month)	16 GFW	16 CFW	16 FD	Wool growth (month)	21 GFW	21 CFW	21 FD	Wool growth (month)
JB Pye 1990a	41	Natural mixed spp.	18	408^{A}	407	408	408	407	407	6	408	408	408	6	—	—	—	—
JB Pye 1991	41	Natural mixed spp.	12	995^{A}	997	934	—	—	—	—	968	968	968	12	921^{F}	907^{F}	908^{F}	8
Katanning 1991	64	Artificial Hc	8	947^{A}	933^{B}	894^{C}	460^{D}	460^{D}	466^{D}	7	871^{E}	871^{E}	879^{E}	13	—	—	—	
CSIRO 1991	60	Artificial Hc	7	1074	1063	—	1063	1050	1056	10	—	—	—	—	1010	1004	1014	11
CSIRO 1992	74	Artificial Tc	13	1058	1072	—	1072	1069	1065	10	—	—	—	—	1059	1057	663	11
Turretfield 1992	48	Artificial Hc	7	1602^{A}	705	1419	699	696	696	6	691	691	691	6	—	—	—	—

[A] Shorn as lambs at weaning. [B] BW at 9 months. [C] BW at 15 months. [D] Shorn at 11 months. [E] Shorn at 17 months. [F] Shorn at 22 months.

per percentage unit change in adult BW, and \$84·29 per extra lamb weaned per ewe. The micron premium (% increase in price for 1 micron decrease in FD) for this index was 5%.

The selection criteria were hogget CFW, FD, and BW measured on the individual with no additional information from relatives. In predicting response, genetic correlations between $\mathrm{FEC}^{0\cdot33}$ and production traits, as suggested in the discussion of this paper (0·10 for CFW at any age, −0·06 for FD at any age, and −0·21 for BW at any age), were used. Economic merit for each trait in the breeding objective (CFW, FD, BW, and NLW) was calculated as the response for that trait, in s.d. units, multiplied by its REV. The aggregate economic merit was the sum of these values for all traits in the breeding objective.

The genetic correlation between FEC and NLW was not estimated for the flocks in this study, as reproductive data were not available at the time that FEC measurements were made due to the age of the animals. Instead, a mean of published estimates (−0·14) was used (Piper 1987; Woolaston *et al.* 1991). The phenotypic s.d. for $\mathrm{FEC}^{0\cdot33}$ was set to 1·0 and heritability was assumed to be 0·25. Phenotypic standard deviations, heritabilities, and phenotypic and genetic covariances between production traits are from Semple *et al.* (1994). As all estimates reported here were very close to zero, phenotypic correlations between $\mathrm{FEC}^{0\cdot33}$ and production traits were kept at zero for all predictions.

Results

Statistical models and heritability estimates

Fixed effects and interactions that had a significant effect on $\mathrm{FEC}^{0\cdot33}$ were reported in detail by Eady *et al.* 1996. Significant effects for individual production traits are given in Table 3. Two-way interactions of fixed effects were not significant with the exception of BL×MG for the trait 21FD in the CSIRO 1991 group, and BL×BRR for WW and BL×MG for 10BW, 10GFW, and 10CFW in the CSIRO 1992 group ($P < 0\cdot05$). Heritability estimates for all traits are summarised in Table 4.

Estimates for production traits were derived only from data from animals that were present in the flocks in years that FEC was measured and may not be the same as other estimates using all information collected in each flock.

Genetic correlations

In the JB Pye group, with the exception of the 10-month shearing of the 1990*a* group (Table 5), the correlations between $\mathrm{FEC}^{0\cdot33}$ and CFW were moderate and negative in sign. A negative correlation was also found between $\mathrm{FEC}^{0\cdot33}$ and 10CFW in the CSIRO 1992 group. Moderate correlations, positive in sign, were found between $\mathrm{FEC}^{0\cdot33}$ and 10CFW in the Katanning 1992 and CSIRO 1991 groups, and between $\mathrm{FEC}^{0\cdot33}$ and 21CFW in the CSIRO 1992 group, and $\mathrm{FEC}^{0\cdot33}$ and 16CFW in the Turretfield 1992 group. $\mathrm{FEC}^{0\cdot33}$ and all expressions of fibre diameter were negatively correlated in the JB Pye 1990*a* and 1991 groups. In the CSIRO 1992 group, $\mathrm{FEC}^{0\cdot33}$ was negatively correlated with 10FD but the correlation at 21 months was essentially zero. In the CSIRO 1991 group, the correlation between $\mathrm{FEC}^{0\cdot33}$ and 10FD was close to zero but was slightly positive at 21 months of age. In the Turretfield 1992 group, the correlation between $\mathrm{FEC}^{0\cdot33}$ and 10FD was slightly negative but close to zero at 16 months of age. The genetic correlation between $\mathrm{FEC}^{0\cdot33}$ and 16BW was negative in all groups where 16BW was recorded. The genetic correlation between $\mathrm{FEC}^{0\cdot33}$ and 10BW was moderately to strongly negative in all but 1 group (CSIRO 1991), but a less consistent result was observed for $\mathrm{FEC}^{0\cdot33}$ and WW. Standard errors of the estimates ranged between 0·13 and 0·28, except for the s.e. (0·36–0·67) of estimates from the JB Pye 1990*a* group.

An average of all estimates was calculated by weighting each estimate in proportion to the reciprocal of its sampling variance (Table 5). The results were correlations with $\mathrm{FEC}^{0\cdot33}$ of −0·20, −0·18, and −0·26 for WW, 10BW, and 16BW, respectively; 0·21, −0·06, and 0·21 for 10GFW, 16GFW, and 21GFW, respectively; 0·21, −0·05, and 0·07 for 10CFW, 16CFW, and 21CFW, respectively; and −0·09, −0·12, and 0·04 for 10FD, 16FD, and 21FD, respectively. Only the pooled estimates of the genetic correlation between $\mathrm{FEC}^{0\cdot33}$ and BW traits were significantly different from zero.

When estimates were pooled for all CFW, FD, and BW traits, the genetic correlations between $\mathrm{FEC}^{0\cdot33}$ and GFW, CFW, FD, and BW were 0·15, 0·10, −0·06, and −0·21, respectively.

Phenotypic correlations

The phenotypic correlations between $\mathrm{FEC}^{0\cdot33}$ and production traits were all close to zero (Table 6).

Correlated response

Using the pooled estimates of the genetic correlation between $\mathrm{FEC}^{0\cdot33}$ and CFW, FD, and BW, selection based on individual information for hogget CFW, FD, and BW would give a correlated response in $\mathrm{FEC}^{0\cdot33}$ of 0·03 s.d. units per s.d. response in aggregate index merit. Assuming a heritability of 0·25 and s.d. of 1 for $\mathrm{FEC}^{0\cdot33}$, this represents a 12% increase in $\mathrm{FEC}^{0\cdot33}$ per s.d. response in aggregate index merit.

Discussion

From the 4 flocks in the present study, there was no obvious deviation from zero in the genetic and phenotypic parameters relating $\mathrm{FEC}^{0\cdot33}$ and wool production traits. Although estimates of the genetic correlation for $\mathrm{FEC}^{0\cdot33}$ with CFW and FD varied with age of testing, this is probably just sampling

Table 3. Significant levels of random and fixed effects in models fitted to production traits recorded in Merino resource flocks

BL, bloodline; MG, management group; DA, dam age; BRR, birth rearing rank; DOB, day of birth; WW, weaning weight; BW, body weight; GFW, greasy fleece weight; CFW, clean fleece weight; FD, fibre diameter; 10, 16, and 21 refer to age in months at measurement

Flock and trait	BL	Sire	Sex	MG	DA	BRR	DOB	Flock and trait	BL	Sire	Sex	MG	DA	BRR	DOB
JB Pye 1990a								CSIRO 1991							
WW	*	*	n.s.	n.a.	**	**	**	WW	**	**	**	n.s.	*	**	**
10BW	*	n.s.	**	n.s.	**	**	*	10BW	**	**	**	**	n.s.	**	**
16BW	n.s.	*	**	**	**	**	*	16BW	—	—	—	—	—	—	—
10GFW	*	**	n.s.	**	**	**	**	10GFW	**	**	n.s.	**	n.s.	**	**
10CFW	*	**	n.s.	**	**	**	**	10CFW	**	**	n.s.	*	**	**	**
10FD	**	**	n.s.	n.s.	n.s.	n.s.	*	10FD	**	**	n.s.	**	*	n.s.	*
16GFW	**	**	**	**	**	**	n.s.	21GFW	**	**	n.a.	**	n.s.	**	**
16CFW	**	**	**	**	**	**	n.s.	21CFW	**	**	n.a.	**	n.s.	**	*
16FD	**	**	n.s.	**	n.s.	n.s.	n.s.	21FD	**	**	n.a.	**	*	n.s.	n.s.
JB Pye 1991								CSIRO 1992							
WW	*	**	n.a.	**	**	**	**	WW	**	**	n.s.	**	n.s.	n.s.	n.s.
10BW	**	**	n.a.	**	**	**	**	10BW	**	**	**	**	n.s.	**	**
16BW	**	**	n.a.	**	n.s.	*	*	16BW	—	—	—	—	—	—	—
16GFW	**	**	n.a.	**	**	**	**	10GFW	**	*	n.s.	**	**	**	**
16CFW	**	**	n.a.	**	**	**	**	10CFW	**	**	n.s.	**	**	**	**
16FD	**	**	n.a.	**	n.s.	**	**	10FD	**	**	**	**	n.s.	**	n.s.
21GFW	**	**	n.a.	**	*	**	n.s.	21GFW	**	**	n.s.	**	**	**	**
21CFW	**	**	n.a.	**	*	**	n.s.	21CFW	**	**	n.s.	**	**	**	**
21FD	**	**	n.a.	**	n.s.	**	n.s.	21FD	**	**	**	n.s.	n.s.	n.s.	n.s.
Katanning 1991								Turretfield 1992							
WW	**	**	**	n.a.	**	**	n.s.	WW	**	**	**	n.a.	**	**	**
10BW	*	**	n.a.	**	**	**	n.s.	10BW	*	**	n.a.	n.a.	n.s.	**	**
HBW	**	**	n.a.	**	*	**	n.s.	16BW	**	**	n.a.	n.s.	n.s.	**	**
10GFW	*	**	n.a.	n.a.	n.s.	**	n.s.	10GFW	**	**	n.a.	n.a.	**	**	**
10CFW	*	**	n.a.	n.a.	n.s.	**	n.s.	10CFW	**	**	n.a.	n.a.	**	**	*
10FD	**	**	n.a.	n.a.	n.s.	n.s.	n.s.	10FD	*	**	n.a.	n.a.	n.s.	*	**
21GFW	**	**	n.a.	**	**	**	n.s.	21GFW	**	**	n.a.	n.a.	*	**	*
21CFW	**	**	n.a.	**	**	**	n.s.	21CFW	*	**	n.a.	n.a.	*	**	n.s.
21FD	**	**	n.a.	**	n.s.	*	**	21FD	**	**	n.a.	n.a.	*	n.s.	**

$^{*}P < 0{\cdot}05$; $^{**}P < 0{\cdot}01$; n.s., not significant; n.a., not applicable where sex and management group were confounded, or both sexes were in same management group, or data from only 1 sex were used.

variation. For CFW, estimates at 10 months of age were generally unfavourable and at 16 and 21 months of age they were close to zero (Table 5). The pooled estimate for the correlation between FD and $\text{FEC}^{0 \cdot 33}$ was unfavourable at both 10 and 16 months of age and close to zero at 21 months of age. The magnitude of the standard errors associated with the individual estimates precluded any of them being significantly different from zero.

The genetic relationship between $\text{FEC}^{0 \cdot 33}$ and BW appeared to be favourable, being generally negative and of the order of 0·2. This is consistent with the result from Merino lines selected for high or low WW, where a favourable correlated response in FEC was apparent (Eady *et al.* 1994).

The genetic correlation of 0·21 between $\text{FEC}^{0 \cdot 33}$ and 10-month GFW is consistent with the observed correlated response in fleece weight in lines selected for divergence in FEC in New Zealand (Morris *et al.* 1997). However, the results for body weight in Merinos appear to be opposite to those found in meat and dual-purpose sheep breeds. In New Zealand, the initial suggestion of an unfavourable correlation between BW and FEC came from differences observed in lines selected for WW. More recent estimates of the genetic correlation between BW and FEC have supported this finding (McEwan *et al.* 1995) in some breeds. However, there is still debate among New Zealand researchers as to the nature of the relationship between FEC and BW (C. A. Morris, pers. comm.).

The apparent difference in sign of the FEC–BW correlation between meat/dual-purpose sheep breeds and Merinos may reflect the different selection pressure that has been placed on the trait in each breed over time. Stronger selection for BW in meat/dual-purpose sheep breeds may have favoured the partitioning of nutrients for BW gain to the extent that other processes (such as immune response) are compromised.

Table 4. Univariate heritability estimates (±s.e.) for $\mathrm{FEC}^{0\cdot 33}$ and production traits in Merino resource flocks

To calculate the pooled estimate, each estimate was weighted in proportion to the reciprocal of its sampling variance. Estimates only include data from animals that were present in the flocks in years that faecal egg count (FEC) was measured and may not be the same as published or yet to be published estimates using all information collected in each flock. WW, weaning weight; BW, body weight; GFW, greasy fleece weight; CFW, clean fleece weight; FD, fibre diameter; 10, 16, and 21 refer to age in months at measurement

Flock	$\mathrm{FEC}^{0\cdot 33}$	WW	10 BW	16 BW	10 GFW	10 CFW	10 FD	16 GFW	16 CFW	16 FD	21 GFW	21 CFW	21 FD
JB Pye	0·07	0·19	0·17	0·28	0·47	0·58	0·40	0·42	0·40	0·70	—	—	—
1990a	±0·12	±0·13	±0·13	±0·15	±0·18	±0·20	±0·16	±0·17	±0·17	±0·21			
JB Pye	0·17	0·37	0·34	0·33	—	—	—	0·36	0·42	0·70	0·34	0·37	0·61
1991	±0·08	±0·11	±0·11	±0·11				±0·12	±0·12	±0·16	±0·11	±0·12	±0·15
Kattanning	0·17	0·32	0·42	0·57	0·61	0·73	0·80	0·48	0·53	0·72	—	—	—
1991	±0·09	±0·11	±0·13	±0·15	±0·21	±0·22	±0·22	±0·14	±0·14	±0·17			
CSIRO	0·42	0·22	0·36	—	0·35	0·33	±0·83	—	—	—	0·37	0·31	0·59
1991	±0·12	±0·08	±0·10		±0·11	±0·10	±0·17				±0·11	±0·10	±0·14
CSIRO	0·40	0·58	0·48	—	0·12	0·17	0·59	—	—	—	0·26	0·28	0·50
1992	±0·11	±0·12	±0·12		±0·07	±0·08	±0·13				±0·09	±0·10	±0·15
Turretfield	0·34	0·20	0·47	0·27	0·30	0·47	0·59	0·38	0·49	0·80	—	—	—
1992	±0·09	±0·08	±0·14	±0·08	±0·11	±0·14	±0·16	±0·13	±0·15	±0·18			
Pooled[A]	0·25	0·29	0·32	0·33	0·25	0·32	0·62	0·40	0·46	0·73	0·31	0·31	0·57
estimate	±0·04	±0·04	±0·05	±0·06	±0·05	±0·05	±0·07	±0·07	±0·07	±0·09	±0·06	±0·06	±0·08

[A] Calculated from $\dfrac{\sum_i \dfrac{X_i}{\sigma_i^2}}{\sum_i \dfrac{1}{\sigma_i^2}} \pm \sqrt{\dfrac{1}{\sum_i \dfrac{1}{\sigma_i^2}}}$

Table 5. Genetic correlations (±s.e.) between $\mathrm{FEC}^{0\cdot 33}$ and production traits in Merino resource flocks

To calculate the pooled estimate, each estimate was weighted in proportion to the reciprocal of its sampling variance. FEC, faecal egg count; WW, weaning weight; BW, body weight; GFW, greasy fleece weight; CFW, clean fleece weight; FD, fibre diameter; 10, 16 and 21 refer to age in months at measurement

Flock	WW	10 BW	16 BW	10 GFW	10 CFW	10 FD	16 GFW	16 CFW	21 FD	21 GFW	21 CFW	21 FD
JB Pye	n.a.	n.a.	−0·13	0·44	0·28	−0·28	0·02	−0·23	−0·53	—	—	—
1990a			±0·67	±0·46	±0·50	±0·54	±0·59	±0·57	±0·36			
JB Pye	−0·20	−0·37	−0·41	—	—	—	−0·32	−0·38	−0·19	−0·13	−0·29	−0·10
1991	±0·25	±0·24	±0·23				±0·25	±0·22	±0·22	±0·27	±0·25	±0·24
Katanning	0·26	−0·16	−0·24	0·30	0·36	0·12	−0·09	−0·06	0·04	—	—	—
1991	±0·28	±0·28	±0·25	±0·27	±0·25	±0·27	±0·28	±0·26	±0·25			
CSIRO	0·40	0·22	—	0·34	0·31	0·02	—	—	—	0·15	0·06	0·11
1991	±0·19	±0·19		±0·19	±0·19	±0·17				±0·20	±0·21	±0·18
CSIRO	−0·48	−0·35	—	0·01	−0·20	−0·21	—	—	—	0·41	0·31	0·04
1992	±0·13	±0·16		±0·28	±0·24	±0·17				±0·18	±0·20	±0·20
Turretfield	−0·40	−0·24	−0·18	0·03	0·28	−0·15	0·16	0·28	−0·04	—	—	—
1992	±0·18	±0·19	±0·19	±0·24	±0·20	±0·20	±0·23	±0·21	±0·19			
Pooled	−0·20	−0·18	−0·26	0·21	0·21	−0·09	−0·06	−0·05	−0·12	0·21	0·07	0·04
estimate	±0·08	±0·09	±0·12	±0·11	±0·11	±0·09	±0·14	±0·13	±0·12	±0·12	±0·13	±0·12

n.a., not estimable.

The same argument may apply to wool production, where the availability of sulfur amino acids is the major rate-limiting factor for keratin production (Reis 1979), and sulfur amino acids also are important precursors for production of immunoglobulins (Cunningham 1978). These issues will be difficult to resolve until there is some understanding of the cost to the animal of mounting a rapid and effective immune response to internal parasites.

Heritability estimates for production traits and $\mathrm{FEC}^{0\cdot 33}$ reported here (Table 4) fall into the general range of published values for Merino sheep (Table 1) but tend to be greater than previous estimates for CFW, FD, and BW in the Katanning Base Flock (Lewer *et al.* 1994) and CFW and FD in the Turretfield Resource Flock (Gifford *et al.* 1994). The estimates from the CSIRO Finewool Flock and the JB Pye Flock, averaged over the 2 years, were similar to those

Table 6. Phenotypic correlations between $\mathrm{FEC}^{0\cdot 33}$ and production traits in Merino resource flocks

FEC, faecal egg count; WW, weaning weight; BW, body weight; GFW, greasy fleece weight; CFW, clean fleece weight; FD, fibre diameter; 10, 16, and 21 refer to age in months at measurement

Flock	WW	10 BW	16 BW	10 GFW	10 CFW	10 FD	16 GFW	16 CFW	16 FD	21 GFW	21 CFW	21 FD
JB Pye 1990a	n.a.	n.a.	−0·10	0·06	0·06	−0·05	−0·03	−0·03	−0·06	—	—	—
JB Pye 1991	0·02	0·01	−0·09	—	—	—	−0·04	−0·04	−0·1	−0·02	−0·01	−0·08
Katanning 1991	−0·06	−0·12	−0·12	0·05	0·05	−0·03	−0·02	0·00	−0·05	—	—	—
CSIRO 1991	0·04	0·04	—	0·04	0·05	0·01	—	—	—	0·02	0·02	0·03
CSIRO 1992	−0·03	−0·05	—	−0·04	−0·04	−0·10	—	—	—	0·04	0·02	−0·04
Turretfield 1992	−0·05	−0·12	−0·06	−0·01	0·04	−0·11	−0·02	0·00	−0·09	—	—	—
Pooled estimate	−0·02	−0·04	−0·09	0·01	0·02	−0·06	−0·03	−0·01	−0·07	0·02	0·02	−0·01

n.a., not estimable.

reported by Swan *et al.* (1995) and Vaez Torshizi *et al.* (1996). Because estimates from the study reported in this paper are based on data from 1 year only, the year parasite resistance was measured, they would be less accurate estimates than those already published for these flocks.

Estimates of genetic correlations varied between flocks both in magnitude and sign. This variation between flocks was not significant and is similar to the variation in genetic correlations reported for wool traits in different Merino flocks. The approach taken in deciding on a suitable figure to use, where genetic parameters are not specifically known for a particular flock, has been to calculate an average from a range of estimates (Ponzoni 1987). Lewer *et al.* (1994) summarised the range in published estimates of genetic correlations for wool traits.

The approach of using a weighted average from a number of flocks can be used for genetic correlations between FEC and production traits, but is open to the danger that genotype×environment interactions may be significant and influence the estimates of genetic correlations, or that true differences do exist between flocks as a result of different gene frequencies or different measurement strategies. For instance, the estimates from the JB Pye Flock are nearly all moderate and similar in sign to what might be expected given the effect of helminth infection on BW, wool production, and FD (Besier *et al.* 1996). Helminth challenge in this environment can be extreme, with anthelmintic treatment required every 4–5 weeks to prevent mortality and clinical signs of disease in young sheep. The impact of larval challenge on wool production can be quite substantial under these conditions (Barger 1982; Albers *et al.* 1989).

However, genetic correlations between FEC and wool production from the other flocks, which were exposed to a lower level of natural parasitism over the period that wool production was measured, did not appear to be consistently different from those in the JB Pye flock. This contrasts with results reported by Albers *et al.* (1987) where the magnitude of the negative genetic correlations between FEC and production traits increased when production was measured during helminth infection. However, in the present study the estimates do not appear to be significantly influenced by the level of parasitism.

Should, then, these estimates from different environments be pooled? The environments in the present study varied in terms of the level of natural helminth challenge that occurred over the period that production was measured. The environment in which production is measured can affect both additive genetic variance for these traits and their covariances. This is even more applicable to disease traits, as incidence will vary with environment and will have a direct effect on the expression of production traits. The range in environments in this study was diverse in terms of helminth challenge, going from relatively low natural challenge in Western Australia and South Australia, to high challenge in the New England environment, to extremely high at Camden. However, looking at the genetic correlations from flocks in each of these areas (Table 5) it is difficult to draw any conclusions about the validity, or otherwise, of pooling estimates from different environments.

The phenotypic correlations do not add much information to this comparison of environments as they were predominantly low or close to zero, suggesting that the measurement of FEC, after a short period of worm infection, is not a useful indicator of production, measured over a considerably longer period. This appears to be a common outcome, with low phenotypic correlations occurring in the study of Albers *et al.* (1987; see Piper and Barger 1988) and in a range of experiments in New Zealand (Baker *et al.* 1991; Bisset *et al.* 1992). In the current study, the only trend that could be observed in the phenotypic correlations (Table 6) was a small, but generally negative, association of $\text{FEC}^{0\cdot33}$ with BW and FD, indicating that the more resistant sheep tended to be phenotypically heavier and produce coarser wool. A more extensive monitoring of FEC over the period for which production was measured may have resulted in stronger phenotypic associations. Conversely, the sheep may not have been exposed to significant natural helminth infection during the period that wool growth was measured. With the exception of the JB Pye Flock, FECs were obtained after a relatively brief artificial worm challenge that, in itself, would have had little effect on production (Kisielewicz *et al.* 1995). Given the routine worm control programs that were used within each flock, natural helminth infection may not have had any measurable impact on production.

Whether these estimates should be pooled or not is best resolved by considering whether the estimates from this study should be used in preference to zero genetic correlations, the parameter values frequently being assumed where ram breeders are selecting for resistance (Pocock *et al.* 1995). Now that there are published estimates from a range of Merino flocks, some of which are significantly different from zero (FEC–BW), there is a case for changing this assumption, at least when predicting likely changes in FEC with selection for production traits. As there appears to be no general trend for them to change with age or level of natural worm challenge, there is a case for pooling all correlations of $\text{FEC}^{0\cdot33}$ with GFW to give an estimate of $0\cdot15$, all correlations of $\text{FEC}^{0\cdot33}$ with CFW to give $0\cdot10$, all correlations of $\text{FEC}^{0\cdot33}$ with FD to give $-0\cdot06$, and all correlations of $\text{FEC}^{0\cdot33}$ with BW to give an estimate of $-0\cdot21$.

Sensitivity analyses can be done to discover the consequences of errors in the genetic parameters, on both predicted and realised gains. Initial studies of this nature (Eady 1998) indicate that if there is danger in assuming a zero correlation between FEC and a production trait, where the true correlation is significantly different, it is to underestimate substantially the change that will occur in reproductive rate. This information can then be used in deciding how much effort should be put into further parameter estimation.

The implications of the genetic covariances estimated in this study need to be considered. The predicted response in FEC was unfavourable when using a Merino breeding objective that ignores parasite resistance. If the estimates suggested for use from this study are a true indication of the genetic covariance between FEC and production traits, selection for production alone will lead to increased susceptibility to internal parasites at the rate of approximately 12% per s.d. of the production index. In a flock with an average generation interval of 3 years and selection intensity of $1\cdot35$, this would represent an increase in FEC of approximately 1% per year.

As the linkage between increasing fleece weight and decreasing FD can be resolved by combining the traits in an index with appropriate economic weights, so too can parasite resistance be included in the breeding objective. Determining the relative emphasis that should be placed on breeding for helminth resistance in Merino breeding objectives for different environments will be a complex task and is not within the scope of this paper. However, it should be noted that in environments where effective control of helminths is increasingly under threat due to anthelmintic resistance, breeders should seriously consider placing some selection emphasis on resistance to avoid losses associated with increased worm burdens.

In what type of environment are these genetic correlations applicable? The genetic parameters estimated here could be applied in the majority of Australian environments where sheep are grazed. With the exception of the JB Pye Flock, all groups studied came from regions where Merino sheep are usually grazed, and also where there is an interest by breeders in selecting sheep for helminth resistance (Anon. 1994). However, it must be recognised that a characteristic of these environments was an effective parasite control program which minimised the impact of worms on production. Phenotypic and genetic parameters under these conditions may be considerably different from those where there is no parasite control (Albers *et al.* 1987). The parameters reported here may be appropriate for use where worm control programs are currently effective but may not be appropriate if increasing anthelmintic resistance causes control programs to break down.

If there is progressive erosion of the effectiveness of anthelmintics with no corresponding development of alternative control strategies, it may be of considerable importance to estimate genetic parameters in a diseased environment to ensure optimal response to selection. Development of anthelmintic resistance is predictable; what is unpredictable is the likelihood of development of alternative worm control strategies. These include the use of biological control agents such as predatory fungi (Waller and Faedo 1996), the use of vaccination to improve host immunity (Miller 1996), and the use of strategic supplementation (Coop and Holmes 1996). Another alternative may be a shift in enterprise mix to cropping or cattle, to reduce sheep numbers and stocking rate. In practice, one or a combination of these strategies may be implemented before the level of worm challenge changes to the extent where the genetic parameters are significantly different. If this is the case, additional parameters in a diseased environment may not be required.

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References

Albers, G. A. A., Gray, G. D., le Jambre, L. F., Piper, L. R., Barger, I. A., and Barker, J. S. F. (1989). The effect of *Haemonchus contortus* on liveweight gain and wool growth in young Merino sheep. *Australian Journal of Agricultural Research* **40**, 419–32.

Albers, G. A. A., Gray, G. D., Piper, L. R., Barker, J. S. F., le Jambre, L. F., and Barger, I. A. (1987). The genetics of resistance and resilience to *Haemonchus contortus* in young Merino sheep. *International Journal for Parasitology* **17**, 1355–63.

Anon. (1994). Nemesis Newsletter No. 2. News from the network. (CSIRO: Armidale.)

Atkins, K. D. (1987). Potential responses to selection in Merino sheep given current industry structure and selection practices. *In* Merino Improvement Programs in Australia'. (Ed. B. J. McGuirk.) pp. 299–312. (Australian Wool Corporation: Melbourne.)

Baker, R. L., Watson, T. G., Bisset, S. A., Vlassoff, A., and Douch, P. G. C. (1991). Breeding sheep in New Zealand for resistance to internal parasites: research results and commercial application. *In* 'Breeding for Disease Resistance in Sheep'. (Eds G. D. Gray and R. R. Woolaston.) pp. 19–32. (Australian Wool Corporation: Melbourne.)

Barger, I. A. (1982). Helminth parasites and animal production. *In* 'Biology and Control of Endoparasites'. (Eds L. E. A. Symons, A. D. Donald, and J. K. Dineen.) pp. 133–55. (Academic Press: Sydney.)

Beattie, A. W. (1962). Relationships among productive characters of Merino sheep in north-western Queensland. 2. Estimates of genetic parameters, with particular reference to selection for wool weight and crimp frequency. *Queensland Journal of Agricultural Science* **19**, 17–26.

Besier, B., Lyon, J., and McQuade, N. (1996). Drench resistance in sheep worms—a big economic cost. *Western Australian Journal of Agriculture* **37**, 60–3.

Bisset, S. A., Vlassoff, A., Morris, C. A., Southey, B. R., Baker, R. L., and Parker, A. G. H. (1992). Heritability of and genetic correlations among faecal egg counts and productivity traits in Romney sheep. *New Zealand Journal of Agricultural Research* **35**, 51–8.

Brown, G. H., and Turner, H. N. (1968). Response to selection in Australian Merino sheep. II. Estimates of phenotypic and genetic parameters for some production traits in Merino ewes and an analysis of the possible effects of selection on them. *Australian Journal of Agricultural Research* **19**, 303–22.

Coop, R. L., and Holmes, P. H. (1996). Nutrition and parasite interactions. *International Journal for Parasitology* **26**, 951–62.

Cunningham, A. J. (1978). 'Understanding Immunology.' (Academic Press: London.)

Cunningham, E. P. (1969). The relative efficiencies of selection indexes. *Acta Agriculturae Scandinavica* **19**, 45–8.

Davis, G. P., and Kinghorn, B. P. (1986). Genetic and phenotypic parameters for growth, wool production and reproductive traits in a line of Merino sheep. *Proceedings of the 3rd World Congress on Genetics Applied to Livestock Production* **11**, 145–50.

Eady, S. J. (1995). Implications of non-normal distribution of faecal egg count for measuring worm resistance in Merino sire evaluation schemes. *Australian Association of Animal Breeding and Genetics* **11**, 79–83.

Eady, S. J. (1998). Worm resistance in a Merino breeding objective—influence of genetic correlations between resistance and production traits. *Proceedings of the 6th World Congress on Genetics Applied to Livestock Production* **27**, 141–4.

Eady, S. J., Woolaston, R. R., and Mortimer, S. I. (1994). Internal parasite resistance of Merino flocks selected for production. *Proceedings of the 5th World Congress on Genetics Applied to Livestock Production* **20**, 289–92.

Eady, S. J., Woolaston, R. R., Mortimer, S. I., Lewer, R. P., Raadsma, H. W., Swan, A. A., and Ponzoni, R. W. (1996). Resistance to nematode parasites in Merino sheep: sources of genetic variation. *Australian Journal of Agricultural Research* **47**, 895–915.

Falconer, D. S. (1989). 'Introduction to Quantitative Genetics.' 3rd Edn. (Longman Scientific and Technical: Harlow, UK.)

Gifford, D. R., Ponzoni, R. W., Ancell, P. M. C., Hynd, P. I., Walkley, J. R. W., and Grimson, R. J. (1994). Genetic studies on wool quality and skin characters of the Merino. *Proceedings of the 5th World Congress on Genetics Applied to Livestock Production* **19**, 409–12.

Gregory, I. P. (1982*a*). Genetic studies of South Australian Merino sheep. III. Heritabilities of various wool and body traits. *Australian Journal of Agricultural Research* **33**, 355–62.

Gregory, I. P. (1982*b*). Genetic studies of South Australian Merino sheep. IV. Genetic, phenotypic and environmental correlations between various wool and body traits. *Australian Journal of Agricultural Research* **33**, 363–73.

Hickson, J. D., Swan, A. A., Kinghorn, B. P. and Piper, L. R. (1995). Maternal effects at different ages in Merino sheep. *Proceedings of the Australian Association of Animal Breeding and Genetics* **11**, 416–20.

James, J. W. (1993). Design of resource flocks. *In* 'Merino Genetic Resource Flocks in Australia'. (Eds. R. W. Ponzoni and D. R. Gifford.) pp. 62–8. (SA Govt: Adelaide.)

James, P. J., Ponzoni, R. W., Walkley, J. R. W., and Whitely, K. J. (1990). Genetic parameters for wool production and quality traits in South Australian Merinos of the Collinsville family group. *Australian Journal of Agricultural Research* **41**, 583–94.

Kisielewicz, B. K., Fraser, J. M., and Eady, S. J. (1995). No effect of a short period of artificial worm challenge on liveweight change in young Merino sheep. *Proceedings of the*

Australian Association of Animal Breeding and Genetics **11**, 674–7.

Lewer, R. P., Woolaston, R. R., and Howe, R. R. (1994). Studies on Western Australian Merino sheep. II. Genetic and phenotypic parameter estimates for objectively measured traits on ram and ewe hoggets using different model types. *Australian Journal of Agricultural Research* **45**, 829–40.

McEwan, J. C., Dodds, K. D., Greer, G. J., Bain, W. E., and Duncan, S. J. (1995). Genetic estimates for parasite resistance traits in sheep and their correlations with production traits. *New Zealand Journal of Zoology* **22**, 177.

McEwan, J. C., Mason, P., Baker, R. L., Clarke, J. N., Hickey, S. M., and Turner, K. (1992). Effect of selection for productive traits on internal parasite resistance in sheep. *Proceedings of the New Zealand Society of Animal Production* **52**, 53–6.

Meyer, K. (1989). Restricted maximum likelihood to estimate variance components for animal models with several random effects using a derivative-free algorithm. *Genetics Selection Evolution* **21**, 317–40.

Miller, H. R. P. (1996). Prospects for the immunological control of ruminant gastrointestinal nematodes: natural immunity, can it be harnessed? *International Journal for Parasitology* **26**, 801–11.

Morley, F. H. W. (1955). Selection for economic characters in Australian Merino sheep. V. Further estimates of phenotypic and genetic parameters. *Australian Journal of Agricultural Research* **6**, 77–90.

Morris, C. A., Bisset, S. A., Vlassoff, A., Baker, R. L., Watson, T. G., and Wheeler, M. (1997). Yearling and ewe fleece weights in Romney and Perendale flocks selected for divergence in faecal nematode egg count. *Proceedings of the Association for the Advancement of Animal Breeding and Genetics* **12**, 50–3.

Mortimer, S. I., and Atkins, K. D. (1989). Genetic evaluation of production traits between and within flocks of Merino sheep. I. Hogget fleece weights, body weight and wool quality. *Australian Journal of Agricultural Research* **40**, 433–43.

Mortimer, S. I., and Atkins, K. D. (1995). Maternal effects influence growth traits of Merino sheep. *Proceedings of the Australian Association of Animal Breeding and Genetics* **11**, 421–4.

Mullaney, P. D., Brown, G. H., Young, S. S. Y., and Hyland, P. G. (1970). Genetic and phenotypic parameters for wool characteristics in fine-wool Merino, Corriedale and Polwarth sheep. *Australian Journal of Agricultural Research* **21**, 527–40.

Piper, L. R. (1987). Genetic variation in resistance to internal parasites. *In* 'Merino Improvement Programs in Australia'. (Ed. B. J. McGuirk.) pp. 351–63. (Australian Wool Corporation: Melbourne.)

Piper, L. R., and Barger, I. A. (1988). Resistance to gastrointestinal strongyles: feasibility of a breeding program. *Proceedings of the 3rd World Congress for Sheep and Beef Cattle Breeding*, INRA, Paris **2**, 593–611.

Pocock, M. J., Eady, S. J., and Abbott, K. A. (1995). *Nemesis* in action—breeding for worm resistance. *Proceedings of the Australian Association of Animal Breeding and Genetics* **11**, 74–8.

Ponzoni, R. W. (1987). WOOLPLAN—design and implications for the Merino industry. *In* 'Merino Improvement Programs in Australia'. (Ed. B. J. McGuirk.) pp. 25–40. (Australian Wool Corporation: Melbourne.)

Reis, P. J. (1979). Effects of amino acids on the growth and properties of wool. *In* 'Nutritional and Environmental Limitations to Wool Growth'. (Eds J. L. Black and P. J. Reis.) pp. 223–42. (University of New England: Armidale.)

Semple, S. J., Atkins, K. D., and Casey, A. E. (1994). 'OBJECT Manual.' (NSW Agriculture: Orange.)

Snedecor, G. W., and Cochran, W. G. (1967). 'Statistical Methods.' 6th Edn. (Iowa State University Press: Ames, IA.)

Swan, A. A., Lax, J., and Purvis, I. W. (1995). Genetic variation in objectively measured wool traits in CSIRO's fine wool flock. *Proceedings of the Australian Association of Animal Breeding and Genetics* **11**, 516–20.

Vaez Torshizi, R., Nicholas, F. W., and Raadsma, H. W. (1996). REML estimates of variance and covariance components for production traits in Australian Merino sheep, using an animal model. 1. Body weight from birth to 22 months. *Australian Journal of Agricultural Research* **47**, 1235–49.

Walkley, J. R. W., Ponzoni, R. W., and Dolling, C. H. S. (1987). Phenotypic and genetic parameters for lamb and hogget traits in a flock of South Australian Merino sheep. *Australian Journal of Experimental Agriculture* **27**, 205–10.

Waller, P. J., and Faedo, M. (1996). The prospects for biological control of the free-living stages of nematode parasites of livestock. *International Journal for Parasitology* **26**, 915–25.

Watson, T. G., Morris, C. A., McEwan, J. C., Hurford, A. P., and Hosking, B. C. (1995). Genetic estimates of relationships between FEC and production traits in research sheep flocks selected for productive performance. *New Zealand Journal of Zoology* **22**, 177–8.

Woolaston, R. R. (1994). Preliminary evaluation of strategies to breed Merinos for resistance to roundworms. *Proceedings of the 5th World Congress on Genetics Applied to Livestock Production* **20**, 281–4.

Woolaston, R. R., and Piper, L. R. (1996). Selection of Merino sheep for resistance to *Haemonchus contortus*: genetic variation. *Animal Science* **62**, 451–60.

Woolaston, R. R., Windon, R. G., and Gray, G. D. (1991). Genetic variation in resistance to internal parasites in Armidale experimental flocks. *In* 'Breeding for Disease Resistance in Sheep'. (Eds. G. D. Gray and R. R. Woolaston.) pp. 1–9. (Australian Wool Corporation: Melbourne).

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