Resistance to nematode parasites in Merino sheep: sources of genetic variation

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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), CSIRO Finewool Flock (Armidale, NSW), and the Trangie D Flock (Trangie, NSW). Faecal egg count (FEC) was used to measure relative resistance of sheep to nematode parasites after either natural or artificial infection with *Haemonchus contortus* and *Trichostrongylus colubriformis*. Differences in $FEC^{0.33}$ between strains and between and within bloodlines were examined and the heritability of this trait was estimated. A low proportion of the total variation in parasite resistance could be attributed to strain and bloodline effects (1 and 3.5%, respectively) after either natural or artificial infection. The major source of genetic variation was found within bloodlines (22.2% of total variation), with individual sires showing a wide range in parasite resistance. Paternal half-sib heritability estimates for $FEC^{0.33}$ were significant ($P < 0.05$) in 9 of the 11 analyses and ranged from 0.07 to 0.42, with a weighted average of 0.22. The influence of the environmental effects of sex, age of dam, birth-rearing rank, and day of birth were also investigated, and were found to be only occasionally significant, accounting for a small proportion ($0.3-2.2\%$) of variation. Management group effects both prior to and at the time of measurement were often significant, and accounted for $2.2-19.4\%$ of variation in FEC. Correction of FEC for effects other than management group would seem to add little to precision of selection. These results have demonstrated that significant genetic variation for nematode parasite resistance exists within a wide range of Merino bloodlines, and within-flock selection of resistant sires appears to be an effective method of improving this trait in Merino sheep.

Additional keywords: heritability, faecal egg count, parasite resistance, variance components.

Introduction

In Australia, gastro-intestinal nematode parasites of sheep have shown an alarming increase in anthelmintic resistance. The latest survey indicates that over 90% of sheep properties show some drench resistance (Overend *et al.* 1994). This increase in anthelmintic resistance has caused increasing difficulties in the control of nematode parasite infections. The unlikely advent of a new family of drugs for parasite control during the next 5–10 years means that these difficulties will only increase as resistance spreads to the most recently developed family of drugs, the avermectins. The utilisation of genetic variation that exists between sheep for natural resistance has been proposed as a means of reducing the reliance on anthelmintics for parasite control (Piper and Barger 1988).

Table 1. Heritability (± s.e.) estimates for transformed FEC after natural and artificial nematode infection in a range of sheep breeds

Breed	Age of sheep (months)	Infection type and no. of FECs	Heritability	Reference
Merino	4–5	Artificial *H. contortus* 1 count, max. 1–3 weekly measurements	0·29±0·03	Woolaston and Piper 1996
Romney and Romney cross	5–8	Natural (*T. colubriformis* and *Ostertagia* spp.), 1 count	0·34±0·19	Watson *et al.* 1986
Merino	18	Artificial *H. contortus*, 1 count	0·23±0·13	Piper 1987
Merino	4–5	Artificial *T. colubriformis* after vaccination with irradiated *T. colubriformis*, av. 5 counts made at weeks 3–7 post infection	0·41±0·04	Woolaston *et al.* 1991
Merino	6–12	Natural, 2 counts in different infection cycles	0·42±0·14	Cummins *et al.* 1991
Romney	5–8	Natural, 2 counts in different infection cycles	0·53±0·15	Baker *et al.* 1991
Romney	5–8	Natural, 1 count	0·27±0·07	Bisset *et al.* 1992
Romney	5	Natural, 1 count	0·13±0·07	McEwan *et al.* 1992
Merino	4–5	Artificial *H. contortus*, 1 count at 4 weeks post infection 1 count at 5 weeks post infection	0·34±0·10 0·26±0·09	Albers *et al.* 1987
Red Maasai	10	Natural, av. 2 counts 2 days apart	0·20±0·08	Baker *et al.* 1994
Romney		Natural infection,		Morris *et al.* 1993
	4	1 count	0·39±0·13	
	6	1 count	0·46±0·14	
Romanov	6–10	Artificial infection, av. 6 counts	0·55	Gruner and Lantier 1995
Polish Long Wool	6–8	Natural, av. 2 counts 2 months apart	0·28±0·16	Gruner and Lantier 1995
Hungarian Merino	6–7	Artificial *H. contortus*, av. 4 counts with second infection imposed	0·49±0·17	Sreter *et al.* 1994

Faecal egg count (FEC) following parasite challenge has been widely adopted as an indirect measure of host resistance. The heritability of FEC has been estimated in a number of breeds of sheep, the majority of estimates falling in the range $0 \cdot 2$–$0 \cdot 4$ (Table 1). The higher estimates have tended to come from flocks where the FECs were made in highly controlled environments (Woolaston et al. 1991) or repeat measurements were made (Baker et al. 1991; Cummins et al. 1991; Gruner and Lantier 1995). The heritability estimates for Australian Merinos have come from 5 bloodlines, and there has been no wider study within this breed to identify genetic variation that may be attributed to strain and bloodline-within-strain.

Variation between Merino strains and bloodlines for production traits has been well documented (Jackson and Roberts 1970; Mortimer and Atkins 1989; Lewer et al. 1992). If a Merino breeder desires to shift fleece weight or fibre diameter in a certain direction, there is information available to help identify suitable bloodlines (Atkins et al. 1995). However, should a breeder wish to improve a less commonly measured trait or a trait that has only regional importance, identifying superior bloodlines is indeed difficult or impossible. Differences between Merino strains in fleece and body traits have largely arisen through selection pressure for particular characteristics felt to be of importance in a region (Chapman et al. 1973). Differences in parasite resistance between strains and bloodlines may have evolved through natural selection or genetic drift. Although there has been little deliberate selection for resistance, differences may also have appeared if associations existed between this disease trait and production traits in the breeding objective.

As strains and bloodlines have tended to develop in regions defined largely by climatic attributes, there may have evolved substantial differences in resistance between these genetic groups on account of the large variation in disease incidence between regions. This study investigates the extent of genetic variation that exists between Merino strains and bloodlines. As many bloodlines as possible were included in the study by using Merino resource flocks already established across Australia. The parasite species used were *Haemonchus contortus*, an important parasite in regions of Australia which have a summer rainfall component, and *Trichostrongylus colubriformis*, a parasite with a wide distribution throughout high rainfall areas in Australia (Anderson et al. 1978; Beveridge and Ford 1982). Sources of genetic and environmental variation in nematode parasite resistance are identified, including the influence of effects such as management group, sex, age of dam, birth rearing status, and day of birth.

Materials and methods

Merino sheep representing a range of bloodlines maintained in resource flocks across Australia were tested for resistance to roundworm parasites. These flocks included the JB Pye Flock (Camden, NSW), Katanning Base Flock (Katanning, WA), Turretfield Merino Resource Flock (Rosedale, SA), CSIRO Finewool Flock (Armidale, NSW), and the Trangie D Flock (Trangie, NSW).

Infective larvae and faecal egg counting

Where artificial infection was used, the larvae were prepared at the CSIRO Pastoral Laboratory, Armidale, from stocks of Kirby strain *H. contortus* and McMaster strain *T. colubriformis*. The origins of these strains were given by Woolaston et al. (1990). Before

August 1992, artificial infections were administered as a known dose of infective larvae via a gelatin capsule. This method was replaced by a semi-automated procedure using a modified vaccination gun (Roux Revolver), which could be calibrated to give a larval dose at least as accurate as the capsule method. For artificial infection, dose rates were 10 000 *H. contortus* or 20 000 *T. colubriformis* L₃ larvae per sheep. Where it was not clear if animals had been previously exposed to natural nematode infection, the sheep were 'primed' with a half dose of infective larvae before the main infection. The 'priming' infection was allowed to persist for 21–28 days, and was terminated with anthelmintic treatment before subsequent reinfection with the same parasite species. At this second infection egg counts were determined.

Where groups were primed, all animals in the mob were similarly infected, with the exception of the *H. contortus* infection of the Turretfield Resource Flock. In this instance, a random selection of half the animals was primed with *H. contortus* larvae to give an indication of the importance of prior exposure to the specific parasite in determining the response to a subsequent infection. Where artificial infection was used, sheep were infected with *H. contortus* in the first year of the study, and in the second year the subsequent drop of sheep was infected with *T. colubriformis*.

Following a challenge period of approximately 28 days for the artificial infections, faecal egg counts were determined using a modified McMaster technique with a lower limit of detection of 100 eggs/g (epg) of faecal material. Bulk faecal cultures were usually, but not always, prepared from each management group to identify the parasite genera present. Egg counts were expressed in terms of epg, and there was no correction for faecal consistency. In the laboratory, the sample preparers and counters were recorded and coded as fixed effects in the subsequent analyses.

Experimental groups and infection type

Table 2 summarises for each resource flock the number of bloodlines, sire families, age of sheep at testing, sex and number of animals tested, type of parasite infection and details of pre-infection priming.

1. JB Pye Flock, University of Sydney, Camden, NSW

The JB Pye Flock, described by Raadsma and Nicholas (1993) and Raadsma *et al.* (1994), was established in 1987 in the Nepean region of NSW, comprising 4 bloodlines. There were 3 medium wool Peppin bloodlines (Plevna, Trangie Fertility and Pye) and 1 fine wool bloodline (Hillcreston). Animals born in 1990 and 1991 (August–September lambing) were used in the resistance study. All nematode parasite infections in the JB Pye flock were from natural challenge. Egg counts in the flock were monitored prior to sampling, and when they reached a mean of 500–1000 epg, faecal samples were taken. The coastal environment with a non-seasonal rainfall of 600 mm per annum was extremely favourable for the survival of infective larvae at pasture. The sheep were continually exposed to infective larvae all year round, as indicated by monitor egg counts, and required regular anthelmintic treatment to prevent both production and livestock losses. Because of the warm and humid conditions, this is not a suitable environment for sheep, and there are no commercial sheep enterprises in this region.

The first group sampled included all of the wethers and approximately one third of the ewes from the 1990 drop. This group had been challenged with footrot before being tested for resistance, but were free of footrot during the period of parasite infection before faecal sampling. These sheep were born at the JB Pye Farm at Camden and were moved after weaning to a separate university property nearby (Mt Hunter) for the footrot challenge. The sheep were randomly allocated to 2 management groups balanced for sire group and sex. The rest of the 1990-drop ewes and 70 1990-drop rams were sampled in 1993 as 3-year-olds. They were located at JB Pye Farm in 2 management groups based on sex. At the time of faecal sampling the ewes were within 1 week of commencement of lambing. The 1991 drop was located at JB Pye Farm in 2 management groups when tested, one comprising ewes and the second comprising rams and wethers.

Table 2. Experimental details for Merino resource flocks tested for resistance to nematode parasites

Hc, *H. contortus*; Tc, *T. colubriformis*

Experimental groups	No. of bloodlines	No. of sire families	Age at testing (mths)	Sex	No. of sheep tested	Infection type and species	Pre-infection priming
JB Pye (1990a)	4	41	18	Ewes	110	Natural	No
				Wethers	298	mixed spp.	
JB Pye (1990b)	4	42	36	Ewes	243	Natural	No
				Rams	70	mixed spp.	
JB Pye (1991)				Ewes	479	Natural	No.
				Rams	109	mixed spp.	
				Wethers	385		
Katanning (1991)	16	64	8	Ewes	478	Artificial	Yes
				Wethers	476	Hc	
Turretfield (1992)	4	48	7	Ewes	816	Artificial	$\frac{1}{2}$ Yes
				Rams	786	Hc	$\frac{1}{2}$ No
CSIRO (1991)	11	60	7	Ewes	552	Artifical	No
				Wethers	524	Hc	
Trangie (1990)	15	23	6	Ewes	301	Artificial Hc	Yes
Katanning (1992)	16	64	8	Ewes	487	Artificial	No
				Wethers	493	Tc	
Turretfield (1993)	4	34	5	Ewes	449	Artifical	No
				Wethers	432	Tc	
CSIRO (1992)	11	74	13	Ewes	573	Artificial	No
				Wethers	499	Tc	
Trangie (1991)	15	23	6	Ewes	324	Artificial	No
				Rams	69	Tc	
Total	50	473			8953		

2. Katanning Base Flock, Great Southern Agricultural Research Institute, WA Department of Agriculture, Katanning, WA

The Katanning Base Flock, comprising 4 strains (Peppin, Collinsville, Bungaree, Independent Group Breeders) each represented by 4 bloodlines, was established in 1981 at Katanning (Lewer *et al.* 1992; Lewer 1993). Details of flock management and the selection of animals were given by Lewer *et al.* (1992). This description does not include the Independent Group Breeder bloodlines but these groups were established in the same manner as the others (R. P. Lewer, pers. obs.). The Great Southern region is characterised by a Mediterranean climate with an annual average rainfall of 470 mm. Nematode parasites are a seasonal problem that requires anthelmintic treatment of young sheep to avoid production losses.

Animals born in 1991 and 1992 (March–April lambing) were used in the parasite resistance study. In both years, the sheep were in 2 management groups based on sex. For the *H. contortus* infection of the 1991 drop, the sheep were primed before the main infection, but this was not considered necessary for the *T. colubriformis* infection of the 1992 drop as monitor egg counts of 0–250 epg for ewes and 0–400 epg for wethers indicated a *Trichostrongylus* spp. infection of sufficient magnitude to trigger their immune systems.

3. Turretfield Merino Resource Flock, SA Department of Agriculture, Rosedale, SA

This flock, consisting of 2 bloodlines for each of 2 strains, was established in 1988 at Turretfield Research Centre, in the wheat–sheep zone of South Australia (Gifford *et al.* 1992; Gifford and Ponzoni 1993). The 2 major family groups of Merinos found in South Australia were represented by 2 studs each: the Collinsville group by Collinsville and Southrose, and the Bungaree group by Anama and East Bungaree. Turretfield receives an annual rainfall of 460 mm, which predominantly falls in the winter. As at Katanning, nematode parasites are a seasonal problem requiring anthelmintic treatment of young sheep to avoid production losses.

Animals born in 1992 and 1993 (April–May lambing) were used in the parasite resistance study. Half the 1992-born group, allocated at random across sire group and sex, were primed for the *H. contortus* infection to allow assessment of the effect of prior exposure to *H. contortus* on the subsequent resistance of the animals. Monitor egg counts of 115–260 epg of *Trichostrongylus* spp. prior to priming suggested the absence of any exposure to *H. contortus*. The 1992-born animals were run in 2 management groups based on sex. Both the ewe and ram groups were infected at Turretfield, but the ewes had been moved to agistment at a property on the Yorke Peninsula at the time of sampling.

The 1993-born progeny were not primed as monitor egg counts, ranging over 100–350 epg, indicated prior exposure to *Trichostrongylus* spp. This group was in 3 management groups: one comprising all ewes, and the wethers split at random into 2 groups. In this year, all sheep remained at Turretfield during the parasite challenge.

4. CSIRO Finewool Flock, Armidale, NSW

The CSIRO Finewool Flock, located at Longford Field Station, Armidale, was established in 1990 (Swan *et al.* 1993). The flock comprised 9 fine wool and 2 medium wool bloodlines. Average annual rainfall is 820 mm, which tends to be summer dominant. Sheep in this region are challenged regularly by nematode parasites, requiring routine anthelmintic treatment to prevent substantial losses in both production and livestock.

Animals born in 1991 and 1992 (October–November lambing) were used in the parasite resistance study. The 1991-born animals were allocated at random to 3 management groups balanced for bloodline, sire, sex, and age of dam. Priming before artificial infection was not considered necessary as sheep of this age on the New England Tablelands have usually been exposed to considerable parasite challenge. This was confirmed by monitor egg counts in excess of 200 epg, before artificial infection, for both the 1991- and 1992-born animals.

The 1992-born progeny were tested for *T. colubriformis* resistance at 13 months of age, an older age than the 1991 group owing to delays caused by a footrot outbreak. These sheep were in 3 management groups, as outlined above, before footrot infection. These groups were then divided on the basis of footrot diagnosis into 5 management groups. Both pre- and post-footrot management groups were fitted as fixed effects in the analysis, but only the post-footrot groups were significant and remained in the analysis. As the prevalence of footrot was relatively low and showed no bloodline or sex effects (A. A. Swan pers. comm.), these groups were still reasonably balanced. There was no differentiation of parasite genera for this infection.

5. Trangie D Flock, NSW Agriculture, Trangie, NSW

The Trangie D Flock was established in 1974–75 at Trangie Agricultural Research Centre on the central western plains of NSW (Mortimer and Atkins 1989; Atkins and Mortimer 1993). Fifteen flocks were formed, comprising 2 fine wool bloodlines, 2 medium wool non-Peppin bloodlines, 10 medium wool Peppin bloodlines, and 1 strong wool South Australian bloodline. The descriptions used in this report are consistent with those used by Mortimer and Atkins (1989). Rainfall at Trangie averages 480 mm/year, and is characterised by its non-seasonality and unreliability. Sheep in this region are not subject to regular parasitism by nematodes.

Ewes born in 1990 and all animals born in 1991 (July–August lambing) were used in the parasite resistance study. Both groups were 'primed' with the respective parasite species before the main infection as the prevalence of nematodes in the Trangie environment and the likelihood of prior exposure were low. In both years all sheep were in a single management group.

Statistical analysis

All FECs were analysed on the cube root scale (Blattman *et al.* 1993; Eady 1995; Woolaston and Piper 1996). Within each resource flock the basic experimental design was a nested hierarchical structure with either 1 or 2 levels, that is, bloodline nested within strain and sire nested within bloodline. Strain was classified as a fixed effect, and bloodline was also classified as a fixed effect when not nested within strain. Bloodline nested within strain was classified as a random effect along with sire-within-bloodline. Least squares analysis of variance (Harvey 1987) was used to estimate the effects of strain (where applicable),

bloodline-within-strain, bloodline, and sire-within-bloodline, as well as the fixed effects of age of dam (maiden $v.$ adult ewes), birth-rearing rank (single-born and reared $v.$ multiple-born and single-reared $v.$ multiple-born and reared lambs), sex (ewe $v.$ wether $v.$ ram), management group or sex/management group where these effects were confounded, sample preparer (3) and counter (3), and first-order interactions of these effects on $FEC^{0\cdot33}$. Day of birth within group was fitted as a covariate. In some flocks management group and sex were confounded, while in others an estimate of both effects was possible. Year effects were confounded with parasite species so each year's data were analysed separately.

The following linear model was used to estimate strain (where applicable), bloodline or bloodline-within-strain, sire-within-bloodline, and error components of variance for $FEC^{0\cdot33}$ for each parasite genus in each resource flock:

$$Y_{hijklmnop} = \mu + st_h + bl_{i:h} + S_{j:i:h} + brr_k + a_l + s_m + m_n + pr_o + ct_p + dob_{Xi}$$

$$+ \text{ 1st order interactions} + e_{hlklmnop}$$

where Y is $FEC^{0\cdot33}$; μ is the common mean; st_h is the effect of the hth strain; bl_i is the effect of the ith bloodline nested within strain; S_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); a_l is the effect of the lth dam age (maiden or mature); s_m is the effect of the mth sex (ewe, wether or ram); m_n is the effect of nth management group; pr_o is the effect of the oth sample preparer; ct_p is the effect of the pth sample counter; dob the regression of phenotype on day of birth; and X_i is the day of birth of animal$_i$; and $e_{hijklmnop}$ is the random error.

The level of significance for each environmental effect was obtained by tests against the error mean square. Significance levels for the effects of strain and bloodline were tested, respectively, against the nested bloodline and sire mean square, and sire effects were tested against the error mean square. The full model containing all main effects was fitted for each flock for the estimation of least-squares constants for environmental effects. Non-significant effects and first-order interactions ($P > 0\cdot05$), plus those interactions which accounted for <2% of the variation in $FEC^{0\cdot33}$, were sequentially excluded from the analyses. The final models for estimation of variance components contained strain (where applicable), bloodline-within-strain/bloodline, sire-within-bloodline, and all significant environmental effects and interactions and non-significant main effects involved in interactions. Where strain, bloodline-within-strain/bloodline, and environmental effects were significant, pair-wise comparisons were made using linear contrasts.

Within-flock variance components for $FEC^{0\cdot33}$ were estimated by the restricted maximum likelihood procedure (DFREML; Meyer 1989) using a sire model. From the ratio of appropriate variance components (within-bloodline variance/within-bloodline plus residual variance), heritability of $FEC^{0\cdot33}$ was estimated for each parasite genera in each resource flock. Approximate standard errors for heritability came from the DFREML analysis. A restricted maximum likelihood (REML) procedure, fitting a sire model within the statistics package SPLUS (StatSci 1993), was used to partition variance between strain, bloodline-within-strain, and sire-within-bloodline. In this analysis, strain, bloodline, and sire were classified as random effects. The degree of consistency of flock means in different years was estimated using product-moment correlations between the least square means.

Results

Parasite infections and species composition

Relatively high FECs (unadjusted) were measured after both natural and artificial infection indicating a substantial parasite burden in all groups with the exception of the CSIRO Finewool flock (1992) where mean FEC was substantially lower (Table 3). In flocks where larval differentiation was performed, the dominant species was generally the one given artificially. However, artificial challenge with *H. contortus* in the Turretfield Resource Flock did not appear to result in an

infection dominated by this species. This infection appeared to be accompanied by significant numbers of naturally acquired *Trichostrongylus* spp. The relatively low egg count, compared to the other *H. contortus* infections, suggests that the establishment of *H. contortus* may have been sub-optimal. *H. contortus* is generally a prolific egg layer compared with *Trichostrongylus* spp. (Clunies Ross and Gordon 1936). The natural infections in the JB Pye Flock varied in species composition between management groups.

Table 3. Mean FEC and proportion of zero counts and parasite genera present after natural and artificial infections of Merino flocks with nematode larvae

Tc, *T. colubriformis*; Hc, *H. contortus*; Ost, *Ostertagia* spp.; Oes, *Oesophagostum* spp. n.d., larval differentiation not determined

Experimental group	Infection type	Management group	Mean FEC (epg)	% Zero counts	Parasite genera present (%)			
					Hc	Tc	Ost	Oes
JB Pye (1990a)	Natural	Group 1	1734	6·9	58	19	23	0
		Group 2			97	1	2	0
JB Pye (1990b)	Natural	Ewes, n.d.	1074	24·0	—	—	—	—
		Rams			0	78	22	0
JB Pye (1991)	Natural	Ewes	6338	0·2	84	14	2	0
		Wethers/rams			96	2	2	0
Katanning (1991)	Artificial Hc	Ewes, n.d.	4452	0·7	—	—	—	—
		Wethers, n.d.			—	—	—	—
Turretfield (1992)	Artificial Hc	Ewes	913	5·4	53	41	6	0
		Rams			52	48	0	0
CSIRO (1991)	Artificial Hc	Group 1	4244	19·7	98	2	0	0
		Group 2			85	13	2	0
		Group 3			96	3	1	0
Trangie (1990)	Artificial Hc	Ewes, n.d.	10851	0·0	—	—	—	—
Katanning (1992)	Artificial Tc	Ewes	2637	0·0	0	90	10	0
		Wethers			0	84	16	0
Turretfield (1993)	Artificial Tc	Ewes	2790	0·5	1	82	13	4
		Wethers			2	89	3	6
CSIRO (1992)	Artificial Tc	5 man. gps, n.d.	311	52·2	—	—	—	—
Trangie (1991)	Artificial Tc	Ewes/rams, n.d.	3894	0·3	—	—	—	—

Environmental effects

Means and standard errors and least squares constants for fixed effects for the 3 infection types are presented in Tables 4 and 5. There were no significant first-order interactions. Management group effects were often highly significant and accounted for $2 \cdot 2$–$19 \cdot 4\%$ of the variation in $FEC^{0 \cdot 33}$. Management group effects alone were not presented in the tabulation of results; however, where management group and sex were confounded the effects were presented.

Sex/management group effects (presented separately from sex effects alone) significantly contributed to $FEC^{0 \cdot 33}$ variation on all occasions (Tables 4 and 5). In 3 of the 4 instances where sex effects were measured, there were significant differences, ewes having lower mean $FEC^{0 \cdot 33}$ than wethers in the JB Pye Flock (1990a) and the CSIRO Finewool Flock (1992), and wethers having lower mean $FEC^{0 \cdot 33}$ than ewes in the CSIRO Finewool Flock (1991). Overall, sex accounted for $0 \cdot 5$–$0 \cdot 8\%$ of the variation in $FEC^{0 \cdot 33}$.

On 3 occasions, birth rearing rank had a significant ($P < 0 \cdot 05$) effect (Table 4 and 5). In 2 instances (Turretfield Resource Flock 1992 and Trangie D Flock

1990), the single-born and single-reared sheep had the highest mean $FEC^{0.33}$. On the third occasion (Turretfield Resource Flock 1993), multiple-born and single-reared sheep had the highest mean $FEC^{0.33}$. Birth rearing rank accounted for a maximum of 2.2% of the total variation in $FEC^{0.33}$.

Age of dam had a significant effect ($P < 0.05$) on only 1 occasion (Turretfield Resource Flock 1992), when it accounted for 0.3% of the variation in $FEC^{0.33}$ and where offspring from mature ewes had a greater egg count than offspring from maiden ewes.

Table 4. Mean and least-squares constants ($\pm$s.e.) for environmental effects on $FEC^{0.33}$ after natural nematode infection

Reproductive status of ewe management groups: np, non-pregnant; pnl, pregnant but non-lactating; pl, pregnant and lactating
Birth rearing rank: SS, single-born and reared; MS, multiple-born, single-reared; MM, multiple-born and reared
Means followed by the same letter for the same fixed effect do not differ significantly at $P = 0.05$

Source	Level	JB Pye 1990a	JB Pye 1990b	JB Pye 1991
Mean		9.62 ± 0.57	7.82 ± 0.82	16.93 ± 0.48
Sex/management group	Ewe np		-2.98 ± 0.64b	-1.47 ± 0.25b
	Ewe pnl		3.31 ± 1.04a	
	Ewe pl		0.42 ± 0.57a	
	Ram		-0.75 ± 0.61ab	1.09 ± 0.34a
	Wether			0.38 ± 0.26a
Sex	Ewe	-0.55 ± 0.28a		
	Wether	0.55 ± 0.28b		
Birth rearing rank	SS	-0.20 ± 0.40	0.19 ± 0.51	0.29 ± 0.28
	MS	-0.43 ± 0.59	0.34 ± 0.74	-0.34 ± 0.35
	MM	0.63 ± 0.50	-0.54 ± 0.59	0.05 ± 0.45
Dam age	Maiden	-0.07 ± 0.38	0.33 ± 0.48	-0.25 ± 0.20
	Adult	0.07 ± 0.38	-0.33 ± 0.48	0.25 ± 0.20
Day of birth		0.03 ± 0.03	-0.04 ± 0.04	0.04 ± 0.02*

* $P < 0.05$.

Day of birth had a significant effect on $FEC^{0.33}$ in 5 of the 11 analyses. In the JB Pye Flock (1991), Turretfield Resource Flock (1992 and 1993), and CSIRO Finewool Flock (1992), day of birth had a significant ($P < 0.05$) and positive effect; that is, the younger the animal at the time of measurement the higher the $FEC^{0.33}$. The regression of day of birth against $FEC^{0.33}$ accounted for approximately 0.4% of variation.

In the Turretfield Resource Flock in 1992, priming with *H. contortus* prior to the artificial infection had no significant effect on the subsequent $FEC^{0.33}$.

Between-bloodline effects

Significant bloodline differences were demonstrated in 5 of the 11 analyses (Table 6 and 7). In the JB Pye Flock, there were significant flock differences in the 1990-drop footrot experimental group and the 1991-drop group after natural infection with mixed parasite genera. Where there were significant differences between bloodlines, the only consistency was that the Trangie bloodline had a higher mean $FEC^{0.33}$ than the Plevna and Hillcreston bloodlines. Correlations between

Table 5. Mean and least-squares constants (±s.e.) for environmental effects on $FEC^{0.33}$ after artificial infection with *H. contortus* and *T. colubriformis*

Birth rearing rank: SS, single-born and reared; MS, multiple-born, single-reared; MM, multiple-born and reared. DOB, day of birth
Means followed by the same letter for the same fixed effect do not differ significantly at $P = 0.05$

Source	Level	*H. contortus* infection				*T. colubriformis* infection			
		Katanning (1991)	Turretfield (1992)	CSIRO (1991)	Trangie (1990)	Katanning (1992)	Turretfield (1993)	CSIRO (1992)	Trangie (1991)
Mean		14·46±0·40	8·09±0·28	11·26±1·15	21·20±1·62	13·37±0·19	13·71±0·28	3·77±0·43	15·21±0·48
Priming	Primed		−0·08±0·08						
	Not primed		0·08±0·08						
Sex/ managemt group	Ewe	2·29±0·15a	0·98±0·08a			0·78±0·08a	0·37±0·08a		
	Ram		−0·98±0·08b			−0·78±0·08b	−0·37±0·08b		
	Wether	−2·29±0·15b							
Sex	Ewe			0·67±0·24a				−0·59±0·20a	−0·13±0·21
	Ram								+0·13±0·21
	Wether			−0·67±0·24b				0·59±0·20b	
Birth rearing rank	SS	0·63±0·31	0·28±0·14a	0·02±0·44	1·39±0·54a	0·01±0·13	−0·14±0·17a	0·03±0·19	−0·26±0·21
	MS	−0·41±0·53	0·01±0·23ab	−0·41±0·70	−1·51±0·75b	−0·13±0·21	0·48±0·21b	0·39±0·27	0·17±0·30
	MM	−0·22±0·34	−0·29±0·15b	0·39±0·57	0·12±0·54ab	0·12±0·15	−0·33±0·28a	−0·42±0·22	0·09±0·20
Dam age	Maiden	−0·18±0·18	−0·26±0·10a	0·57±0·55	0·11±0·48	0·00±0·09	0·00±0·08	0·25±0·23	−0·01±0·20
	Adult	0·18±0·18	0·26±0·10b	−0·57±0·55	−0·11±0·48	0·00±0·09	0·00±0·08	−0·25±0·23	0·01±0·20
DOB		0·00±0·00	0·04±0·01**	−0·03±0·03	0·07±0·04	0·01±0·01	0·02±0·01*	0·04±0·02*	0·02±0·02

* $P < 0.05$; ** $P < 0.01$.

bloodline means measured in different years were not significantly different from zero (1990a and 1990b, $r = 0 \cdot 41$; 1990a and 1991, $r = 0 \cdot 54$; 1990b and 1991, $r = 0 \cdot 26$).

In the Katanning Base Flock there was a strain effect for the *H. contortus* infection (Table 7) with the Peppins having the highest $FEC^{0 \cdot 33}$ and the Bungaree the lowest. However, these differences were not evident with the *T. colubriformis* infection when $FEC^{0 \cdot 33}$ in all the strains was similar. There were no significant differences between bloodlines-within-strains, after artificial infection with either *H. contortus* or *T. colubriformis* larvae (Table 7). The correlation between bloodline means for each infection, without fitting strain, was very close to zero ($r = -0 \cdot 05$).

Table 6. Analysis of variance and estimates of variance components (VC) for $FEC^{0 \cdot 33}$ ($\pm$s.e.) after natural infection with mixed nematode genera

Source	JB Pye 1990a		JB Pye 1990b		JB Pye 1991	
	Analysis of variance					
	d.f.	MS	d.f.	MS	d.f.	MS
Bloodline	3	333·85**	3	14·00	3	139·23*
Sire	37	25·78	38	40·70*	37	46·88**
Error	363	20·07	268	26·61	920	22·81
	Partitioning of variance					
	VC	%	VC	%	VC	%
Bloodline	3·03±2·71	12·8	0·00±0·00	0	0·32±0·70	1·3
Sire	0·38±0·61	1·6	1·53±1·16	5·4	1·05±0·48	4·2
Error	20·25±1·51		26·75±2·30		22·78±1·06	

* $P < 0 \cdot 05$; ** $P < 0 \cdot 01$.

There were no strain or bloodline-within-strain effects on $FEC^{0 \cdot 33}$ in the Turretfield Resource Flock for either the *H. contortus* or *T. colubriformis* infections (Table 7). There was no significant relationship between bloodline means for the 2 infections ($r = 0 \cdot 29$).

In the CSIRO Finewool Flock, there were significant differences between bloodlines (Table 7). Bloodline 6 had a consistently higher $FEC^{0 \cdot 33}$ after both the *H. contortus* and *T. colubriformis* infections, whereas bloodlines 7 and 9 had consistently lower $FEC^{0 \cdot 33}$ for the 2 types of infection. Overall, the association between bloodline means for the 2 infections, although positive, was not statistically significant ($r = 0 \cdot 35$).

There were no strain or bloodline-within-strain effects in the Trangie D Flock after artificial infection with *H. contortus* (Table 7). After infection with *T. colubriformis*, there were bloodline differences within the Peppin strain (Table 7), with MP4 and MP6 showing the lowest $FEC^{0 \cdot 33}$ and MP5, MP7, and MP8 the highest. Bloodline means for the 2 infections were not strongly correlated, and the relationship was not statistically significant ($r = 0 \cdot 34$).

Within-strain and bloodline effects

Significant sire effects were demonstrated in 9 of the 11 analyses. Sire effects on $FEC^{0 \cdot 33}$ after natural infection in the JB Pye Flock (Table 6) were significant for 2 of the 3 measurements, resulting in low to moderate heritability estimates

Table 7. Analysis of variance and estimates of variance components (VC) for $FEC^{0.33}$ ($\pm$s.e.) after artificial infection with *H. contortus* and *T. colubriformis*

Source	*H. contortus* infection								*T. colubriformis* infection							
	Katanning (1991)		Turretfield (1992)		CSIRO (1991)		Trangie (1990)		Katanning (1992)		Turretfield (1993)		CSIRO (1992)		Trangie (1991)	

Analysis of variance

Source	d.f.	MS	d.f.	MS	d.f.	MS	d.f.	MS	d.f.	MS	d.f.	MS	d.f.	MS	d.f.	MS
Strain	3	181·40**	1	318·45			3	16·94	3	14·87	1	7·65			3	3·14
Bl:Strain	12	22·69	2	88·50	10	436·43*	11	59·92	12	10·69	2	16·52	10	296·99**	11	16·43**
Sire	48	31·61**	44	40·91**	49	174·44**	15	69·21*[A]	48	10·42**	30	8·60*	63	33·00**	16	8·01[A]
Error	889	18·52	1549	10·08	1010	58·26	284	34·96	915	5·24	843	5·54	992	12·96	375	5·95

Partitioning of variance

Source	VC	%	VC	%	VC	%	VC	%	VC	%	VC	%	VC	%	VC	%
Strain	0·68±0·70	3·4	0·30±0·57	2·5			0·00±0·00	0	0·02±0·05	0·4	0±0	0			0·00±0·00	0
Bl:Strain	0·00±0·32	0	0·08±0·20	0·7	2·92±2·29	4·3	0·00±2·58	0	0·08±0·00	0	0·03±0·01	0·5	2·80±1·41	16·3	0·34±0·37	5·2
Sire	0·69±0·40	3·5	1·00±0·38	8·4	6·79±2·14	9·9	2·21±1·84	6·4[A]	0·32±0·13	5·8	0·11±0·08	2·0	1·41±0·42	8·2	0·19±0·29	2·9[A]
Error	18·60±0·92		10·57±0·97		58·62±2·65		34·89±3·31		5·16±0·24		5·55±0·00		12·96±0·58		6·05±0·56	

Levels of significance are *$P < 0.05$, **$P < 0.01$.
[A] From separate analysis of variance within the Peppin strain as only this group had sire pedigrees recorded.

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(Table 8). Significant sire effects were found, after artificial infection with *H. contortus,* in all flocks examined (Table 7), resulting in moderate heritability estimates within the range $0 \cdot 17$–$0 \cdot 42$. The heritability estimates for the *T. colubriformis* infection tended to be more variable, with no significant sire effects in the Trangie D Flock (Table 7) and in the Turretfield Resource Flock; in the latter flock, heritability estimates were inconsistent between sex/management groups (Table 8).

The model used for estimating heritability in each flock included all significant fixed effects. Where dam age, birth rearing rank, and day of birth had a significant effect on $FEC^{0 \cdot 33}$, additional heritability estimates were made excluding these fixed effects as they are not routinely recorded in commercial studs. The heritability estimates, unadjusted for these fixed effects, were the same as, or very close to, those estimated using the model that included all significant effects (Table 8).

Table 8. Heritability estimates for $FEC^{0 \cdot 33}$ ($\pm$ s.e.) in Merino resource flocks after natural infection with nematode parasites and artificial infection with *H. contortus* and *T. colubriformis*

To calculate average heritability each heritability estimate was weighted in proportion to the reciprocal of the sampling variance of the estimate

Flock	Natural	H. contortus	T. colubriformis
JB Pye 1990a	$0 \cdot 07 \pm 0 \cdot 12$		
JB Pye 1990b	$0 \cdot 26 \pm 0 \cdot 17$		
JB Pye 1991	$0 \cdot 17 \pm 0 \cdot 08$		
JB Pye 1991[A]	$0 \cdot 17 \pm 0 \cdot 08$		
Katanning (1991)		$0 \cdot 17 \pm 0 \cdot 09$	
Turretfield (1992)		$0 \cdot 34 \pm 0 \cdot 09$	
Turretfield (1992)[A]		$0 \cdot 34 \pm 0 \cdot 09$	
CSIRO (1991)		$0 \cdot 42 \pm 0 \cdot 12$	
Trangie (1990)		$0 \cdot 33 \pm 0 \cdot 23$	
Katanning (1992)			$0 \cdot 24 \pm 0 \cdot 08$
Turretfield (1993)			$0 \cdot 09 \pm 0 \cdot 06$ all sheep[B]
Turretfield (1993)			$0 \cdot 23 \pm 0 \cdot 13$ ewes
Turretfield (1993)			0 wethers
Turretfield (1993)[A]			$0 \cdot 11 \pm 0 \cdot 07$
CSIRO (1992)			$0 \cdot 40 \pm 0 \cdot 11$
CSIRO (1992)[A]			$0 \cdot 41 \pm 0 \cdot 11$
Trangie (1991)			$0 \cdot 11 \pm 0 \cdot 18$
Weighted average	$0 \cdot 17$	$0 \cdot 32$	$0 \cdot 21$

[A] Estimated using model excluding dam age, birth rearing rank, and day of birth.
[B] Estimate used in weighted average.

Variance components

The genetic components of variance for $FEC^{0 \cdot 33}$ after natural parasite infection and artificial infection with *H. contortus* and *T. colubriformis* are given in Table 6 and 7 where strain, bloodline, and sire were classified as random effects. Consistent REML estimates for the sire component of variance were obtained using DFREML and SPLUS. In the Trangie D Flock, bloodline and sire components of variance were estimated from the Peppin bloodlines only as these were the groups for which sire pedigree data were recorded (Table 7). Genetic sources of variation

in $FEC^{0.33}$ showed differences between and within infection type. However, the within-flock genetic component (sire component $\times$ 4) was greater than the between-strain or bloodline components on most occasions. The relationship between within-bloodline genetic and other sources of variation was consistent within infection type; however, the degree of variance attributed to strain and bloodline varied between the *H. contortus* and *T. colubriformis* infections. Results from an average of all analyses are presented graphically in Fig. 1.
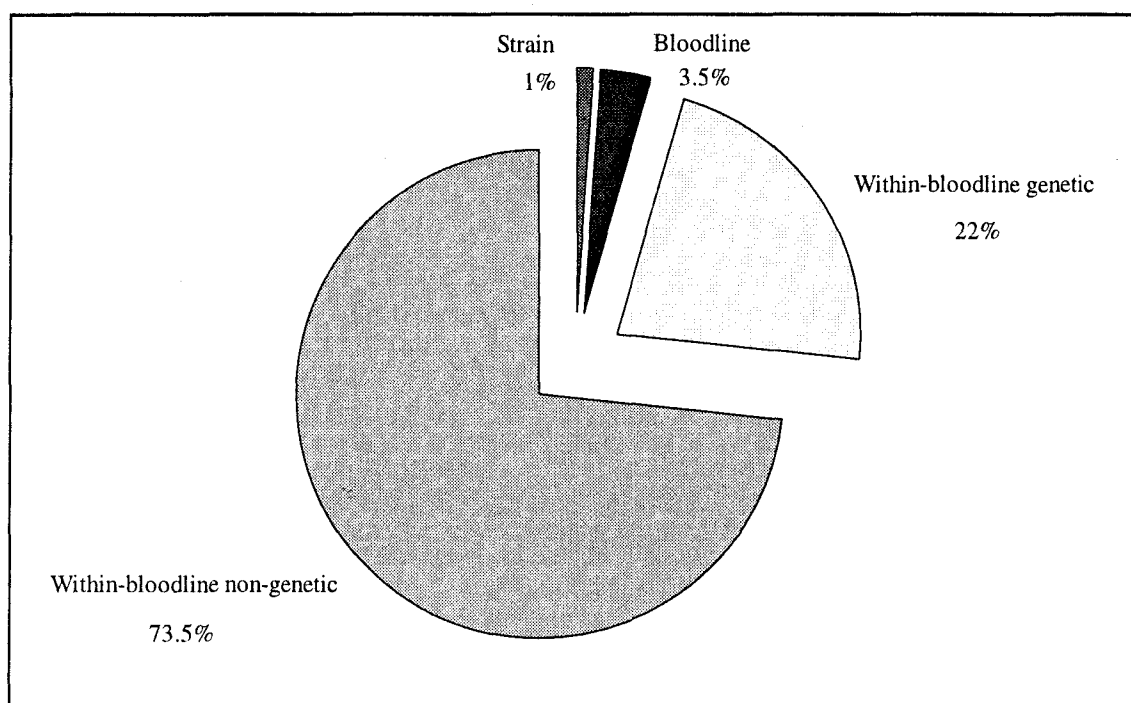
Fig. 1. Sources of variation in $FEC^{0.33}$ (%) across all resource flocks and infection types.

Discussion

The results of this study indicate that there is little genetic variation in nematode resistance between Merino strains and bloodlines. In the flocks studied, a relatively low proportion of variation in resistance could be attributed to strain and bloodline differences after either natural parasite challenge or artificial infection with *H. contortus* or *T. colubriformis*. Resistance does not appear to be under strong natural selection or to be highly correlated with other traits under selection. The major source of genetic variation for FEC was found within bloodlines, with individual sires showing a wide range in resistance in their progeny. Sources of environmental variation in resistance were only occasionally significant and accounted for a small proportion of variance in $FEC^{0.33}$.

Environmental effects

In this study, sex effects on FEC were inconsistent in nature which is in agreement with Woolaston and Piper (1996), who reported no consistent differences between ewe and ram weaners when run together over a number of years in both random bred and *Haemonchus* selection line flocks. It is unlikely that sheep will

be run as mixed-sex groups post-weaning, so there would be little call for routine correction factors in any event.

Management group effects were consistently large and contributed significantly to FEC variation. In many cases, these effects could not be separated from the sex of the animals. But if sex effects are likely to be small or non-significant, most of the variation between management groups could be attributed to differences in availability of infective larvae on the pasture and/or the level of nutrition of the sheep in each management group. Where there are genetic links across management groups, adjusting for management group during the period of parasite infection prior to measurement would be essential for analysis. Adjusting for management groups earlier in the life of the animals may also be desirable, as in some flocks management groups prior to weaning had a significant carry-over effect on FEC at a later age. This result highlights the conditions under which valid comparisons of animals can be made for parasite resistance. It would be inappropriate to make comparisons of the resistance of bloodlines in wether trials where the sheep are brought together only after weaning. However, comparisons of sires in central test situations where all offspring are born and managed together are valid.

Estimates of the environmental effect of dam age can be biased if the flock is responding to selection because younger ewes are the result of a greater number of years of selection than older ewes. However, this type of bias is largely avoided in the resource flocks used in this study, as each flock was very close to randomly bred, ewe selections being made at random and rams purchased from the original stud or selected from within each flock at random. There may have been some genetic change in flocks where rams were purchased each year from the original stud, given that stud was making genetic gain, but this would be unlikely for a trait such as resistance when no direct selection was being practiced. Age of dam had a significant effect on FEC on only one occasion, and reports from previous studies have shown the effect to be inconsistent (Albers *et al.* 1987; Woolaston and Piper 1996) or non-significant (Woolaston *et al.* 1991; Hygate and Cummins, unpublished data). Day of birth was generally not important, and although significant in a third of the cases, the effect was small. From these results it appears that both age of dam and day of birth effects can largely be ignored when including parasite resistance in a breeding objective.

Studies of fleece traits and body weight have shown that birth rearing rank is the main environmental effect that exerts a significant and consistent influence on hogget performance (Brown *et al.* 1966; Gregory and Ponzoni 1981; Mortimer and Atkins 1989; Lewer *et al.* 1992) in Merino sheep. In the flocks tested for parasite resistance, birth rearing rank did not have such a large effect on FEC, and was significant in only 3 of the 11 analyses. The trend for single-born animals to have a greater FEC than twin-born is consistent with reports from other flocks where birth type had a significant effect (Woolaston *et al.* 1991; Woolaston and Piper 1996; Hygate and Cummins, unpublished data). Possible reasons for twins appearing to be more resistant to nematode parasites than singles are difficult to imagine, as it is generally accepted that twin-born lambs are more susceptible to infection. The expectation is that sheep with a maternal handicap are generally lighter in bodyweight and would be more susceptible to parasites than their better fed cohorts. Woolaston and Piper (1996) suggested that differential weaning (earlier for offspring of first lamb ewes and ewes rearing multiples) may interact with the immunological development

of the sheep, and when measured post-weaning, those having the longest time to overcome the stress of weaning (diet transition) are in some way favoured.

The effect of prior exposure to the specific parasite used for artificial infection did not appear to be important on the one occasion it was investigated. Although the primed and unprimed sheep ran together, the prevailing weather conditions should have precluded the unprimed animals from being infected by *H. contortus* larvae hatching from eggs deposited by the primed sheep. The infected sheep would have commenced passing eggs in their faeces about 18–21 days after infection. The lower temperature limit for *H. contortus* egg development is approximately 10 and 7°C, respectively, for mean and minimum air temperatures (Besier and Dunsmore 1993). Mean and minimum air temperature during the period the sheep were infected, until they were moved onto a clean pasture, were 10 and 5°C, respectively. Therefore, it is unlikely any eggs would have developed to infective larvae. In southern Australia, it is uncommon for sheep to be naturally exposed to *H. contortus* in autumn and winter. Monitor counts prior to artificial infection showed no indication of *H. contortus* presence, but there were low levels of *Trichostrongylus* spp. The primed and unprimed animals had similar egg counts in the subsequent infection, indicating that the measured immune response may not be specific to helminth genera. This conclusion is supported by observations showing considerable cross resistance to a range of helminth species in Merinos selected for resistance to one specific parasite (Woolaston *et al.* 1990).

The occurrence of significant fixed effects did not appear to be related to the magnitude of mean FEC, and in flocks where there were significant effects, they accounted for only a small proportion of the variation (0·3–2·2%). Therefore, it is reasonable to conclude that leaving FEC measurements unadjusted for birth rearing type, age of dam, and birth date will cause little loss of selection efficiency for this trait. A similar scenario appears to exist for footrot (Raadsma *et al.* 1994), dermatophilosis (Woolaston *et al.* 1995), and fleece rot and body strike (McGuirk and Atkins 1984; Raadsma *et al.* 1989; Raadsma 1991) in Merinos where birth rearing type, age of dam, and age at measurement within a contemporary group did not significantly contribute to variation in these diseases. This may be a characteristic of disease traits in general.

Few breeders are able to correct for effects such as birth bearing type, age of dam, and birth date within the one age group because they generally do not record female pedigrees and lambing dates. Therefore, the heritability assumed for FEC in most breeding programs should be that estimated without fitting these effects. As these environmental effects were only occasionally significant, and, if so, accounted for only a small proportion of variance, it is predictable that heritability estimates without fitting these effects should be very close to the estimates when all significant effects were fitted, as was found with these data. This is in contrast to the adjustments for environmental effects needed for estimation of heritability of wool traits and body weight, which are often influenced by birth rearing type, age of dam, and birth date, even when measured at 15–16 months of age (Gregory and Ponzoni 1981; Mortimer and Atkins 1989; Lewer *et al.* 1992).

Between-strain and bloodline effects

The differences in FEC between strains were generally unpredictable and inconsistent. In the Trangie D Flock, where fine wool and medium wool stains

were compared, there were no clear differences in resistance, despite the large environmental differences in which these 2 strains originated. In the Katanning Base Flock, there was no significant difference between medium and strong wool Merino strains, but these strains originated in environments that were less diverse in terms of parasite exposure. Traditionally, fine wool strains have evolved in the higher rainfall regions of the New England and Southern Tablelands in New South Wales, the western districts of Victoria, and regions of Tasmania; the medium wools on the drier slopes and plains of New South Wales and Victoria; and the strong wool strains in the pastoral and cropping regions of South Australia. Despite the diverse level of disease prevalence the different strains would have experienced, results from this study suggest it would be difficult to choose a strain that will consistently and predictably express an advantage in terms of parasite resistance.

Bloodline differences between infections (years) were also inconsistent as indicated by the low correlation between bloodline means for each year. This could be due to the different parasite species used for each infection. The relative resistance of the bloodlines could be characteristic of infection type, but this is unlikely as sheep selected for and against resistance to a particular parasite species tended to show a similar level of divergence when challenged with other unrelated species (Woolaston et al. 1990). There may be significant genotype × year interactions for this trait, unlike wool and body weight (Mortimer and Atkins 1989), with year effects potentially having a large effect on disease prevalence. However, the inconsistent ranking of bloodlines across the 2 years is more likely due to the low precision with which individual bloodline means were estimated, and few conclusions can be drawn from this study as to the actual difference in resistance that may exist between particular bloodlines.

A similar result was reported for footrot in the JB Pye Flock (Raadsma et al. 1994), where relative differences between bloodlines after natural challenge with Dichelobacter nodosus were not consistent and no single flock could be considered more resistant or susceptible to footrot.

These results suggest that there is little potential at present for breeders to improve the resistance levels of their flocks by finding a single source of resistant rams, firstly because the differences between strains and bloodlines were in most cases small, and secondly they were not predictable. It is not possible to sample from the total population of Merino bloodlines, and this limitation should be recognised when interpreting these results. However, for breeders interested in making genetic progress towards greater parasite resistance, it is pleasing to know that improvement should be achievable by concentrating on the selection of resistant rams within bloodlines.

Within-bloodline effects

There was a significant sire effect on $FEC^{0 \cdot 33}$ on all but 2 occasions and the lack of significance in these instances was in flocks where numbers of progeny per sire group were small. The estimates of heritability ranged from $0 \cdot 07$ to $0 \cdot 40$, which is consistent with previously published estimates summarised in Table 1. There were no obvious differences in heritability estimates with the different type of parasite infection, but in the Turretfield Resource Flock in 1993 there was a significant difference in the estimate between sexes, with a zero estimate of

heritability for expression in wethers and $0 \cdot 23$ for females. This result, in the context of the other estimates from both this study and elsewhere, suggests that some environmental effect was operating in the wether flock to preclude genetic differences being identified. The mean egg count was significantly lower in the wethers than the ewe flock (2594 $v.$ 2979 epg, respectively, $P < 0 \cdot 01$) but still in excess of 1000 epg, the mean level of infection suggested by Eady and Woolaston (1992) to be confident of detecting genetic differences. The maturity of the immunological response may have varied between the 2 sexes owing to different levels of exposure to infective larvae or differing planes of nutrition prior to the challenge infection. There is good evidence that genetic differences in resistance develop after exposure to infective larvae, and that until the immune system is triggered by a primary infection, resistant and susceptible sheep are very similar in their FEC (Windon 1991). For some reason, the wethers may not have had sufficient exposure prior to the artificial infection or may have experienced a poorer plane of nutrition than their female half-sibs. In the light of such results, consideration needs to be given to the time and conditions under which resistance is measured to ensure there is a maximum opportunity for genetic differences to be expressed. Given that the animals have had prior exposure to helminths and FECs are of sufficient magnitude to indicate a patent infection (Eady and Woolaston 1992), the only way to determine if genetic differences are being expressed is to identify if sire effects are significant. It is unlikely that conditions would operate where sire effects are significant, but bloodline effects are not due to environmental factors associated with the infection.

Conclusions

The partitioning of FEC variance (Fig. 1) clearly demonstrates that the major source of genetic variation for resistance in flocks in this study exists within bloodlines, rather than between strains or bloodlines. The consistent heritability estimates from different resource flocks/environments add substance to the belief that nematode parasite resistance can be favourably controlled in any Merino flock where the breeder has an interest in this trait. Within-flock selection of individual sires that exhibit resistance appears to be the most effective method of improvement compared to bloodline selection. Results from sire evaluation schemes (Eady 1995) will aid in the identification of resistant sires across flocks, allowing breeders to exploit the genetic variation that is apparent in the breed as a whole. However, before breeding strategies that involve selection for parasite resistance in addition to production traits can be designed, estimates of genetic, phenotypic, and environmental correlations need to be made.

Acknowledgments

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