

## **Chapter 4 Resistance to Nematode Parasites in Merino Sheep: Sources of Genetic Variation**

### **4.1 Introduction**

As described in Chapter 2 and 3, 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 from 0.2 to 0.4 (See Table 2.2 for summary). 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 five 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 resistance between strains and bloodlines may have evolved through natural selection or genetic drift. Although there has been little deliberate selection for internal parasite 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 large differences 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 internal parasite resistance are identified including the influence of effects such as management group, sex, age of dam, birth rearing status and day of birth.

## **4.2 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).

### **4.2.1 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 gelatine 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* and 20,000 *T. colubriformis* L<sub>3</sub> larvae

per sheep. In some instances, the sheep were "primed" with a half dose of infective larvae before the main infection where it was not clear if animals had been previously exposed to natural nematode infection. Where animals were "primed", the 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, only a random selection of half the animals were 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, FECs were determined using a modified McMaster technique with a lower limit of detection of 100 epg. Bulk faecal cultures were usually, but not always, prepared from each management group to identify the parasite genera present. Faecal samples collected from the JB Pye and CSIRO Finewool flocks and Trangie D Flock were chilled and transported to the CSIRO Pastoral Research Laboratory at Armidale for counting. Faecal samples collected from the Turretfield Resource Flock and Katanning Base Flock were counted on site by CSIRO staff. Within 6-36 hours of collection, a 2g sample of faecal material was weighed and 15 ml of water added to arrest egg development (Levine and Todd 1975). Before counting, samples were mixed with an electric drill attachment and 35 ml of saturated salt solution was added. Samples were again mixed thoroughly with the pipette used to load the counting slides. Samples were counted within 24-120 hours of collection, depending on the number of animals in the group. Egg counts were expressed in terms of epg of faecal material. There was no correction for faecal consistency.

In the laboratory, the sample preparations and counters were recorded and coded as fixed effects in the subsequent analyses. The preparing and counting team consisted of the

same people over the duration of these studies although not all were present every time. Members of the team systematically rotated between counting and preparing. In most instances, samples were randomised for counting in order to avoid any bias that might have occurred by counting them in ear-tag order. In some flocks, sire groups were tagged sequentially and counting in tag order would have confounded counting sequence with sire group.

Laboratory procedures for handling large groups of samples were developed during these studies. Where possible computer files of tag numbers were obtained before sampling and pre-printed labels were used at the time of sampling. From the same data file, sample identification sheets and data recording sheets were prepared for use in the laboratory. This system greatly reduced transcription errors in the sheep yards at sampling and later during laboratory procedures such as weighing and counting.

## **4.2.2 Genetic resource flocks**

Table 4.1 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.

### **4.2.2.1 JB Pye Flock, University of Sydney, Camden, NSW**

#### **4.2.2.1.1 Origin and replacement policy**

The JB Pye flock was established in 1987 at Camden in the Nepean region of NSW and comprised four Merino bloodlines. The primary objective in establishing the flock was to estimate the heritability of resistance to footrot, and to estimate phenotypic and genetic correlations between footrot resistance and all major production traits, including other economically important diseases (Raadsma and Nicholas 1993).

Table 4.1 Experimental details for Merino resource flocks tested for resistance to nematode parasites: experimental groups, number of bloodlines, number of sire families, age at testing, sex and number of animals tested, infection type and species and pre-infection priming

Experimental groups	No. of bloodlines	No. of sire families	Age at testing (mths)	Sex of animals	No. animals 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)	4	41	12	Ewes	479	Natural	No
				Rams	109	mixed spp	
				Wethers	385		
Katanning (1991)	16	64	8	Ewes	478	Artificial	Yes
				Wethers	476	Hc <sup>A</sup>	
Turretfield (1992)	4	48	7	Ewes	816	Artificial	½ Yes
				Rams	786	Hc	½ No
CSIRO (1991)	11	60	7	Ewes	552	Artificial	No
				Wethers	524	Hc	
Trangie (1990)	15	23	6	Ewes	301	Artificial	Yes
						Hc	
Katanning (1992)	16	64	8	Ewes	487	Artificial	No
				Wethers	493	Tc <sup>B</sup>	
Turretfield (1993)	4	34	5	Ewes	449	Artificial	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		

<sup>A</sup> Hc - *H. contortus*.

<sup>B</sup> Tc - *T. colubriformis*.

The bloodlines in the JB Pye flock were Plevna (medium-wool Peppin); Trangie Fertility (medium-wool Peppin); Pye (medium-wool Peppin); and Hillcreston (fine-wool Saxon). The Trangie Fertility and Pye bloodlines were not genetically distinct, as rams from the Trangie bloodline had been used in the Pye bloodline at some stage of their history. However, for all sheep sampled here, replacement sires were bred and selected from within each flock. Replacement males were chosen at random from within each sire group at lamb marking and remaining males were castrated. A description of flock management is given by Raadsma *et al.* (1994).

#### 4.2.2.1.2 Experimental groups and infection type

Animals born in 1990 and 1991 (August-September lambing) were used in the parasite resistance study. All internal parasite infections in the JB Pye flock were from natural challenge. Egg counts in the flock were monitored before sampling and when they reached a mean between 500-1000 epg, faecal samples were taken. The sheep were continually exposed to infective larvae all year round, as indicated by monitor egg counts done on 10-15 animals in the flock.

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 moved after weaning to a separate university property near by (Mt Hunter) for the footrot challenge. The sheep were randomly allocated to two 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 two management groups based on sex. At the time of faecal sampling the ewes were within 1 week of commencement of lambing. The 1991 drop were located at JB Pye Farm in two management groups when tested, one comprising ewes and the second comprising rams and wethers.

#### 4.2.2.1.3 Location

The temperate coastal climate of the Nepean region has a non-seasonal rainfall average of 600 mm per annum. The sheep were run on a mixture of semi-improved and irrigated pasture based on clover and rye grass. This environment favours the survival of nematode parasites so that sheep are under constant challenge and require regular anthelmintic treatment to prevent both production and livestock losses. Because of the warm and wet conditions this is not a suitable environment for sheep and there are no commercial sheep enterprises in this region.

#### 4.2.2.2 Katanning Base Flock, Great Southern Agricultural Research Institute, WA Department of Agriculture, Katanning, WA

##### 4.2.2.2.1 Origin and replacement policy

The Katanning Base Flock was established in 1981 at Katanning, situated in the south western sheep/wheat belt of Western Australia. Four studs were chosen to represent each of the four main types of Merino sheep bred in Western Australia: Bungaree, Collinsville, Peppin and performance-based group breeding schemes (Table 4.2). The basis for selection of each flock was strain purity and its influence on the industry through ram sales (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 (Lewer, pers. comm.).

Table 4.2 Merino strains and bloodlines in the Katanning Base Flock (Lewer 1993)

Peppin	Collinsville	Bungaree	Independent Group Breeders
Colvin	Barloo	Bungadale	Corke
Condeena	Ejanding	Glenbyrne	Honey
Cranmore Park	Lewisdale	Hagley	Webb
Woolkabin	Mianelup	Quailerup	Young

##### 4.2.2.2.2 Experimental groups and infection type

Animals born in 1991 and 1992 (March-April lambing) were used in the parasite resistance study. In both years, the sheep were in two 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 the 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.

#### 4.2.2.2.3 Location

The Great Southern region is characterised by a Mediterranean climate, and receives about 450-500 mm of rain per annum. Pastures are based predominantly on subterranean clover. Internal parasites are a seasonal problem that requires anthelmintic treatment of young sheep to avoid production losses.

#### **4.2.2.3 Turretfield Merino Resource Flock, SA Department of Agriculture, Rosedale, SA**

##### 4.2.2.3.1 Origin and replacement policy

This flock was established in 1988 at Turretfield Research Centre, in the wheat-sheep zone of South Australia. The two major family groups of Merinos found in South Australia were represented by two studs each; the Collinsville group by Collinsville and Southrose, and the Bungaree group by Anama and East Bungaree (Gifford *et al.* 1992).

Five hundred foundation ewes, either cast-for-age ewes or surplus ewe hoggets, were contributed by each stud. Annually about 15 rams were purchased from each of the four contributing studs. Sire selection was dependent on information available in the individual studs. Random selections of flock rams were obtained from those performance-tested at 10 to 12 months of age (Anama and Southrose) or from various price grades established by the stud master (Collinsville and East Bungaree) (Gifford and Ponzoni 1993). Ewes were selected at random from those born within the resource flocks. There was no repeat mating of sires between years.

#### 4.2.2.3.2 Experimental groups and infection type

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, before priming, suggested the absence of any exposure to *H. contortus*. The 1992 born animals were run in two management groups based on sex. Both the ewe and ram groups were infected at Turretfield but the ewes had been moved to agistment at Sandilands on the Yorke Peninsula at the time of sampling.

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

#### 4.2.2.3.3 Location

Turretfield has an average annual rainfall of 460 mm, 60-70% falling between May and September. The pastures consist of subterranean clover and Wimmera ryegrass. In this environment, internal parasites are a seasonal problem requiring young sheep to be treated with anthelmintic to prevent losses in production.

### 4.2.2.4 CSIRO Finewool Flock, Arridale, NSW

#### 4.2.2.4.1 Origin and replacement policy

The CSIRO Finewool Flock at Arridale, on the New England Tablelands, was established in 1990 (Swan *et al.* 1995). The flock comprises 9 fine wool bloodlines, 1 medium wool Peppin and 1 medium wool non-Peppin bloodline (Table 4.3). The

medium wools were included as a link to previous (and current) research which has concentrated on those genotypes rather than as a strain comparison, and so strain was not included in the analysis of data from this flock. Selection of bloodlines was based on factors such as industry influence, geographical location and willingness to participate.

Selection of the foundation animals was left to the contributors, with the proviso that the animals should be a representative sample of the bloodline. Rams were purchased each year from the stud level and were similar to those generally available to the commercial industry. Each year a link sire was repeat mated to allow for optimal genetic analysis.

Table 4.3 Merino bloodlines in the CSIRO Finewool Flock (Swan *et al.* 1993)

Description	Bloodline
New England Finewool	Emu Creek Europambela Mirani
NSW Central Tablelands Finewool	Grathlyn
NSW Southern Tablelands Finewool	Hillcreston Legerton Merryville
Victorian Finewool	Wurrock
Tasmanian Finewool	Mount Morrison
NSW Medium Peppin	Hazeldean
NSW Medium non-Peppin	Woodside

#### 4.2.2.4.2 Experimental groups and infection type

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 one of three 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 before artificial infection, in excess of 200 epg 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 due 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 sire or sex effects (Swan pers comm.), these groups were still reasonably balanced. There was no differentiation of parasite genera for this infection.

#### 4.2.2.4.3 Location

The Finewool Flock runs at Longford Field Station, 40 km west of Armidale. The property is largely comprised of improved native pastures sown to phalaris, subterranean clover and rye grass. Average annual rainfall is 820 mm and is summer dominant. Sheep in this region are regularly challenged by internal parasites and routine anthelmintic treatment is required to prevent substantial losses in both production and livestock.

#### 4.2.2.5 Trangie D Flock, NSW Agriculture, Trangie, NSW

##### 4.2.2.5.1 Origin and replacement policy

The Trangie D Flock was established in 1974-75 at Trangie Agricultural Research Centre on the central western plains of NSW. Fifteen flocks were formed, comprising two fine wool bloodlines, two medium wool non-Peppin bloodlines, ten medium wool Peppin bloodlines and one strong wool South Australian bloodline. The descriptions used in this report are consistent with those used by Mortimer and Atkins (1989).

Details of the selection and management of the sheep have been given by Mortimer and Atkins (1989). The bloodlines in the Trangie D Flock were maintained as discrete breeding units until 1983 when a subset of the bloodlines (8) were then used in a crossbreeding experiment. This was called the Trangie C Flock (Atkins and Mortimer 1993). Replacement rams for the Trangie C Flock and the 7 remaining bloodlines of the D Flock were bred within each bloodline and chosen at random within the flocks rather than bought from their original source. Rams were used only for one year. The sheep measured for FEC were the purebred bloodlines of the C Flock and the 7 remaining bloodlines of the D Flock.

#### 4.2.2.5.2 Experimental groups and infection type

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 one management group.

#### 4.2.2.5.3 Location

Rainfall at Trangie averages 480 mm per annum and is non-seasonal but extremely variability and unreliable. The sheep were grazed on pastures comprised of native grass species with a large component of barley grass and medics. Sheep in this region are not subject to regular parasitism by internal nematodes.

### 4.2.3 Statistical analysis

All FECs were analysed on the cube root scale (Blattman *et al.* 1993, Woolaston and Piper 1996, Chapter 3). Within each resource flock the basic experimental design was a nested hierarchical structure with either one or two 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 versus adult ewes), birth-rearing rank (single-born and reared versus multiple-born and single-reared versus multiple-born and reared lambs), sex (ewe versus wether versus ram), management group or sex/management group where these effects were confounded, sample preparer and counter and first order interactions of these effects on FEC<sup>0.33</sup>. Day of birth 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<sup>0.33</sup> for each parasite genus in each resource flock:

$$Y_{hijklmnopq} = \mu + st_h + bl_{i:h} + S_{j:i:h} + brr_k + a_l + s_m + m_n + pr_o + ct_p + b(\bar{X} - X_q) + \text{interactions} + e_{hijklmnop}$$

where Y is FEC<sup>0.33</sup>;  $\mu$  is the common mean;  $st_h$  is the effect of the  $h$ th strain;  $bl_i$  is the effect of the  $i$ th bloodline nested within strain;  $S_j$  is the effect of the  $j$ th sire nested within bloodline;  $brr_k$  is the effect of the  $k$ th birth rearing type (single born and reared, multiple born and single reared, multiple born and reared);  $a_l$  is the effect of the  $l$ th dam age (maiden or mature);  $s_m$  is the effect of the  $m$ th sex (ewe, wether or ram);  $m_n$  is the effect of  $n$ th management group;  $pr_o$  is the effect of the  $o$ th sample preparer;  $ct_p$  is the effect of the  $p$ th sample counter;  $b$  is the regression of phenotype on day of birth and  $\bar{X}$  is the mean day of birth and  $X_q$  is the day of birth for animal <sub>$q$</sub>  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. The full model

containing all main effects was fitted for each flock for the estimation of least-squares constants for environmental effects. Non-significant ( $P>0.05$ ) effects and interactions, plus those interactions which accounted for less than 2% of the variation in  $FEC^{0.33}$  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  $FEC^{0.33}$  were estimated by the restricted maximum likelihood procedure (DFREML, Meyer 1989) using a sire model. From the appropriate variance components, heritability of  $FEC^{0.33}$  was estimated for each parasite genera in each resource flock. Approximate standard errors for heritability came from the DFREML analysis. A REML procedure fitting a sire model within the statistics package Splus (StatSci 1993) was used to partition variance between strain, bloodline-within-strain/bloodline and sire-within-bloodline. Associations between flock means in different years were estimated using product-moment correlations between the least square means.

## **4.3 Results**

### **4.3.1 Parasite infections and species composition**

Relatively high FECs were measured after both natural and artificial infection indicating a significant parasite burden in all groups with the exception of the CSIRO Finewool Flock (1992) where mean FEC was substantially lower (Table 4.4). 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 to *Trichostrongylus* spp (Clunies Ross and Gordon 1936). The natural infections in the JB Pye Flock varied in species composition between management groups.

### 4.3.2 Environmental effects

Means and standard errors and least squares constants for fixed effects for the three infection types are presented in Tables 4.6 and 4.7. Management group effects were often highly significant and accounted for 2.2% to 19.4% of the variation in  $FEC^{0.33}$ . Management group effects alone were not presented in the tabulation of results, although where management group and sex were confounded the effects were presented.

Sex/management group effects (presented separately from sex effects alone) significantly contributed to  $FEC^{0.33}$  variation on all occasions (Tables 4.6 and 4.7). In three of the four instances where sex effects were measured, there were significant differences, ewes having lower mean  $FEC^{0.33}$  than wethers in the JB Pye Flock (1990a) and the CSIRO Finewool Flock (1992), and wethers having lower mean  $FEC^{0.33}$  than ewes in the CSIRO Finewool Flock (1991). Overall, sex accounted for 0.5% to 0.8% of the variation in  $FEC^{0.33}$ .

On three occasions, birth rearing rank had a significant ( $p < 0.05$ ) effect (Table 4.5 and 4.6). In two instances (Turretfield Resource Flock 1992 and Trangie D Flock 1990), the single-born and 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  $FEC^{0.33}$ .

Table 4.4 Mean FEC and proportion of zero counts and parasite genera present after natural and artificial infections with nematode larvae in Merino flocks tested for resistance

The following abbreviations have been used for parasite genera, Tc = *T. colubriformis*, Hc = *H. contortus*, Os = *Ostertagia* spp., Oes = *Oesophagostum* spp.

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 - nd <sup>A</sup>	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	Ewes - nd	4452	0.7	-	-	-	-
	Hc	Wethers - nd			-	-	-	-
Turretfield (1992)	Artificial	Ewes	913	5.4	53	41	6	0
	Hc	Rams			52	48	0	0
CSIRO (1991)	Artificial	Group 1	4244	19.7	98	2	0	0
	Hc	Group 2			85	13	2	0
		Group 3			96	3	1	0
Trangie (1990)	Artificial	Ewes - nd	10851	0.0	-	-	-	-
	Hc							
Katanning (1992)	Artificial	Ewes	2637	0.0	0	90	10	0
	Tc	Wethers			0	84	16	0
Turretfield (1993)	Artificial	Ewes	2790	0.5	1	82	13	4
	Tc	Wethers			2	89	3	6
CSIRO (1992)	Artificial	5 man. gps - nd	311	52.2	-	-	-	-
	Tc							
Trangie (1991)	Artificial	Ewes/rams - nd	3894	0.3	-	-	-	-
	Tc							

<sup>A</sup> Larval differentiation not determined.

Age of dam had a significant effect ( $P<0.05$ ) on only one 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 from offspring from maiden ewes.

Table 4.5 Mean and least-squares constants ( $\pm$ standard error) for environmental effects on  $FEC^{0.33}$  after natural nematode infection with mixed parasite genera

The following abbreviations have been used for reproductive status of ewe management groups: np = non-pregnant, p nl = pregnant but non-lactating, p l = pregnant and lactating. The following abbreviations have been used for birth rearing rank: SS = single born and reared, MS = multiple-born and single reared, MM = multiple born and reared. DOB = day of birth.

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

Means with different superscripts for the same fixed effect differ significantly ( $P<0.05$ ).

Level of significance for DOB effect is \*  $P<0.05$ .

Table 4.6 Mean and least-squares constants ( $\pm$ standard error) for environmental effects on FEC<sup>0.33</sup> after artificial infection with *H. contortus* and *T. colubriformis*

The following abbreviations have been used for birth rearing rank: SS = single born and reared, MS = multiple-born and single reared, MM = multiple born and reared. DOB = day of birth.

<i>H. contortus</i> infection				<i>T. colubriformis</i> infection					
Source	Level	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/ management group	Ewe	2.29±0.15 <sup>a</sup>	0.98±0.08 <sup>a</sup>			0.78±0.08 <sup>a</sup>	0.37±0.08 <sup>a</sup>		
	Ram		-0.98±0.08 <sup>b</sup>			-0.78±0.08 <sup>b</sup>	-0.37±0.08 <sup>b</sup>		
	Wether	-2.29±0.15 <sup>b</sup>							
Sex	Ewe			0.67±0.24 <sup>a</sup>				-0.59±0.20 <sup>a</sup>	-0.13±0.21
	Ram							0.59±0.20 <sup>b</sup>	0.13±0.21
	Wether			-0.67±0.24 <sup>b</sup>					
Birth rearing rank	SS	0.63±0.31	0.28±0.14 <sup>a</sup>	0.02±0.44	1.39±0.54 <sup>a</sup>	0.01±0.13	-0.14±0.17 <sup>a</sup>	0.03±0.19	-0.26±0.21
	MS	-0.41±0.53	0.01±0.23 <sup>ab</sup>	-0.41±0.70	-1.51±0.75 <sup>b</sup>	-0.13±0.21	0.48±0.21 <sup>b</sup>	0.39±0.27	0.17±0.30
	MM	-0.22±0.34	-0.29±0.15 <sup>b</sup>	0.39±0.57	0.12±0.54 <sup>ab</sup>	0.12±0.15	-0.33±0.28 <sup>a</sup>	-0.42±0.22	0.09±0.20
Dam age	Maiden	-0.18±0.18	-0.26±0.10 <sup>a</sup>	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±0.10 <sup>b</sup>	-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 <sup>**</sup>	-0.03±0.03	0.07±0.04	0.01±0.01	0.02±0.01 <sup>*</sup>	0.04±0.02 <sup>*</sup>	0.02±0.02

Means with different superscripts for the same fixed effect differ significantly (P<0.05).

Level of significance for DOB effects is \*P<0.05 and \*\* P<0.01.

Day of birth had a significant effect on  $FEC^{0.33}$  in five of the 11 analyses. In the JB Pye Flock (1991), Turretfield Resource Flock (1992 and 1993) and in the 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  $FEC^{0.33}$ .

### 4.3.3 Between-bloodline effects

Significant bloodline differences were demonstrated in five of the 11 analyses (Tables 4.7 and 4.8). In the JB Pye Flock, there were significant flock differences in the 1990 drop footrot experimental group and the 1991 drop after natural infection with a mixed parasite genera (Figure 4.1). 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 (Figure 4.1). Correlations between bloodline means measured in different years were not significantly different from zero (1990a and 1990b,  $r=0.41$ ; 1990a and 1991,  $r=0.54$ ; 1990b and 1991,  $r=0.26$ ).

Table 4.7. Analysis of variance for  $FEC^{0.33}$  after natural infection with mixed nematode genera

Source	JB Pye 1990a		JB Pye 1990b		JB Pye 1991	
	d.f.	Mean square	d.f.	Mean square	d.f.	Mean square
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

Levels of significance are \* $P<0.05$ , \*\* $P<0.01$ .

In the Katanning Base Flock there was a strain effect for the *H. contortus* infection (Table 4.8) with the Peppins having the highest  $FEC^{0.33}$  and the Bungaree the lowest (Figure 4.2). However, these differences were not evident with the *T. colubriformis*

infection when FEC<sup>0.33</sup> in all the strains was similar (Figure 4.2). There were no significant differences between bloodlines-within-strains, after artificial infection with either *H. contortus* or *T. colubriformis* larvae (Table 4.8). The correlation between bloodline means (Figure 4.3), without fitting strain, for the two infections was very close to zero ( $r=-0.05$ ).

Table 4.8. Analysis of variance for FEC<sup>0.33</sup> after artificial infection with *H. contortus* and *T. colubriformis*

<i>H. contortus</i> infection								
Source	Katanning (1991)		Turretfield (1992)		CSIRO (1991)		Trangie (1990)	
	d.f.	Mean square	d.f.	Mean square	d.f.	Mean square	d.f.	Mean square
Strain	3	181.40**	1	318.45			3	16.94
Bloodline (Strain)	12	22.69	2	88.50	10	436.43*	11	59.92
Sire	48	31.61**	44	40.91**	49	174.44**	15	69.21* <sup>A</sup>
Error	889	18.52	1549	10.08	1010	58.26	284	34.96
<i>T. colubriformis</i> infection								
Source	Katanning (1992)		Turretfield (1993)		CSIRO (1992)		Trangie (1991)	
	d.f.	Mean square	d.f.	Mean square	d.f.	Mean square	d.f.	Mean square
Strain	3	14.87	1	7.65			3	3.14
Bloodline (Strain)	12	10.69	2	16.52	10	296.99**	11	16.43** <sup>A</sup>
Sire	48	10.42**	30	8.60*	63	33.00**	16	8.01
Error	915	5.24	843	5.54	992	12.96	375	5.95

Levels of significance are \*P<0.05, \*\*P<0.01.

<sup>A</sup> From separate analysis of variance within the Peppin strain as only this group had sire pedigrees recorded.

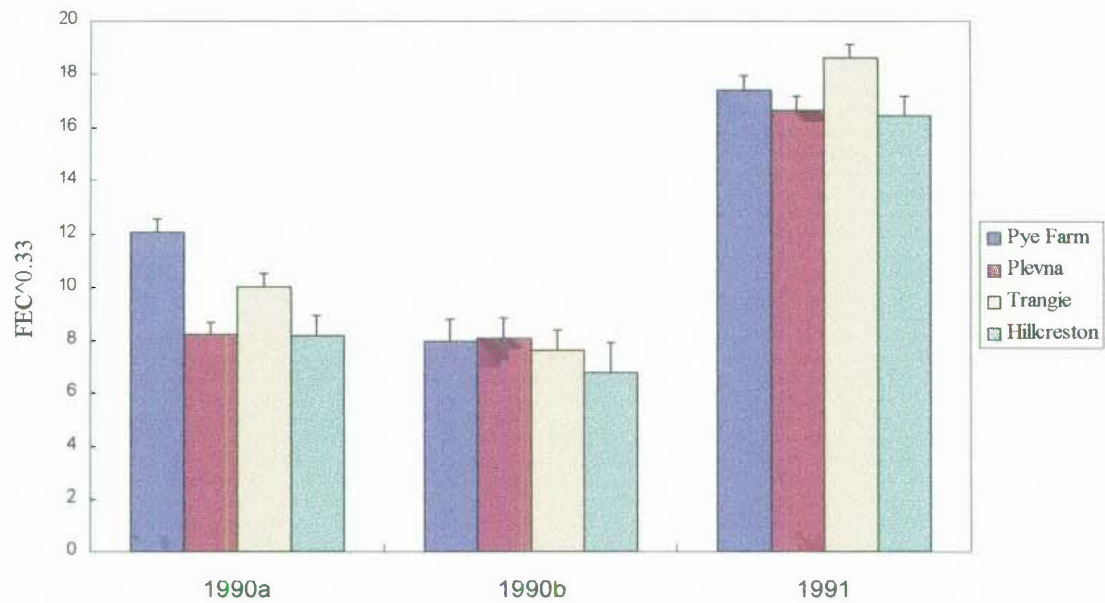


Figure 4.1 Mean FEC<sup>0.33</sup> for bloodlines in the JB Pye Flock after natural infection of the 1990 and 1991 born sheep with mixed nematode genera.

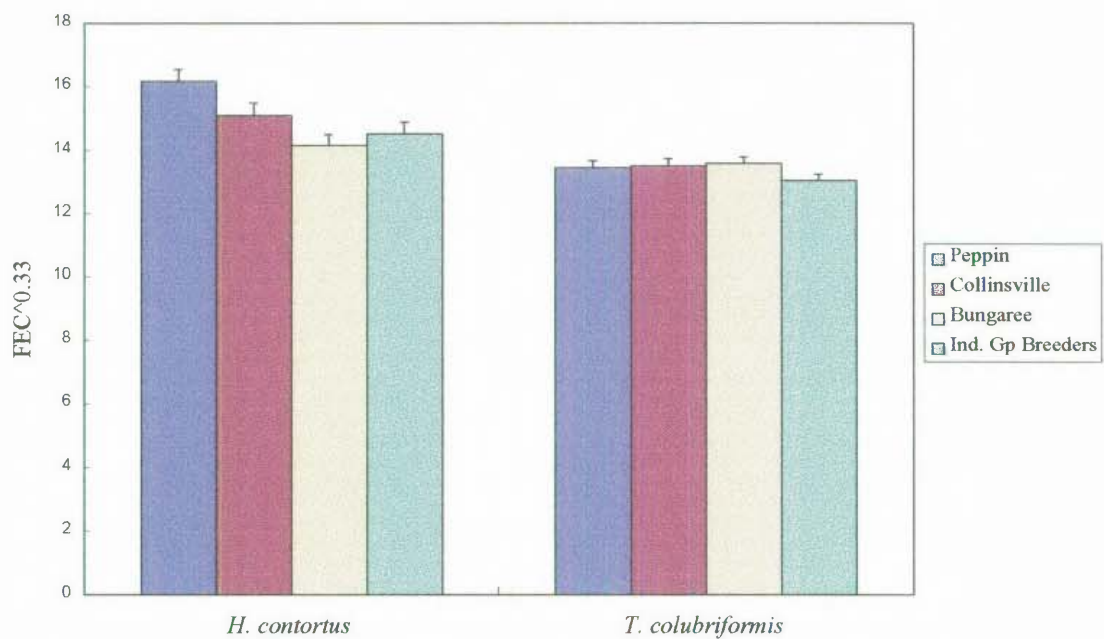


Figure 4.2 Mean FEC<sup>0.33</sup> of Merino strains represented in the Katanning Base Flock after artificial infection with *H. contortus* (1991 drop) and *T. colubriformis* (1992 drop).

There were no strain or bloodline-within-strain effects on  $FEC^{0.33}$  in the Turretfield Resource Flock for either the *H. contortus* or *T. colubriformis* infections (Table 4.8). Bloodline means only are presented in Figure 4.4. There was no significant relationship between bloodline means for the two infections ( $r=0.29$ ).

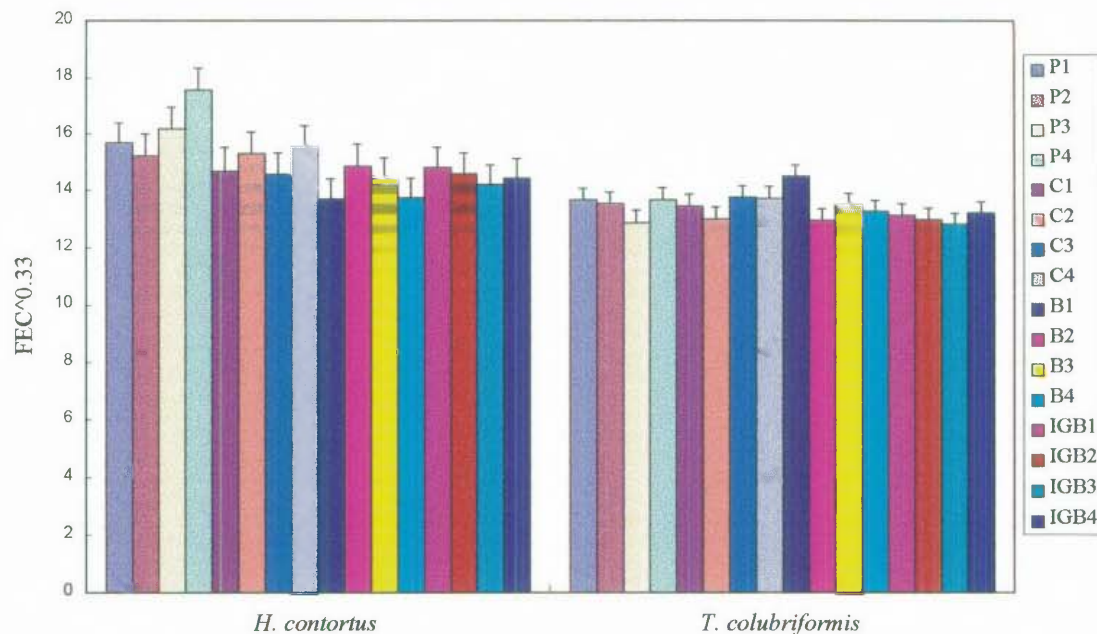


Figure 4.3 Mean  $FEC^{0.33}$  for bloodlines in the Katanning Base Flock after artificial infection with *H. contortus* (1991 drop) and *T. colubriformis* (1992 drop). Bloodline codes have been randomised to maintain confidentiality of individual results.

In the CSIRO Finewool Flock, there were significant differences between bloodlines (Table 4.8). Bloodline 6 had a consistently higher  $FEC^{0.33}$  after both the *H. contortus* and *T. colubriformis* infections (Figure 4.5) whereas Bloodlines 7 and 9 had consistently lower  $FEC^{0.33}$  for the two types of infection. Overall, the association between bloodline means for the two infections, although positive, was not statistically significant ( $r=0.35$ ). There were no strain or bloodline-within-strain effects in the Trangie D Flock after artificial infection with *H. contortus* (Table 4.8). After infection with *T. colubriformis*, there were bloodline differences within the Peppin strain (Table 4.8) with MP 4 and MP 6 showing the lowest  $FEC^{0.33}$  and MP 5, MP 7 and MP 8 the highest (Figure 4.6). Bloodline means for the two infections were not strongly correlated and the relationship was not statistically significant ( $r=0.34$ ).

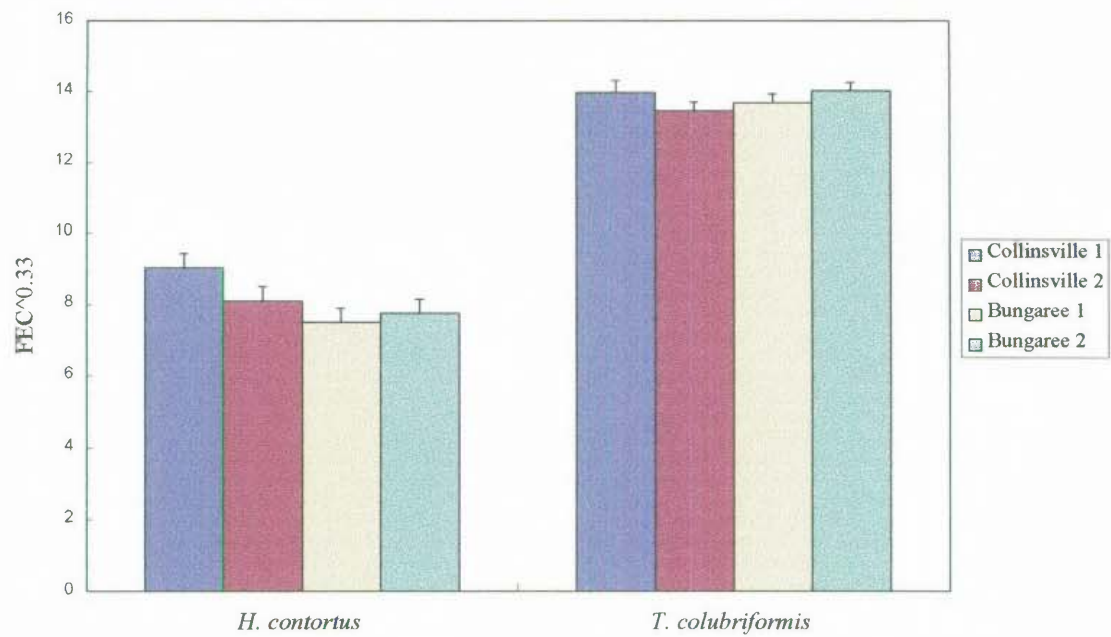


Figure 4.4 Mean FEC<sup>0.33</sup> for bloodlines in the Turretfield Resource Flock after artificial infection with *H. contortus* (1992 drop) and *T. colubriformis* (1993 drop). Bloodline codes have been randomised to maintain confidentiality of individual results.

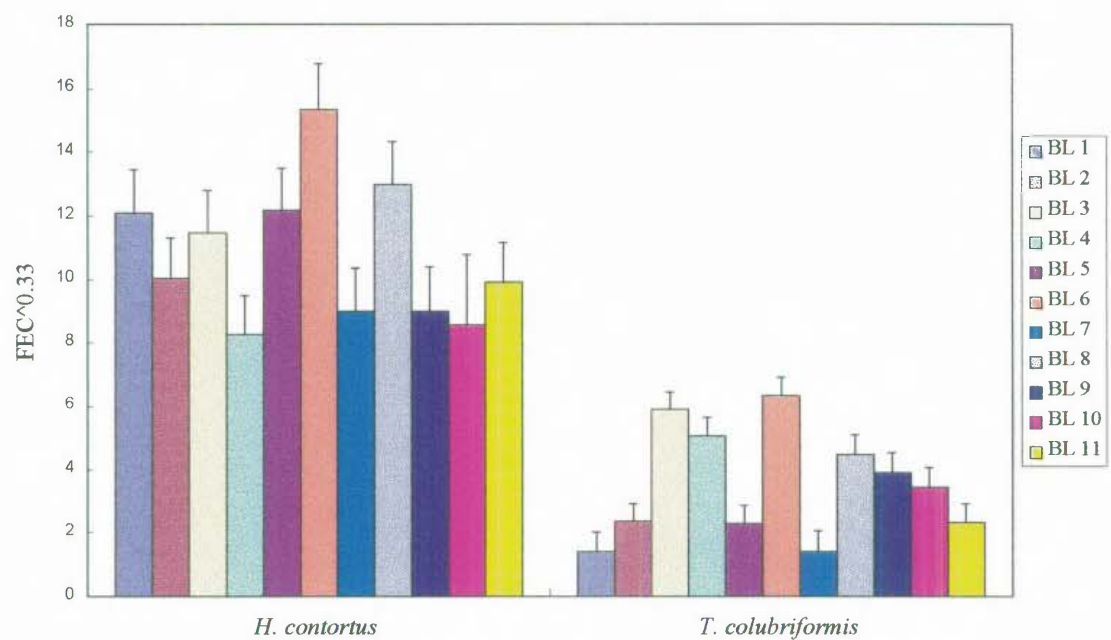


Figure 4.5 Mean FEC<sup>0.33</sup> for bloodlines in the CSIRO Finewool Flock after artificial infection with *H. contortus* (1991 drop) and *T. colubriformis* (1992 drop). Bloodline codes have been randomised to maintain confidentiality of individual results.

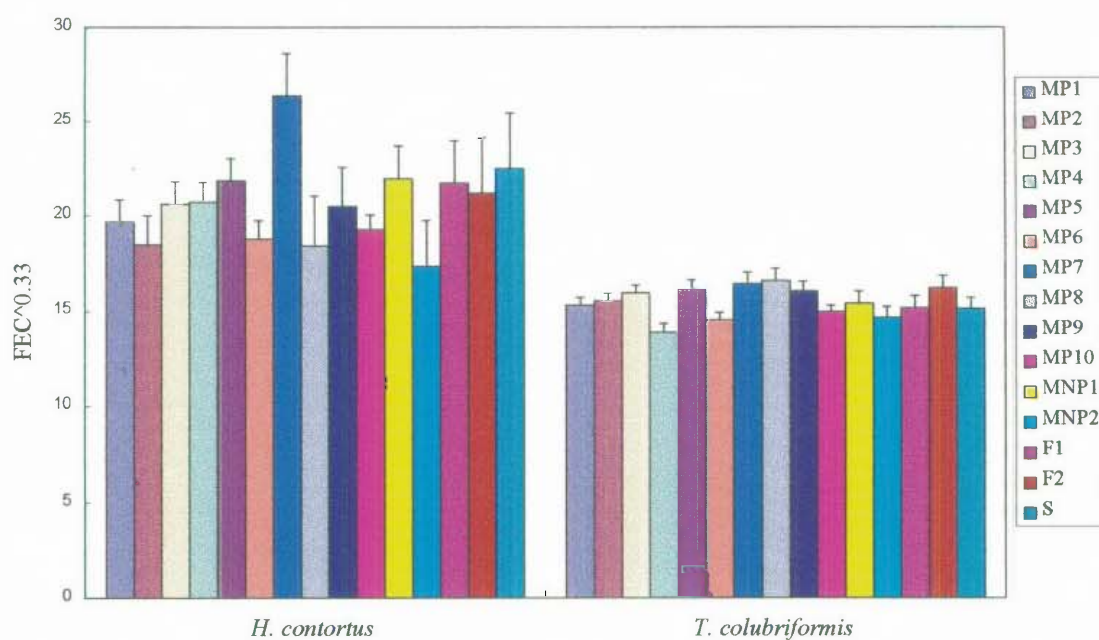


Figure 4.6 Mean  $FEC^{0.33}$  for bloodlines in the Trangie D Flock after artificial infection with *H. contortus* (1990 drop) and *T. colubriformis* (1991 drop).

#### 4.3.4 Within-strain and bloodline effects

Significant sire effects were demonstrated in nine of the 11 analyses. Sire effects on  $FEC^{0.33}$  after natural infection in the JB Pye Flock (Table 4.7) were significant for two of the three measurements resulting in low to moderate heritability estimates (Table 4.9). Significant sire effects were found, after artificial infection with *H. contortus*, in all flocks examined (Table 4.8) resulting in moderate heritability estimates within the range of 0.17 to 0.42. The heritability estimates for the *T. colubriformis* infection tended to be more variable with no significant sire effects in the Trangie D Flock (Table 4.8) and in the Turretfield Resource Flock, in the latter flock heritability estimates being inconsistent between sex/management groups (Table 4.9). Overall heritability estimates for  $FEC^{0.33}$  averaged  $0.21 \pm 0.03$  when weighted by the reciprocal of the sampling variance.

### 4.3.5 Variance Components

The components of variance for  $FEC^{0.33}$  after natural parasite infection and artificial infection with *H. contortus* and *T. colubriformis* are given in Tables 4.10 and 4.11. 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 4.11). Genetic sources of variation in  $FEC^{0.33}$  showed differences between and within infection type. However, the within-flock genetic component (sire component multiplied by four) 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, although 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 Figure 4.7.

Table 4.9 Heritability estimates for  $FEC^{0.33}$  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	Infection type		
	Natural	<i>H. contortus</i>	<i>T. colubriformis</i>
JB Pye 1990a	0.07±0.12		
JB Pye 1990b	0.26±0.17		
JB Pye 1991	0.17±0.03		
Katanning (1991)		0.17±0.09	
Turretfield (1992)		0.34±0.09	
CSIRO (1991)		0.42±0.12	
Trangie (1990)		0.33±0.23	
Katanning (1992)			0.24±0.08
Turretfield (1993)			0.09±0.06 all sheep <sup>A</sup>
Turretfield (1993)			0.23±0.13 ewes
Turretfield (1993)			0.00 wethers
CSIRO (1992)			0.40±0.11
Trangie (1991)			0.11±0.18
Weighted average <sup>B</sup>	0.16±0.05	0.29±0.05	0.18±0.04

<sup>A</sup> Estimate used in weighted average.

<sup>B</sup> Calculated from 
$$\frac{\sum_i \frac{X_i}{\sigma_i^2}}{\sum_i \frac{1}{\sigma_i^2}} \pm \sqrt{\frac{1}{\sum_i \frac{1}{\sigma_i^2}}}$$

Table 4.10 Estimates of variance components for FEC<sup>0.33</sup> after natural infection with nematode parasites

Source	JB Pye 1990a		JB Pye 1990b		JB Pye 1991	
	Variance component	%	Variance component	%	Variance component	%
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	

Table 4.11 Estimates of variance components for FEC<sup>0.33</sup> (±standard error) after artificial infection with *H. contortus* and *T. colubriformis*

Bl:Strain = bloodline nested within strain.

<i>H. contortus</i> infection								
Source	Katanning (1991)		Turretfield (1992)		CSIRO (1991)		Trangie (1990)	
	Variance component	%	Variance component	%	Variance component	%	Variance component	%
Strain	0.68±0.70	3.4	0.30±0.57	2.5			0.00±0.00	0.0
Bl:Strain	0.00±0.32	0.0	0.08±0.20	0.7	2.92±2.29	4.3	0.00±2.58	0.0
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
Error	18.60±0.92		10.57±0.97		58.62±2.65		34.89±3.31	

<i>T. colubriformis</i> infection								
Source	Katanning (1992)		Turretfield (1993)		CSIRO (1992)		Trangie (1991)	
	Variance component	%	Variance component	%	Variance component	%	Variance component	%
Strain	0.02±0.05	0.4	0.00	0.0			0.00±0.00	0.0
Bl:Strain	0.08±0.00	0.0	0.03±0.01	0.5	2.80±1.41	16.3	0.34±0.37	5.2
Sire	0.32±0.13	5.8	0.11±0.08	2.0	1.41±0.42	8.2	0.19±0.29	2.9
Error	5.16±0.24		5.55±0.00		12.96±0.58		6.05±0.56	

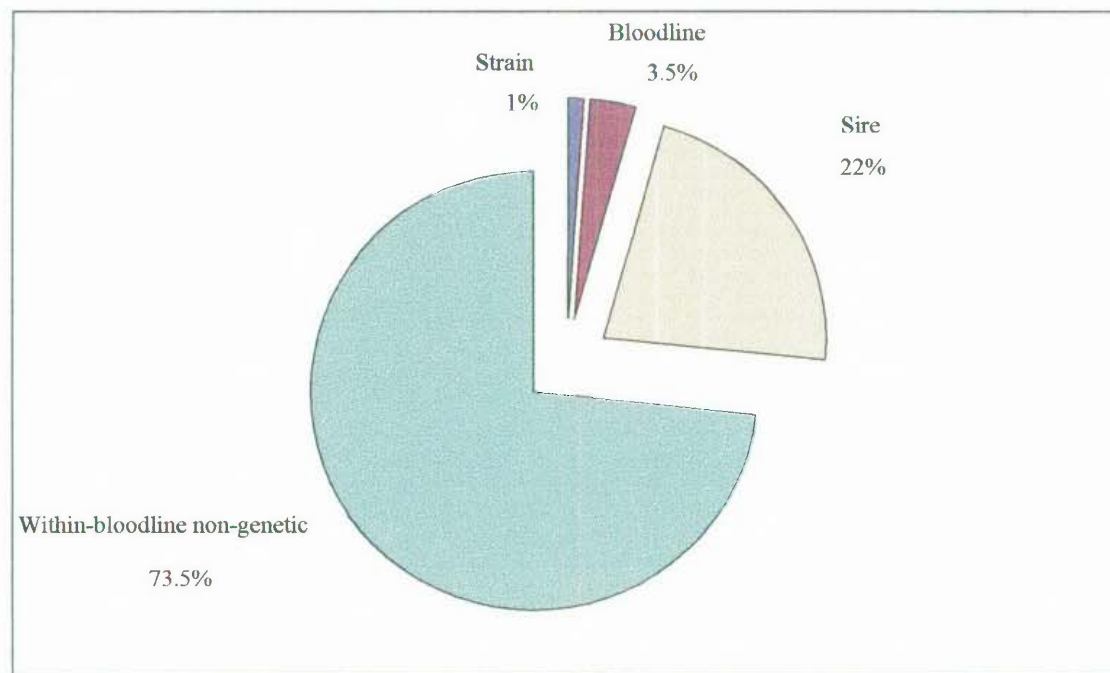


Figure 4.7 Sources of variation in FEC (%) across all resource flocks and infection types.

## 4.4 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*. From the lack of between flock variation 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 FEC variance.

#### 4.4.1 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. Therefore, adjusting for management groups 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 only brought together 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 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 a flock grade or selected from replacements at random. There may have been some genetic change in flocks where rams were purchased each year from the original stud, given that the stud was making genetic gain, but this would be unlikely for a trait such as resistance when no direct selection was being practised. 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; 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 three 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 at risk during 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 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°C and 7°C respectively for mean and mean 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°C 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 the autumn and winter months. 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 to 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), 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 the environmental effects were only occasionally significant and, if so, accounted for only a small proportion of variance, it is unlikely that heritability estimates calculated without fitting these effects will vary significantly from those reported here. This is in contrast to the adjustments for environmental effects needed for estimation of heritability of wool traits and bodyweight, 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).

#### **4.4.2 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 strains were compared, there were no clear differences in resistance despite the large environmental differences in which these two 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 resistance.

Bloodline differences between infections (years) were also inconsistent. The low correlation between bloodline means for each year may indicate an interaction of bloodline and 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 x 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 two 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.

#### **4.4.3 Within-bloodline effects**

There was a significant sire effect on  $FEC^{0.33}$  on all but two 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 0.09 to 0.40, which is consistent with previously published estimates summarised in Chapter 2, Table 2.2. 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 males and 0.23 for females (Table 4.9). This result, in the context of the other estimates both from 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 epg versus 2979 epg, respectively,  $F < 0.01$ ) 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 two sexes due 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 significant, due to environmental factors associated with the infection.

## 4.5 Conclusions

The partitioning of FEC variance (Figure 4.7) clearly demonstrates that the major source of genetic variation for resistance, in flocks in this study, exists within bloodlines, rather than between strain 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 (Chapter 3) 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 should be made.