

Chapter 5 Internal Parasite Resistance of Merino Flocks Selected for Production

5.1 Introduction

The response observed in flocks selected for FEC has demonstrated that breeding for parasite resistance can meet with success (Woolaston *et al.* 1991). The relative importance of disease resistance in a breeding objective will be determined in part by the genetic correlations between the measured resistance trait, FEC, and other economically important production traits in the breeding objective. Estimates of genetic correlations between FEC and production traits in random bred Merino flocks (Table 5.1) have been close to zero but are characterised by large standard errors. In an experiment conducted by Albers *et al.* (1987) correlations between FEC and wool growth and FEC and liveweight change were essentially zero when these production traits were measured under worm free conditions, but when infected with *H. contortus*, the correlations were moderate and negative in sign. In New Zealand studies, estimates of genetic correlations between FEC and the production traits of greasy fleece weight and body weight have varied, but have been unfavourable on a number of occasions (Table 5.1).

Another approach to determining if FEC and production traits are correlated at the genetic level, is to examine correlated responses in flocks under selection for one of the traits of interest. However, any examination of selection flocks for a correlated response, where the foundation animals were not allocated at random or measured for the trait of interest, and the selection lines are not replicated, is open to error as initial differences between lines and genetic drift cannot be quantified (Henderson 1989). However, in many instances it cannot be predicted at the outset of an experiment which traits may subsequently become of interest, and examination of selection flocks is of value given the deficiencies of this approach are recognised.

Within some flocks selected for production in New Zealand, there appears to have been a negative correlated response between production and resistance to internal

parasite infection, as measured by FEC (Table 5.2). In 8 out of 10 instances, where young animals from a positive selection flock for production were compared with a control flock of the same origin, the selected flock demonstrated a higher FEC. The flocks in which there appeared to be a correlated response in FEC were single trait selection lines for weaning weight (Woodlands), 12 month greasy fleece weight (Woodlands, Whatawhata, Massey Uni.), hogget body weight (Whatawhata, Woodlands) and a production index including number of lambs born, weaning weight and hogget fleece weight (Woodlands). This fleece weight result was consistent in all selection flocks in New Zealand (Table 5.2). Upon examination of Australian flocks selected for helminth resistance (Table 5.3), there is little evidence of a correlated response in any production traits for Merinos, but there is evidence in New Zealand flocks of an unfavourable response, in terms of GFW, to selection for FEC. Results of McMillan *et al.* (1992) monitoring reproductive rate (Table 5.3) should be interpreted with care as they were from very early years of the experiment (remembering that ewes lag behind lambs in generation number).

Table 5.1 Genetic correlation (\pm standard error) between FEC and greasy (GFW) and clean fleece weight (CFW), fibre diameter (FD), weaning weight (WW), liveweight gain (LWG), hogget body weight (HBW), reproduction rate (RR) and dag score (DS) in a range of sheep breeds

Reference	Breed	No of sires	Genetic correlation							
			GFW	CFW	FD	WW	LWG	HBW	RR	DS
Watson <i>et al.</i> 1986	Romney	35	na	na	na	na	-0.43	na	na	-0.7
Baker <i>et al.</i> 1991	Romney cross	33	na	na	na	na	0.49	na	na	-0.26 \pm 0.24
	Wallaceville						0.02 \pm 0.25			
Baker <i>et al.</i> 1991	Romney	60	na	na	na	na	-0.16 \pm 0.21	na	na	0.34 \pm 0.20
	Wairunga									
Bisset <i>et al.</i> 1992	Romney ^A	60	-0.31 \pm 0.16	na	na	0.09 \pm 0.22	-0.48 \pm 0.21	-0.26 \pm 0.21	na	0.45 \pm 0.19
	Hawkes Bay									
McEwan <i>et al.</i> 1995a	Romney ^A	139	0.14 \pm 0.14	na	na	na	na	0.15 \pm 0.15	na	na
	Apex		0.16 \pm 0.13	na	na	na	na	0.18 \pm 0.13	na	na
	Coopworth ^u		0.02 \pm 0.22	na	na	na	na	0.24 \pm 0.20	na	na
McEwan <i>et al.</i> 1995a	SRDG	82	0.25 \pm 0.18	na	na	na	na	0.04 \pm 0.18	na	na
	Romney ^B	na	na	0.14 \pm 0.17	-0.14 \pm 0.12	na	na	-0.15 \pm 0.16	na	na
Woolaston 1990	Random bred	na	na	na	na	na	na	na	na	na
Woolaston <i>et al.</i> 1991	Merino	na	na	-0.05 \pm 0.25	0.11 \pm 0.22	na	na	0.08 \pm 0.34	-0.22	na
	Control line	na	na	na	na	na	na	na	na	na
Albers <i>et al.</i> 1987 (worm free)	Merino	60	na	-0.17 \pm 0.30	-0.25 \pm 0.26	na	-0.01 \pm 0.25	na	na	na
	Merino	60	na	-0.02 \pm 0.32	-0.26 \pm 0.27	na	-0.29 \pm 0.26	na	na	na
Albers <i>et al.</i> 1987 (worm infected)	Merino	60	na	-0.53 \pm 0.27	-0.39 \pm 0.23	na	-0.39 \pm 0.31	na	na	na
	Merino	44	na	-0.66 \pm 0.28	-0.41 \pm 0.24	na	-0.68 \pm 0.34	na	na	-0.42 \pm 0.29
Karlsson and Greeff 1996	Merino	44	na	na	na	na	na	na	na	0.24 \pm 0.29
McEwan (unpublished) ^B	Apex	253	-0.11 \pm 0.10	na	na	na	na	-0.03 \pm 0.10	na	na
	Coopworth ^B	629	0.03 \pm 0.09	na	na	na	na	-0.04 \pm 0.08	na	na
	SRDG	629	0.25 \pm 0.07	na	na	na	na	0.24 \pm 0.08	na	na
	Romney ^B	629	0.23 \pm 0.07	na	na	na	na	0.18 \pm 0.06	na	na

^A Baker *et al.* (1991) is a preliminary report of the data presented by Bisset *et al.* (1992).

^B McEwan (unpublished) includes McEwan *et al.* (1995).

Table 5.2 Correlated response in FEC in flocks selected for production

Reference	Flock	Selection criteria	Year commenced	Effect on FEC
Garrick <i>et al.</i> 1992	Massey Uni.	Hogget GFW	1956	↑
Watson <i>et al.</i> 1986	Ruakura High Fertility Romney	Multiple birth ^A	1948	↑
McEwan <i>et al.</i> 1992	Woodlands	Index	1973	↑
		Dam NLB	1973	↑
		100 day weight ^B	1973	↑
		Hogget GFW	1973	↑
Morris and Bisset (unpublished)	Woodlands	100 day weight ^B	1973	↑
		Hogget GFW	1973	↑
	Tokanui	Hogget body wt	1973	0
	Whatawhata	Hogget GFW	1967	↑
		Hogget body wt	1967	0

^A No actual control line comparison.

^B Same line sub-sampled at two sites.

Given the body of information, it is likely that the results from New Zealand selection flocks indicate a realised genetic correlation between FEC and fleece weight. However, from the Australian parasite selection lines, there is little evidence of such a relationship in Merino sheep. This experiment examines the helminth resistance of Merino flocks selected for production, to test the hypothesis that there have been no correlated responses in FEC. These flocks include divergent selection lines for fleece rot, the study of which may indicate whether there is any genetic link between disease traits.

Table 5.3 Correlated response in greasy (GFW) and clean fleece weight (CFW), fibre diameter (FD), weaning weight (WW), hogget body weight (HBW), reproduction rate (RR), live weight gain (LWG) and dag score (DS) in flocks selected for helminth resistance

Reference	Flock	Selection criteria	Year commenced	Effect on production trait of selecting for resistance							
				GFW	CFW	FD	WW	HBW	RR	LWG	DS
Windon <i>et al.</i> 1993	Trichostrongylus selection lines	Response to <i>T. colubriformis</i> vaccination	1980	0 ^A	0	0	na	na	na	0	na
Woolaston (unpublished data)	Haemonchus selection lines	FEC following artificial infection with <i>H. contortus</i>	1978	0	0	0	na	0	0	na	0
McMillan <i>et al.</i> 1992	Ruakura FEC selection lines	FEC at 5 and 8 months of age	1985	na	na	na	na	na	0	na	na
Douch <i>et al.</i> 1995	Wallaceville lines	FEC at 5 and 8 months of age	1979	na	na	na	0	0	na	0	↑ ↑ 0
	Tokanui lines	FEC at 5 and 8 months of age	1985	na	na	na	0	↓ ^B	na	↓ ^B	0
Morris and Bisset (unpublished data)	Wallaceville lines	FEC at 5 and 8 months of age	1979	↓	na	na	na	na	↑	na	na

^A Number of symbols indicates number of times the trait was recorded in experiment.

^B May be the result of founder effects, because the control line was not intermediate between high and low lines.

5.2 Materials and methods

5.2.1 History of the selection flocks

The eight Merino flocks used in this study were bred at the Agricultural Research Centre at Trangie, situated on the central western plains of New South Wales, an environment where internal parasites are usually not prevalent. The worm control program comprised two drenches per year for young sheep and a single drench for adult sheep. The flocks consisted of a control line plus divergent selection lines for weaning weight, clean fleece weight, fleece rot and a positive fertility line. The Random flock (number of progeny tested, $n=76$) was of the same genetic origin as the Weaning Weight Plus ($n=39$) and Minus ($n=26$) lines (Pattie 1965) and the Fleece Weight Plus ($n=62$) and Minus ($n=51$) lines (Pattie and Barlow 1974), and was similar to but not of the same origin as the fleece rot Susceptible ($n=74$) and Resistant ($n=96$) lines (Mortimer 1991) and Fertility line ($n=50$) (Atkins and Robards 1976).

The Weaning Weight and Fleece Weight flocks were single trait selection lines. The Susceptible and Resistant flocks were selected on a combination of fleece rot scores and body strike. The Fertility flock was selected for high net reproductive rate, growth rate and wool production. Initial selection of sheep for each flock and selection history are given below.

5.2.1.1 Random line

This flock was established in 1951. Ten rams and a flock of 100 ewes were chosen at random from the Trangie Base flock. The flock was then closed and replacement rams and ewes selected at random each year subject to restrictions on black wool, deformity and fertility (Pattie 1965).

5.2.1.2 Weaning weight lines

These flocks were established in 1951. Sheep for the two flocks were selected on the basis of high or low weaning weight from the Trangie Base flock. As weaning weight was not available for ewes born in 1945 and 1946, their ten-month weight was used for selection. Since initial establishment the flocks have been closed, and replacements selected annually for either high or low weaning weight (Pattie 1965).

5.2.1.3 Fleece weight lines

These flocks were established in 1951. Sheep for the two flocks were selected from the Trangie Base flock on the basis of their clean fleece weight. Since initial establishment the flocks have been closed, and replacements (16-18 months of age) selected annually for either high or low clean fleece weight (Pattie and Barlow 1974).

5.2.1.4 Resistant and susceptible fleece rot lines

These flocks were established in 1974. The initial rams originated from the Trangie Fertility flock and they were allocated to either the Resistant or Susceptible flock on the basis of fleece rot infection after artificial wetting. Ewes were selected from the Trangie Selection Demonstration flock on the basis of naturally occurring fleece rot. There were a number of introductions of rams from the Fertility flock from 1976 to 1979 based on fleece rot response to artificial wetting. The flocks were closed in 1980 and ram replacements selected on the basis of fleece rot after both natural and artificial wetting and fly strike incidence. For 1982 and later matings, all hogget replacement ewes for both flocks have been selected at random (See Mortimer 1991 for full details).

5.2.1.5 Fertility flock

The fertility flock of 400 ewes was established in 1959. The ewes were chosen from various other flocks at Trangie and were not selected on the basis of their fertility. Initially, rams used in the flock were offspring of highly fertile ewes from the weaning weight plus selection flock and the Trangie Nucleus flock. In 1966 the flock was closed and subsequently all replacements were bred within the flock. Only rams born and raised as multiples were considered for selection. Rams were culled on low growth rates to weaning and low hogget fleece weight with the final selection being made on the basis of each ram's dam fertility index. Any ewe failing to rear at least one lamb to weaning in any year was culled. All twin born hogget ewes were selected and the remaining replacement ewes selected from the single born ewes with the highest hogget fleece weights (Atkins and Robards 1976).

5.2.2 Experimental details

Progeny from all flocks, totaling 45 sire groups, were born at the research station at Trangie in July-August 1992. The sheep were shorn as lambs in October 1992 and were moved in December 1992 to the Agricultural Research and Advisory Station, Condobolin approximately 200 km south west of Trangie. The sheep were run in two management groups based on sex. Male progeny remained entire. Liveweights, greasy fleece weights and fleece rot scores (Atkins and Mortimer 1989) were recorded prior to shearing in mid-October, 1993. All of the sheep were scored for fleece rot except the Fleece Minus line which did not have sufficient wool to score adequately. The sheep were faecal sampled on 7 October, 1993, 35 days after an artificial infection with 20,000 *Trichostrongylus colubriformis* larvae. Egg counts were made using the modified McMaster technique. FEC were transformed (cube root) and least squares were used to determine the appropriate statistical model and to estimate flock means.

5.2.3 Statistical analysis

The following linear model was used to estimate sire and error components of variance and covariance for the traits examined in this study:

$$Y_{ijklmn} = \mu + fl_i + S_{j;i} + brr_k + a_l + s_m + b(\bar{X} - X_n) + \text{interactions} + e_{ijklmn}$$

where Y is the observed trait; μ is the common mean; fl_i is the effect of the i th flock; $S_{j;i}$ is the effect of the j th sire nested within flock; 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, mature); s_m is the effect of the m th sex (female, entire male); b is the regression of phenotype on day of birth and \bar{X} is the mean day of birth and X_n is the day of birth for animal $_n$ and e_{ijklmn} is the random error. First order interactions of main effects were tested for significance and sequentially omitted from the model if non-significant ($P < 0.05$) or accounted for less than 2% of the variation. The final model used for each trait is given in Table 5.4.

Table 5.4 Significant levels of random and fixed effects in models fitted to production traits recorded in Merino resource flocks

DA = dam age; BRR = birth rearing rank; DOB = day of birth; Flk x Sex = flock by sex interaction.

Trait	Flock	Sire	Sex	DA	BRR	DOB	Flk x Sex
FEC ^{0.33}	*	*	**	ns	ns	ns	*
WW	**	ns	**	**	**	**	ns
Flc Rot	**	*	ns	ns	ns	ns	*
14GFW	**	*	ns	*	**	*	ns
14BW	**	*	**	*	**	*	**

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

Genetic parameters were estimated by fitting an animal model with DFREML (Meyer 1989). Maternal pedigrees were not included in the analysis as it was not within the scope of this work to investigate maternal effects for each trait. Least squares

estimates for genetic correlations were also made to provide approximate standard errors for the DFREML estimates (as DFREML does not estimate standard errors).

5.3 Results

The mean untransformed FEC for the ram management group was 2160 epg (n=206) and for the ewe management group was 1682 epg (n=268), this difference being highly significant ($P<0.001$). Birth rearing rank had a significant effect on $FEC^{0.33}$ with the single born and reared (SS) sheep having a FEC of 1907 epg (n=223), multiple born and single reared (MS) sheep 1597 epg (n=98), and multiple born and reared (MM) sheep 2052 epg (n=153). The difference between SS and MS was significant, as was that between MS and MM. Flock means for weaning weight, $FEC^{0.33}$, fleece rot score, greasy fleece weight and hogget liveweight are presented in Table 5.5. There was a significant difference between the Weaning Weight lines in $FEC^{0.33}$, with the Plus line having a lower $FEC^{0.33}$ than the Minus line ($P<0.001$). In the other selection groups there were no significant differences in $FEC^{0.33}$ between divergent lines. Sire effects were also significant ($P<0.001$), with an overall heritability estimate for $FEC^{0.33}$ of 0.63 ± 0.20 . From the DFREML analysis, genetic correlations between $FEC^{0.33}$ and fleece rot, hogget liveweight, greasy fleece weight and weaning weight were -0.20, 0.12, 0.30 and 0.19, respectively. Least squares estimates were similar (-0.25 ± 0.26 , -0.12 ± 0.43 , 0.37 ± 0.30 and 0.10 ± 0.56) and not significantly different from zero.

5.4 Discussion and conclusion

No evidence could be found to support the New Zealand findings (Garrick *et al.* 1992; Watson *et al.* 1995) of an unfavourable correlated response in FEC as a result of selection for either body weight, fleece weight or a production index that includes fertility, fleece weight and weaning weight. The response in wool production shown by the Fleece Plus flock compared to the Random flock was estimated to be 1% per annum over the period 1952 to 1977 (McGuirk 1980). The annual divergence between

the Fertility flock and the Random flock was estimated to be 1.8% for lambs weaned per ewe joined, 1.3% for hogget clean fleece weight and 0.8% for weaning weight (Atkins 1980). Wool production improved in the Fertility flock as much as in the Fleece Plus flock, and no increase in FEC was observed in either flock. This consistent pattern suggests that the genetic correlation between FEC and wool production in Merino sheep is close to zero under conditions of low exposure to parasite challenge as was the case in this experiment.

Table 5.5 Least squares mean (\pm standard error) for FEC at 14 months of age (FEC), weaning weight (WW), fleece rot score (Flc Rot), greasy fleece weight (14GFW) and bodyweight (14BW) at 14 months of age for Merino selection flocks

Flock	Random	WW Plus	WW Minus	Flc Wt Plus	Flc Wt Minus	Flc Rot Suscept.	Flc Rot Resist.	Fertility
FEC (epg ^{0.33})	10.51 ^{bc} ± 0.78	8.37 ^a ± 1.03	11.17 ^{cd} ± 1.12	10.47 ^{bz} ± 0.95	9.11 ^{ab} ± 0.96	11.54 ^{cd} ± 0.91	12.77 ^d ± 0.93	11.10 ^c ± 0.98
WW (kg)	19.1 ^c ± 0.4	21.7 ^{de} ± 0.5	15.6 ^a ± 0.6	18.6 ^c ± 0.5	17.4 ^b ± 0.5	22.8 ^e ± 0.4	21.2 ^d ± 0.4	22.0 ^{de} ± 0.5
Flc Rot Score	0.48 ^{cd} ± 0.18	1.16 ^e ± 0.23	0.18 ^{bc} ± 0.26	0.70 ^d ± 0.22	nm	1.83 ^f ± 0.21	0.18 ^b ± 0.21	0.09 ^a ± 0.24
14GFW (kg)	3.6 ^c ± 0.1	3.3 ^b ± 0.1	3.1 ^b ± 0.1	4.7 ^f ± 0.1	1.4 ^a ± 0.1	4.4 ^e ± 0.1	3.9 ^d ± 0.1	4.0 ^d ± 0.1
14BW (kg)	35.5 ^c ± 0.8	38.8 ^{de} ± 1.0	28.9 ^a ± 1.0	33.0 ^b ± 1.0	33.4 ^b ± 0.9	38.9 ^e ± 0.8	37.2 ^d ± 0.8	41.1 ^f ± 0.7

^a Means within rows with different superscripts differ significantly ($P < 0.05$).

^{nm} Not measured.

The significant difference in FEC between the Plus and Minus weaning weight lines (8.37 versus 11.17) may indicate a favourable correlated response. Due to the climate and drenching schedule, the environment at Trangie should have been virtually worm free, resulting in an estimate of correlated response free of infection. Published estimates of genetic correlations between FEC and liveweight at various ages in relatively parasite free conditions do not predict such a result. Under such conditions Woolaston *et al.* (1991) and Albers *et al.* (1987) reported that correlations between FEC and body weight in Merino sheep were not significantly different from zero.

In New Zealand genetic correlations have varied across flocks. In a flock of Romneys (Bisset *et al.* 1992), the correlations between FEC and weaning weight, 7 month weight and weight gain were negative (-0.05, -0.29 and -0.36, respectively) which suggests FEC should fall as animals are selected for increased weaning weight. In contrast other estimates from Romney and Coopworth flocks (McEwan *et al.* 1995) are positive, with genetic correlations between FEC and 8 month body weight averaging 0.15. The genetic correlations between FEC and weaning weight and FEC and hogget body weight reported in this paper were not significantly different from zero (0.19 and 0.12, respectively). The Fertility selection flock showed no correlated response in FEC even though weaning weight increased by a similar amount per annum (0.7%, Davis 1987) to that observed in the Weaning Weight Plus flock (0.8%, Atkins 1980). Even though there appeared to be a favourable response in FEC to selection for weaning weight, the inconsistency of results would make it unwise to predict a favourable response in body weight to selection for FEC in Merino sheep.

The Fleece Rot Resistant and Susceptible lines also displayed a similar FEC, suggesting no correlated response for this trait. The estimated genetic correlation between FEC and fleece rot was not significantly different from zero. However, it should be recognised that these results may have been affected by the occurrence of fleece rot during the parasite infection. The genetic correlation between FEC and fleece rot has been estimated in a larger random bred flock to be -0.49 ± 0.20 (Eady and Raadsma, unpublished data) but this estimate also suffers from the limitation that both disease traits were present concurrently. The reported association between FEC and fleece rot may vary with differing incidence of the two diseases. Consequently, these estimates may have low utility in predicting correlated responses to selection when both diseases do not occur concurrently. One way of obtaining an unbiased estimate of the genetic correlation between two disease traits, when they occur independently, is to replicate related populations in a diseased and disease-free environment (Baker 1991). This could be done by splitting half-sib families at random and running half of them in a worm-free environment while measuring fleece rot, and vice versa for the other half.

Generally by the age of 14 months sheep have developed a strong natural immunity to internal parasites (Gibson and Parfitt 1972). Even so there is still evidence of genetic variation in FEC at this age. Piper (1987) reported heritability estimates of 0.23 for log transformed FEC in 18 month old rams and there is evidence that the differences in FEC observed at a young age (6-7 months) persist in adult sheep (Woolaston 1992). Early estimates of 0.84 ± 0.14 and 0.55 ± 0.14 have been reported for the genetic correlation between FEC at approximately 5 and then 8 months of age, in Coopworth and Romney flocks respectively (McEwan *et al.* 1995a). With information from additional animals, these have been updated (McEwan, unpublished data) to 0.65 ± 0.07 and 0.71 ± 0.05 , for Coopworth and Romney flocks respectively. There are no estimates for the genetic correlation between early and later measurement of FEC in Merino sheep. Future work should focus on providing this information, as FEC in weaners may be the expression of a different trait to FEC in older sheep showing a more mature immune response. The estimate of heritability from this study, 0.63, was considerably higher than previous estimates of 0.23 (Piper 1987), 0.30 (Woolaston *et al.* 1991), 0.34 (Watson *et al.* 1986) and results from Chapter 4.

Selection for FEC in Australian Merinos has not resulted in an adverse correlated response in fleece weight, fibre diameter, body weight or fertility (Woolaston, unpublished data), although there has been one report each of lower GFW and body weight (probably founder effect) from New Zealand flocks selected for resistance. If the apparent negligibly correlated responses in the Merino parasite selection lines are indicative of the true relationship between FEC and production traits, sheep breeders can place emphasis on parasite resistance knowing there should be no antagonistic response in production traits. However, current estimates of genetic correlations and results from selection flocks are unacceptably imprecise and this area of breeding for disease resistance still requires further elucidation to allow confidence in the incorporation of parasite resistance into sheep breeding programmes.

Chapter 6 Resistance to Internal Parasites in Merino Sheep: Correlation With Production Traits

6.1 Introduction

Once it has been demonstrated that there is significant additive genetic variance for a trait such that it will respond to selection, the genetic and phenotypic relationships between that trait and others of importance need to be established. These estimates of phenotypic and genetic covariation provide some of the necessary information for traits to be subsequently combined in a selection index. Heritability estimates for a range of traits that are important in a wool producing enterprise are given in Table 6.1. Greasy and clean fleece weight are moderately heritable while the heritability of fibre diameter and body weight tends to be higher. The most important genetic association between these traits is the unfavourable correlation of clean fleece weight with fibre diameter, as it is these two traits that are the major contributors to economic gain in a Merino breeding program.

The heritability of resistance to helminth parasites has been estimated in a number of Merino flocks and is moderate in value (Chapter 4). However, estimates of genetic correlations between the resistance trait of FEC and production traits, used so far to evaluate strategies for breeding for helminth resistance (Woolaston 1994), have come from a relatively small data set in one environment. The author highlighted the critical need for more robust estimates, as the merit of breeding for improved helminth resistance was affected by assumptions made for genetic parameters to a greater extent than by assumptions of the costs associated with parasite infection.

In general, the genetic relationship between disease resistance and production has been assumed to be unfavourable as demonstrated in both dairy cattle (Dunklee *et al.* 1994; Jones *et al.* 1994; Lund *et al.* 1994) and beef cattle (Frisch 1981; Vercoe and Frisch 1981). Correlations between FEC and production traits have come under examination in sheep in New Zealand as the result of observed differences in FEC in

fleece weight and liveweight selection lines, the high fleece weight lines having higher FECs (Watson *et al.* 1995). Studies with Romney sheep showed a consistent, but low unfavourable genetic correlation (0.13-0.25) between FEC and liveweight at 8 months of age and hogget fleece weight at 12 months of age (McEwan, unpublished data). (See Chapter 5 for review of correlated responses and genetic correlations).

Table 6.1. Heritability estimates (\pm standard error) for hogget greasy fleece weight, clean fleece weight, fibre diameter and body weight and genetic correlation (\pm standard error) between clean fleece weight and fibre diameter for a range of Merino flocks

Reference	Strain	Heritability estimates				Genetic correlation CFW-FD
		GFW	CFW	FD	BWT	
Morley 1955	Peppin	0.40 \pm 0.06	0.47 \pm 0.07	na ^A	0.36 \pm 0.08	na
Beattie 1962	Peppin	0.35 \pm 0.18	0.34 \pm 0.18	0.57 \pm 0.17	0.54 \pm 0.20	0.16
Brown and Turner 1968	Peppin	0.42 \pm 0.05	0.40 \pm 0.05	0.47 \pm 0.04	0.65 \pm 0.04	0.16 \pm 0.08
Mullaney <i>et al.</i> 1970	Finewool	0.32 \pm 0.07	0.24 \pm 0.07	0.46 \pm 0.07	na	0.39 \pm 0.11
Gregory 1982a, 1982b	Bungaree	0.27 \pm 0.05	0.25 \pm 0.05	0.75 \pm 0.08	0.40 \pm 0.06	-0.06 \pm 0.11
Davis and Kinghorn 1986	Peppin	0.55 \pm 0.12	0.49 \pm 0.13	0.78 \pm 0.19	0.68 \pm 0.16	0.46 \pm 0.15
Walkley <i>et al.</i> 1987	Koonoona	0.30 \pm 0.09	0.37 \pm 0.10	0.45 \pm 0.10	na	0.21 \pm 0.16
Mortimer and Atkins 1989	Multiple	0.29 \pm 0.06	0.30 \pm 0.06	0.48 \pm 0.07	0.34 \pm 0.06	0.40 \pm 0.11
James <i>et al.</i> 1990	Collinsville	0.34 \pm 0.12	0.39 \pm 0.13	0.42 \pm 0.13	na	-0.12 \pm 0.26
Lewer <i>et al.</i> 1994	Multiple	0.30-0.42	0.26-0.44	0.47-0.59	0.27-0.50	0.26-0.29
Gifford <i>et al.</i> 1994	SA	na	0.44 \pm 0.02	0.36 \pm 0.02	na	na
Swan <i>et al.</i> 1995	Finewool	0.32	0.28	0.67	na	0.31

^A Not available.

To date, in the Merino breed the genetic correlations between FEC and the production traits of greasy fleece weight, clean fleece weight, fibre diameter, hogget body weight and reproductive performance have been assumed to be close to zero or slightly favourable (Woolaston 1994). These values were based on estimates from the control line of the *H. contortus* selection flock and a CSIRO random bred flock (Woolaston *et al.* 1991) at Armidale, NSW. Helminth infections in these sheep were effectively

controlled using the regional management program based on paddock changes and anthelmintic treatment. Studies in Merino flocks selected for production traits in a relatively parasite free environment (Chapter 5) have shown no evidence of a correlated response in FEC, with the exception of the weaning weight lines where there was indication of a favourable association between FEC and weaning weight. The hypothesis to be tested in this experiment is that the genetic correlations between FEC and production traits in Merino sheep are close to zero when measured under conditions of effective helminth control.

6.2 Materials and methods

6.2.1 Genetic resource flocks

Merino sheep representing a range of bloodlines, managed in resource flocks across Australia, were tested for resistance to helminth parasites. These flocks (JB Pye Flock, Camden, NSW; Katanning Base Flock, Katanning, WA; Turretfield Merino Resource Flock, Rosedale, SA; CSIRO Finewool Flock, Armidale, NSW and the Trangie D Flock, Trangie, NSW) were previously described in Chapter 4. All experimental groups as defined and tested for internal nematode resistance in Chapter 4 were used in this study except for those groups where production data were unavailable (Turretfield 1993 and Katanning 1992 groups), sire information was limited (Trangie 1990 and 1991 groups) and age of FEC measurement (36 months) and reproductive status (pregnant) were not consistent with that of other experimental flocks (JB Pye 1990b).

6.2.2 Measurement of FEC and production traits

The measurement of parasite resistance (FEC) was as described in Chapter 4. All FECs were cube root transformed for analysis. Table 6.2 gives details of the production traits that were measured in the flocks and the number of sire families in each flock. Production data was limited to the drops where there was a FEC because

sampling variances for FEC and wool traits and their covariance are more uniform with this use of data (James 1993). Number of animals measured for each pair of traits is given in Table 6.2. Body weights were measured at weaning (WW), 10 months of age (10BW) and/or 16 months of age (16BW). Depending on experimental flock greasy fleece weight, clean fleece weight, and fibre diameter were measured at approximately 10 months (10CFW, 10GFW, 10FD respectively), 16 months (16GFW, 16CFW, 16FD) and 21 months (21GFW, 21CFW, 21FD) of age with either 6-7 or 10-13 months wool growth (see Table 6.2).

In the JB Pye flock all sheep were first shorn as weaners at 4 months of age. Animals were allocated to a footrot experimental group or the breeding replacement group. Those in the footrot group were next shorn at 10 months of age. All sheep were shorn at 16 and 22 months of age. For the 1990 born sheep only data from the footrot group (the JB Pye 1990a group) were used to estimate genetic correlations between FEC and fleece traits at 10 and 16 months. For the 1991 drop, data from both the footrot and breeding groups were used to estimate genetic correlations between FEC and fleece measurements. The 16 month and 22 month fleece data were used to maximise animals per sire group as only the footrot group was shorn at 10 months of age. To make the wool growth period equivalent for the two management groups, the 16 month fleece data for the footrot group were the sum of their 10 and 16 month measurements. Estimates of genetic correlations between FEC and WW, 10BW and 16BW were based on data from the footrot group (1990a) and both groups in 1991.

In the Katanning Base Flock all sheep were first shorn as weaners at 4 months of age. The ewes were next shorn at 11 months of age and all sheep were shorn at 17 months of age. Genetic correlations were estimated between FEC and 11 month fleece traits in the ewes and the 17 month fleece traits for all animals.

Table 6.2 Numbers of sire families and number of animals recorded for pairings of FEC and each production trait in each experimental flock

Flock	Traits															
	No of sire families	WW	10 BW	16 BW	10 GFW	10 CFW	10 FD	Wool growth (mth)	16 GFW	16 CFW	16 FD	Wool growth (mth)	21 GFW	21 CFW	21 FD	Wool growth (mth)
JB Pye 1990a	41	408 ^A	407	408	408	407	407	6	408	408	408	6	-	-	-	-
JB Pye 1991	41	995 ^A	997	934	-	-	-	-	968	968	968	12	921 ^F	907 ^F	908 ^F	8
Katanning 1991	64	947 ^A	933 ^B	894 ^C	460 ^D	460 ^D	466 ^D	7	871 ^E	871 ^E	879 ^E	13	-	-	-	-
CSIRO 1991	60	1074	1063	-	1063	1050	1056	10	-	-	-	-	1010	1004	1014	11
CSIRO 1992	74	1059	1072	-	1072	1060	1065	10	-	-	-	-	1050	1057	1062	11
Turretfield 1997	48	1602 ^A	705	1419	699	696	696	6	691	691	691	6	-	-	-	-

^A Shorn as lambs at weaning.

^B 9 month BW.

^C 15 month BW.

^D 11 month shearing.

^E 17 month shearing.

^F 22 month shearing.

To make the wool growth period equivalent for the two sexes, the 17 month data for the ewes were the sum of their 11 month and 17 month measurements. Therefore, the 17 month fleece trait estimates for this flock are not entirely independent from the first. Genetic correlations between FEC and WW, 10BW and 16BW were estimated using data from both sexes.

In the CSIRO Finewool Flock all sheep were first shorn at 10 months of age and again at 21 months of age. Genetic correlations between FEC and fleece traits at both shearings were estimated. Estimates of genetic correlations between FEC and WW and 10BW were based on data from both sexes.

In the Turretfield resource flock all sheep were first shorn as weaners at 4 months of age. The rams were next shorn at 10 months of age and all sheep were shorn at 16 months of age. Genetic correlations between FEC and fleece traits were based on data from the 10 and 16 month shearing of rams as the only fleece measurement available for the ewes was GFW at 16 months. Estimates of the genetic correlation between FEC and WW and FEC and 16BW used data from both sexes, while for 10BW only data from rams were available.

6.2.3 Statistical analysis

The following linear model was used to estimate sire and error components of variance and covariance for the traits examined in this study:

$$Y_{ijklmno} = \mu + bl_i + S_{j:i} + br_r_k + a_l + s_m + g_n + b(\bar{X} - X_o) + \text{interactions} + e_{ijklmno}$$

where Y is an observed trait; μ is the common mean; bl_i is the effect of the i th bloodline; S_j is the effect of the j th sire nested within bloodline; br_r_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, mature); s_m is the effect of the m th sex (female, castrate male, entire male); g_n is the effect of n th management group; b is the regression of phenotype on day of birth and \bar{X} is the mean day of birth

and X_o is the day of birth for animal o and $e_{ijklmno}$ is the random error. First order interactions of main effects were tested for significance and sequentially omitted from the model if non-significant ($P < 0.05$) or accounted for less than 2% of the variation. The final model used for each production trait is given in Table 6.3, with significant interactions reported in the text of the results. FECs were cube root transformed before analysis (Chapter 3) and the models fitted for this trait are given in Chapter 4.

Variance and covariance components were estimated by the restricted maximum likelihood procedure, using a derivative-free algorithm and fitting an animal model in all bivariate analyses (DFREML, Meyer 1989). Maternal pedigrees were not included in the analysis. Standard errors for heritability came from the DFREML analyses and for genetic correlations were calculated as suggested by Falconer (1989, p 317). Pooled estimates for phenotypic correlations were calculated by transforming each r value to a Fisher's z value and weighting it by the reciprocal of its mean square (Snedecor and Cochran 1967, p 187). Pooled estimates for genetic correlations were calculated by weighting each estimate by the reciprocal of its sampling variance. All pooled estimates came from grouping traits according to age at measurement.

6.3 Results

6.3.1 Statistical models and heritability estimates

Fixed effects and interactions that had a significant effect on $FEC^{0.33}$ were reported in detail in Chapter 4. Significant effects for individual production traits are given in Table 6.3. Two-way interactions of fixed effects were not significant with the exception of $bl \times g$ for the trait 21FL in the CSIRO 1991 group, and $bl \times brr$ for WW and $bl \times g$ for 10BW, 10GFW and 10CFW in the CSIRO 1992 group ($P < 0.05$). Heritability estimates for all traits are summarised in Table 6.4.

Table 6.3 Significant levels of random and fixed effects in models fitted to production traits recorded in Merino resource flocks.
BL = bloodline; MG = management group; DA = dam age; BRR = birth rearing rank; DOB = day of birth

Flock and trait	BL	Sire	Sex	MG	DA	BRR	DOB	Flock and trait	BL	Sire	Sex	MG	DA	BRR	DOB
JB Pye 1990a															
WW	*	*	ns ^A	na ^B	**	**	**	CSIRO 1991	WW	**	**	ns	*	**	**
10BW	*	ns	**	ns	**	**	*	10BW	**	**	**	**	ns	**	**
16BW	ns	*	**	**	**	**	*	16BW	**	**	**	**			
10GFW	*	**	ns	**	**	**	**	10GFW	**	**	ns	**	ns	**	**
10CFW	*	**	ns	**	**	**	**	10CFW	**	**	ns	*	**	**	**
10FD	**	**	ns	ns	ns	ns	*	10FD	**	**	ns	**	*	ns	*
16GFW	**	**	**	**	**	**	ns	21GFW	**	**	na	**	ns	**	**
16CFW	**	**	**	**	**	**	ns	21CFW	**	**	na	**	ns	**	*
16FD	**	**	ns	**	ns	ns	ns	21FD	**	**	na	**	*	ns	ns
JB Pye 1991															
WW	*	**	na	na	na	na	na	CSIRO 1992	WW	*	ns	na	na	na	na
10BW	**	**	na	**	**	**	**	10BW	**	**	**	**	ns	ns	ns
16BW	**	**	na	**	ns	*	*	16BW	**	*	ns	**	ns	**	**
16GFW	**	**	na	**	**	**	**	10GFW	**	*	ns	**	**	**	**
16CFW	**	**	na	**	**	**	**	10CFW	**	**	ns	**	**	**	**
16FD	**	**	na	**	ns	**	**	10FD	**	**	**	**	ns	**	ns
21GFW	**	**	na	**	*	**	ns	21GFW	**	**	ns	**	**	**	**
21CFW	**	**	na	**	*	**	ns	21CFW	**	**	ns	**	**	**	**
21FD	**	**	na	**	ns	**	ns	21FD	**	**	**	ns	ns	ns	ns
Katanning 1991															
WW	**	**	**	na	**	**	ns	Turretfield 1992	WW	**	**	na	**	**	**
10BW	*	**	na	**	**	**	ns	10BW	*	**	na	na	ns	**	**
16BW	**	**	na	**	*	**	ns	16BW	**	**	na	ns	ns	**	**
10GFW	*	**	na	na	ns	**	ns	10GFW	**	**	na	na	**	**	**
10CFW	*	**	na	na	ns	**	ns	10CFW	**	**	na	na	**	**	*
10FD	**	**	na	na	ns	ns	ns	10FD	*	**	na	na	ns	*	**
21GFW	**	**	na	**	**	**	ns	21GFW	**	**	na	na	*	**	*
21CFW	**	**	na	**	**	**	ns	21CFW	*	**	na	na	*	**	ns
21FD	**	**	na	**	ns	*	**	21FD	**	**	na	na	*	ns	**

^Ans = P>0.05, * P<0.05, ** P<0.01. ^BNot applicable where sex and management group were confounded or both sexes were in same management group or data from only one sex were used.

Table 6.4. Univariate heritability estimates (\pm standard error) for $FEC^{0.33}$ and production traits in Merino resource flocks

Estimates only include data from animals that were present in the flocks in years that FEC was measured and may not be the same as published or yet to be published estimates using all information collected in each flock.

Flock	Trait													
	FEC	WW	10 BW	16 BW	10 GFW	10 CFW	10 FD	16 GFW	16 CFW	16 FD	21 GFW	21 CFW	21 FD	
JB Pye	0.07	0.19	0.17	0.28	0.47	0.58	0.40	0.42	0.40	0.70	-	-	-	
1990a	±0.12	±0.13	±0.13	±0.15	±0.18	±0.20	±0.16	±0.17	±0.17	±0.21				
JB Pye	0.17	0.37	0.34	0.33	-	-	-	0.36	0.42	0.70	0.34	0.37	0.61	
1991	±0.08	±0.11	±0.11	±0.11				±0.12	±0.12	±0.16)	±0.11	±0.12	±0.15	
Katanning	0.17	0.32	0.42	0.57	0.61	0.73	0.80	0.48	0.53	0.72	-	-	-	
1991	±0.09	±0.11	±0.13	±0.15	±0.21	±0.22	±0.22	±0.14	±0.14	±0.17				
CSIRO	0.42	0.22	0.36	-	0.35	0.33	0.83	-	-	-	0.37	0.31	0.59	
1991	±0.12	±0.08	±0.10		±0.11	±0.10	±0.17				±0.11	±0.10	±0.14	
CSIRO	0.40	0.58	0.48	-	0.12	0.17	0.59	-	-	-	0.26	0.28	0.50	
1992	±0.11	±0.12	±0.12		±0.07	±0.08	±0.13				±0.09	±0.10	±0.15	
Turretfield	0.34	0.20	0.47	0.27	0.30	0.47	0.59	0.38	0.49	0.80	-	-	-	
1992	±0.09	±0.08	±0.14	±0.08	±0.11	±0.14	±0.16	±0.13	±0.15	±0.18				
Weighted	0.25	0.29	0.32	0.33	0.25	0.32	0.62	0.40	0.46	0.73	0.31	0.31	0.57	
average	±0.04	±0.04	±0.05	±0.06	±0.05	±0.05	±0.07	±0.07	±0.07	±0.09	±0.06	±0.06	±0.08	

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

6.3.2 Genetic Correlations

The correlations between $FEC^{0.33}$ and CFW were moderate and negative in sign on all occasions in the JB Pye group with the exception of the 10 month shearing of the 1990a group (Table 6.5). A negative correlation was also found between $FEC^{0.33}$ and 10CFW in the CSIRO 1992 group. Moderate correlations, positive in sign, were found between $FEC^{0.33}$ and 10CFW in the Katanring 1992 and CSIRO 1991 groups, and between $FEC^{0.33}$ and 21CFW in the CSIRO 1992 group, and $FEC^{0.33}$ and 16CFW in the Turretfield 1992 group. $FEC^{0.33}$ and all expressions of fibre diameter were negatively correlated in the JB Pye 1990a and 1991 groups. In the CSIRO 1992 group, $FEC^{0.33}$ was negatively correlated with 10FD but the correlation at 21 months was essentially zero. In the CSIRO 1991 group the correlation between $FEC^{0.33}$ and 10FD was close to zero but was slightly positive at 21 months of age. In the Turretfield 1992 group the correlation between $FEC^{0.33}$ and 10FD was lowly negative but close to zero at 16 months of age. The genetic correlation between $FEC^{0.33}$ and 16BW was negative in all groups. The genetic correlation between $FEC^{0.33}$ and 10BW was moderately to strongly negative in all but one group (CSIRO 1991), but a less consistent result was observed for $FEC^{0.33}$ and weaning body weight. Standard errors of the estimates ranged between 0.13 and 0.28, except for the standard error (0.36-0.67) of estimates from the JB Pye 1990a group.

An average of all estimates was calculated by weighting each estimate in proportion to the reciprocal of its sampling variance (Table 6.5). The results were correlations with $FEC^{0.33}$ of -0.20, -0.18 and -0.26 for WW, 10BW and 16BW respectively; 0.21, -0.06 and 0.21 for 10GFW, 16GFW and 21GFW respectively; 0.21, -0.05 and 0.07 for 10CFW, 16CFW and 21CFW respectively; and -0.09, -0.12 and 0.04 for 10FD, 16FD and 21FD respectively.

6.3.3 Phenotypic correlations

The phenotypic correlations between $FEC^{0.33}$ and production traits were all close to zero. However, there was a trend towards a slightly negative association between $FEC^{0.33}$ and all expressions of fibre diameter and body weight (Table 6.6).

6.4 Discussion and conclusion

From the six flocks in this study there was no decisive pattern in the genetic and phenotypic parameters relating FEC and production traits. The genetic correlation between FEC and clean wool production appeared to be dependent on the age of testing for clean fleece weight. Estimates at 10 months of age were generally unfavourable and at 16 and 21 months of age they were close to zero. The pooled estimate for the correlation between fibre diameter and FEC was unfavourable at both 10 and 16 months of age and close to zero at 21 months of age. The magnitude of the standard errors associated with the individual estimates precluded any of them being significantly different from zero. The genetic relationship between FEC and body weight appeared to be favourable, being generally negative in sign and of the order of -0.2. This is consistent with the result from Merinos lines selected for high or low weaning weight, where a favourable correlated response in FEC was apparent (Chapter 5).

The results for 10 month clean fleece weight are similar to those reported in New Zealand for fleece weight at 12 months of age. However, the results for liveweight appear to be the opposite in Merinos to that found in meat and dual-purpose sheep breeds. In New Zealand the initial suggestion of an unfavourable correlation between liveweight and FEC came from differences observed in lines selected for weaning weight, and as such was unsubstantiated. More recent estimates of the genetic correlation between liveweight and FEC have supported this finding (McEwan, unpublished data) in some breeds. However, there is still debate amongst New Zealand researchers as to the nature of the relationship between FEC and body weight (Morris, personal communication).

Table 6.5. Genetic correlations (\pm standard error) between FEC^{0.33} and production traits in Merino resource flocks

To calculate the pooled correlation each estimate was weighted in proportion to the reciprocal of the sampling variance of the estimate.

Flock	Trait											
	WW	10 BW	16 BW	10 GFW	16 GFW	10 CFW	16 CFW	10 FD	16 FD	21 GFW	21 CFW	21 FD
JB Pye 1990a	na ^A	na	-0.13 ± 0.67	0.44 ± 0.46	0.02 ± 0.59	-0.23 ± 0.57	-0.53 ± 0.36	-0.28 ± 0.54	-	-	-	-
JB Pye 1991	-0.20 ± 0.25	-0.37 ± 0.24	-0.41 ± 0.23	- ± 0.50	-0.32 ± 0.25	-0.38 ± 0.22	-0.19 ± 0.22	- ± 0.27	-0.13 ± 0.27	-0.29 ± 0.25	-0.10 ± 0.24	-
Katanning 1991	0.26 ± 0.28	-0.16 ± 0.28	-0.24 ± 0.25	0.30 ± 0.27	-0.09 ± 0.28	-0.06 ± 0.26	0.04 ± 0.25	0.12 ± 0.27	-	-	-	-
CSIRO 1991	0.40 ± 0.19	0.22 ± 0.19	- ± 0.19	0.34 ± 0.19	- ± 0.17	- ± 0.17	- ± 0.17	0.02 ± 0.17	0.15 ± 0.20	0.06 ± 0.21	0.11 ± 0.18	-
CSIRO 1992	-0.43 ± 0.13	-0.25 ± 0.16	- ± 0.16	-0.20 ± 0.24	- ± 0.24	- ± 0.24	- ± 0.24	-0.21 ± 0.17	- ± 0.18	-0.21 ± 0.20	-0.04 ± 0.20	-
Turretfield 1992	-0.40 ± 0.18	-0.24 ± 0.19	-0.18 ± 0.19	0.03 ± 0.24	0.16 ± 0.23	0.28 ± 0.21	-0.04 ± 0.19	-0.15 ± 0.20	-	-	-	-
Pooled ^B estimate	-0.20 ± 0.08	-0.18 ± 0.09	-0.26 ± 0.12	0.21 ± 0.11	-0.06 ± 0.14	-0.05 ± 0.13	-0.12 ± 0.12	-0.09 ± 0.09	0.21 ± 0.12	0.07 ± 0.13	0.04 ± 0.12	-

^A Inestimable.

^B 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 6.6. Phenotypic correlations between $FEC^{0.33}$ and production traits in Merino resource flocks

Flock	Trait											
	WW	10 BW	16 BW	10 GFW	10 CFW	10 FD	16 GFW	16 CFW	16 FD	21 GFW	21 CFW	21 FD
JB Pye 1990a	na ^A	na	-0.10	0.06	0.06	-0.05	-0.03	-0.03	-0.06	-	-	-
JB Pye 1991	0.02	0.01	-0.09	-	-	-	-0.04	-0.04	-0.1	-0.02	-0.01	-0.08
Katanning 1991	-0.06	-0.12	-0.12	0.05	0.05	-0.03	-0.02	0.00	-0.05	-	-	-
CSIRO 1991	0.04	0.04	-	0.04	0.05	0.01	-	-	-	0.02	0.02	0.03
CGIRC 1992	-0.03	-0.05	-	-0.04	-0.04	-0.10				0.04	0.02	0.04
Turretfield 1992	-0.05	-0.12	-0.06	-0.01	0.04	-0.11	-0.02	0.00	-0.09	-	-	-
Pooled estimate	-0.02	-0.04	-0.09	0.01	0.02	-0.06	-0.03	-0.01	-0.07	0.02	0.02	-0.01

^A Inestimable.

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

The same argument may apply to wool production, where the availability of sulphur amino acids is the major rate limiting factor for keratin production (Reis 1979), and sulphur amino acids also being important precursors for production of immunoglobulins (Cunningham 1973). These issues will be difficult to resolve until there is some understanding of the cost to the animal of mounting a rapid and effective immune response.

Heritability estimates for production traits and FEC reported here, fall into the general range of published values for Merino sheep (Table 6.1) but tended to be greater than previous estimates for CFW, FD and BW in the Katanning Base Flock (Lewer *et al.* 1994) and CFW and FD in the Turretfield Resource flock (Gifford *et al.* 1994). The estimates from the CSIRO Finewool Flock, averaged over the two years, were similar to those reported by Swan *et al.* (1995). Because these estimates are based on only one year's data, the year parasite resistance was measured, they would be less accurate estimates than those already published for these flocks.

The genetic correlation estimates varied between flocks both in magnitude and sign. This variation between flocks is similar to the variation in genetic correlations reported for wool traits in different Merino flocks. The approach taken in deciding on a suitable figure to use, where genetic parameters are not specifically known for a particular flock, has been to calculate an average from a range of estimates (Ponzoni 1987). Lewer *et al.* (1994) summarised the trends in published estimates of genetic correlations for wool traits. The approach of using a weighted average from a number of flocks can be used for genetic correlations between FEC and production traits, but is open to the danger that genotype \times environment interactions are significant and are influencing the estimates of genetic correlations, or that true differences do exist between flocks as a result of different gene frequencies or different measurement

strategies. For instance, the estimates from the JB Pye Flock are nearly all moderate and similar in sign to what might be expected given the effect of helminth infection on liveweight, wool production and fibre diameter. Helminth challenge in this environment was extreme with anthelmintic treatment required every 4-5 weeks to prevent mortalities and clinical signs of disease. The impact of larval challenge on wool production can be quite substantial under these conditions (Barger 1982; Albers *et al.* 1989).

Genetic correlations between FEC and wool production from the other flocks, which were exposed to a lower level of natural parasitism over the period that wool production was measured, tended to be opposite in sign to those from the JB Pye Flock. This is a similar result to that reported by Albers *et al.* (1987) where the magnitude of the negative genetic correlations between FEC and production traits increased when production was measured during helminth infection. However, statistically these estimates are not significantly different.

The question then is, should these estimates from different environments be pooled? The environments in this study varied in terms of the level of natural helminth challenge that occurred over the period production was measured. The environment in which production is measured can affect both additive genetic variance for these traits and their covariances. With disease traits this is even more applicable as disease incidence will vary with environment and will have a direct effect on the expression of production traits. The range in environments in this study was diverse in terms of helminth challenge, going from relatively low natural challenge in WA and SA, to high challenge in the New England environment, to extremely high at Camden. However, looking at the genetic correlations from flocks in each of these areas it is difficult to draw any conclusions. There perhaps is some indication that in the Camden environment (JB Pye 1991), the relationship between FEC and production is stronger and in the direction expected, given the general effect of parasites on production.

The phenotypic correlations do not add much information to this comparison of environments as they were predominantly low or close to zero. This suggests that the

measurement of FEC at one point in time was not a useful indicator of current production in that environment. This appears to be a common outcome, with low phenotypic correlations occurring in the study of Albers *et al.* (1987, see Piper and Barger 1988) and in a range of New Zealand experiments (Baker *et al.* 1991; Bisset *et al.* 1992). In the current study the only trend that could be observed in the phenotypic correlations was a small, but generally negative, association of FEC with BW and FD, indicating that the more resistant sheep tended to be heavier and produce coarser wool. A more extensive monitoring of FEC over the period for which production was measured may have resulted in stronger phenotypic associations. Conversely, the sheep may not have been exposed to significant natural helminth infection during the period wool growth was measured. With the exception of the JB Pye Flock, FECs were obtained after a relatively brief artificial worm challenge that, in itself, would have had little effect on production (Kisielewicz *et al.* 1995). Given the routine worm control programs that were used within each flock, natural helminth infection may not have had any measurable impact on production.

The issue of whether these estimates should be pooled or not perhaps is best resolved by addressing the question of whether the estimates from this study should be used in preference to zero genetic correlations, which are the parameter values currently being used where ram breeders are selecting for resistance (Pocock *et al.* 1995). The results from this study do suggest a case for changing this practice, at least when predicting likely changes in FEC with selection for production traits. Although none of the estimates are significantly different from zero and they vary across flocks and ages of fleece measurement there appears to be no general trend for them to change with age or level of natural worm challenge. There may be a case for pooling all correlations of FEC with greasy fleece weight to give an estimate of 0.15, all correlations of FEC with clean fleece weight to give 0.10, all correlations of FEC with FD to give -0.06 and all correlations of FEC with body weight to give an estimate of -0.21. Sensitivity analyses can be done to discover the consequences of errors in the genetic parameters, on both predicted and realised gains. This information can then be used in deciding how much effort should be put into further parameter estimation. This type of analysis is reported in Chapter 7.

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

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