Chapter 7 Sensitivity of Genetic Response to Errors in Estimates of Genetic Correlations Between Production Traits and FEC

7.1 Introduction

The consequences of including helminth resistance in a Merino breeding objective will be largely dependent on its relative economic value (REV) and the genetic co-variances between the disease trait and important production traits. Multi-trait selection index theory can be used to predict response in individual traits and in aggregate genotype, but will depend on the accuracy with which the phenotypic and genetic parameters, and the relative economic values, are estimated.

The impact of "errored" parameters and economic values was explored by Ponzoni (1987) for a Merino breeding objective. This was done by changing some of the assumed WOOLPLAN phenotypic and genetic parameters to specific values indicated by estimates from other populations. The relative economic values were also varied giving additional weight to wool production relative to liveweight. The changes in phenotypic and genetic parameters resulted in different predictions of genetic gain, although the correlation between the different indices was close to 1, ranging from 0.96 to 1. In the case where the economic values were changed, the differences in predicted genetic gains were quite substantial but the correlation between indices was relatively high (0.91). The conclusion drawn from this work was that the ability to predict accurately the genetic gain in various traits can be significantly affected by changes in the assumed parameters and REVs, but selection of animals based on the overall index score is relatively unchanged. In practical terms, it is nearly the same individual sheep that will be identified as superior regardless of the parameters or REVs used. This conclusion applies to the combinations of parameters and REVs that were specifically evaluated and may not necessarily hold in every situation.

Using a multiple trait selection index, Piper and Barger (1988) examined the benefits of breeding for improved resistance under conditions of mild or moderate parasitism where the genetic correlation of FEC with wool production and liveweight varied. The model used did not allow for parasitism-induced changes in the (co)variance matrix among production traits, an area where there is little information. Benefits were expressed in terms of the direct effect that including FEC had on the production traits, rather than any economic benefit ascribed to FEC itself. Using genetic correlations which were estimated in a relatively parasite-free environment as being close to zero, there was very little to be gained by including parasite resistance in the selection index. However, under conditions of moderate parasitism, where the genetic correlations between FEC and production were negative and greater in magnitude, inclusion of resistance in the selection index resulted in significant additional gains in wool production and reproductive rate, which more than offset unfavourable changes in fibre diameter. The conclusion made from this work was that the merit of including parasite resistance in a selection index is dependent on the actual level of production loss due to parasitism.

The concept, used by Piper and Barger (1988), of ascribing a zero economic value to helminth resistance and assessing its merit in the breeding objective through its effect on production traits has continued with the use of a desired gain index (Brascamp 1984) as outlined by Woolaston (1994). A desired gain for FEC is specified (as a proportion of the total gain possible) while changes in production traits are optimised by the selection index. The true economic value of parasite resistance is yet to be accurately estimated and will vary greatly for flocks in different environments, depending on the amount of parasite challenge experienced and the cost of adequate control strategies. To overcome this current lack of knowledge, a desired gain is assumed for disease resistance, which then allows an implied REV to be calculated for FEC. The effect of selecting for a desired gain in FEC is examined in terms of its impact on other traits in the breeding objective. The results of this type of analysis are sensitive to the genetic correlations between the restricted trait and the traits for which the aggregate merit is maximised (Brascamp 1984). The consequences of using "errored" parameters needs to be investigated and this information will assist in

deciding how much effort needs to be put into improving the accuracy of parameter estimates.

An alternative approach to that used by Ponzoni (1987) for testing the sensitivity of genetic gain to changes in phenotypic and genetic parameters, is to compare genetic response under three different scenarios. The first is predicted response when "errored" parameters are used, for example the genetic correlations between FEC and production traits currently being used are zero and these may be considered "errored" if the "true" values are found to be the estimates from Chapter 6; the second is actual response achieved where "errored" parameters are used to determine the selection policy in a population where a different set of "true" parameters exist; and the third is predicted response given the "true" parameters are known and used.

The first and third scenario involve the straightforward prediction of response as given by the following equation using the respective "errored" and "true" sets of parameters.

$$\text{Response in selection index (\$)} = i\frac{b'G}{\sqrt{b'Pb}}a$$

where P = phenotypic covariance matrix of selection criteria

G = genetic covariance matrix for selection criteria and objective traits

i = selection intensity

a = vector of economic weights

b = $P^{-1}Ga$

For the second scenario the "errored" index weights (b values) are used in conjunction with the "true" P and G matrices in the response equation, the "errored" b values being calculated from the "errored" P and G matrices. The derivation of the response formula using b values from one set of parameters with another set of parameters follows from James (1982), who shows that the correlation between an optimal index (I) and a sub-optimal index (I_A) is:

$$r_{II_A} = \frac{b' P b_A}{\sqrt{(b' P b)(b'_A P b_A)}}$$

The simulations carried out in this chapter are used to investigate the consequences of assuming zero genetic correlations between FEC and production traits, which is current practice, when a different set of "true" parameters exist in a population. A range of "true" parameters is investigated for each trait, to identify which production trait-FEC correlation has the most influence on genetic gain.

7.2 Materials and methods

The program used for predicting genetic gain (SELIND; Cunningham 1969) was modified by Hickson (1996) to allow the combination of "errored" b values with "true" P and G matrices for predicting response. The following descriptions are used for the genetic response in the three scenarios:

"Errored" prediction = predicted response when "errored" parameters are used. For example, using zero genetic correlations for FEC and production traits, to predict genetic response, may result in an "errored" prediction if they vary from the "true" parameters.

"Achieved" response = predicted response achieved where "errored" parameters are used to determine the selection policy in a population where a different set of "true" parameters exist.

"True" prediction = predicted response given the "true" parameters were known and used.

In assessing the outcome of using "errored" parameters the main comparisons were between the "errored" prediction and the "achieved" response. For each prediction there were 14 objective traits and 4 index traits (selection criteria). Trait names are as defined in Chapter 6 and are summarised in Table 7.1 with the REVs for production traits. These REVs are the same as those specified for WOOLPLAN (Ponzoni 1988) which give a 5% micron premium. The units for CFW and body weight are

percentages of the mean, rather than kg as used by Ponzoni (1988), with a standard deviation of 14% and 10% respectively. The REVs for traits measured at 16 months compared to 21 months reflect the assumptions made regarding flock structure. With the sale of surplus ewes and all wethers after shearing at 16 months of age and the greater value of fleece grown at this age, the ratio of hogget to adult REVs is lower than anticipated given the number of expressions of adult traits.

A range of implied REVs for FEC was calculated to give a specified desired gain in the "errored" prediction of response (Table 7.2). This was done by specifying the gain in FEC (as a proportion of total gain possible) and allowing the change in production traits to be optimised in accordance with their REVs. This was achieved by using the restricted index method described by Brascamp (1984). From this procedure an implied REV is calculated and, when used in index calculations in combination with the production trait REVs, ensures the specified gain in FEC. It is important to note that the relationship between these desired gains and the REVs for FEC are specific to the assumptions used in predicting trait responses. Should the genetic parameters or amount of information from relatives change, the implied REVs for a specific desired gain will also change. The genetic and phenotypic correlations and heritability used for the production traits are given in Table 7.3. One source of information was assumed for each animal, that being its own measurement.

The effect of varying the genetic correlations was assessed in terms of the impact on the aggregate economic merit of the production traits (production index), which was calculated from the response per trait in standard deviation units multiplied by the appropriately scaled relative economic value for each trait. Also presented is the effect on the desired gain in FEC of assumptions about changing genetic correlations.

In all of the predictions the "errored" parameters were defined as zero genetic correlations between FEC and production traits. These were defined as "errored" as they are the current parameters being used in breeding programs and the following analyses were designed to assess the consequences of using zero genetic correlations should the "true" values be different. The phenotypic correlations were kept at zero for all predictions as there was little evidence from results in Chapter 6 or other

published experiments that they differ from zero, and estimates of phenotypic correlations are generally very accurate.

7.2.1 Sensitivity analysis

A sensitivity analysis was carried out to determine the influence of the genetic correlation between FEC and production traits on the "achieved" response in production index. The question being asked was what is the outcome of using zero genetic correlations if the "true" values are something different, the range in "true" values being anything between -1 to +1. The production traits were grouped into four categories to reduce the number of combinations of values to be investigated. These groupings were fleece weight at all ages both clean and greasy, fibre diameter at all ages, body weight at all ages and reproduction rate. The genetic correlation of each type of trait, with FEC, was varied one grouping at a time in increments of 0.2 from -1 to +1, or until the genetic covariance matrix was non-positive definite. For example, when correlations for the fleece weight grouping were varied, all correlations between clean and greasy fleece weight at all ages had the same genetic correlation with FEC. This example is shown in Table 7.1 for the correlation of -0.4 between FEC and fleece weight.

With the range of combinations of genetic correlations being tested it was highly probable that the genetic covariance matrix for some combinations would be non-positive definite, implying that some of the assumed genetic correlations had impossible values. To assess the permissibility of each combination of genetic correlations a sub-routine, described by Hill and Thompson (1978), was added to the selection index program to test that the genetic covariance matrix was (semi)positive definite and the eigenvalues were greater than zero.

7.2.2 Comparison of zero genetic correlations with current estimates

The "true" genetic correlations of production traits with FEC investigated were those estimated in Chapter 6 for fleece and body weight traits (Table 7.1) and called the

"current" estimates. Adult body weight data were not available from the resource flocks so a value of -0.1 was assumed for the genetic correlation between this trait and FEC. This value was selected to be the same sign as the estimates for 10 month and 16 month body weight, -0.18 and -0.26 respectively, but was conservative in magnitude. Reproductive rate data from resource flocks were also unavailable, so the estimate made by Woolaston *et al.* (1991) of -0.22 was used for this trait. The estimates from Chapter 6 plus those detailed above for adult body weight and reproductive rate are referred to in the rest of this chapter as the "current" estimates, as they summarise all current estimates for Merino sheep in Australia.

7.2.3 Effect of reproductive rate correlation on production index

A further combination of parameters was investigated comprising the "current" genetic correlations between FEC and production traits but with the correlation between FEC and reproductive rate set to zero. These correlations are summarised in Table 7.1.

Table 7.2 Implied REVs for FEC to give a specified desired gain in the "errored" prediction of response

Desired gain in FEC using "errored" prediction (proportion)	Gain in FEC using "errored" prediction (trait units)	Implied REV for FEC ($)
0	0	0
0.1	0.025	-4.03
0.2	0.05	-8.18
0.3	0.075	-12.59
0.4	0.1	-17.47
0.5	0.125	-23.11
0.6	0.15	-30.02
0.7	0.175	-39.24
0.8	0.2	-53.37
0.9	0.225	-82.66

Table 7.1 Objective and index traits, phenotypic standard deviations, relative economic values and genetic correlations with FEC used to predict genetic response

Objective Trait	16 GFW	21 GFW	16 CFW	21 CFW	16 FD	21 FD	16 BW	21 BW	10 GFW	10 CFW	10 FD	10 BW	RR	FEC
Units	%	%	%	%	µm	µm	%	%	%	%	µm	%	lambs/ ewe	sd units
Phenotypic sd	14	14	14	14	1.5	1.7	10	10	14	14	1.5	10	0.6	1.0
Index trait			✔		✔		✔							✔
Economic values ($)	0	0	0.87	0.99	-4.56	-4.56	0.32	0.06	0	0	0	0	84.29	See Table 7.2
"Errored" genetic correlations	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
"True"[A] genetic correlations for sensitivity analysis	-0.40	-0.40	-0.40	-0.40	0.00	0.00	0.00	0.00	-0.40	-0.40	0.00	0.00	0.00	
"Current" or "True" genetic correlations[D] for comparison with zero estimates	-0.06	0.21	-0.05	0.07	-0.12	0.04	-0.26	-0.10[B]	0.21	0.21	-0.09	-0.18	-0.22[C]	
"Current" or "True" genetic correlations (with RR set to zero) for comparison with zero estimates	-0.06	0.21	-0.05	0.07	-0.12	0.04	-0.26	-0.10[B]	0.21	0.21	-0.09	-0.18	0.00	

[A] An example of correlations used in sensitivity analysis where traits were grouped.
[B] Assumed value as adult liveweight was not included in data from the resource flocks.
[C] From Woolaston *et al.* (1991) as reproductive rate was not included in data from the resource flocks.
[D] From Table 6.5.

7.3 Results

7.3.1 Sensitivity analysis

Permissible genetic correlations of FEC with fleece weight traits ranged from -0.6 to +0.6, and for fibre diameter, body weight traits and reproductive rate, ranged from -0.8 to +0.8. The change in aggregate merit of the production traits (production index) was symmetrical as the genetic correlation varied in absolute value either side of zero. The percentage difference in production index between the "errored" prediction and the "achieved" response is presented graphically for each trait group for genetic correlations -0.6 to +0.6 (Figures 7.1, 7.2, 7.3, 7.4). Recall that all responses are driven by index weights calculated assuming "errored" correlations of zero. Comparing the results over the same range of correlations for each trait group shows that the "achieved" response in production index is influenced to the greatest extent by the genetic correlations between FEC and fleece weight, followed by FEC and reproductive rate, then FEC and fibre diameter, and least by the correlations between FEC and body weight.

7.3.2 Comparison of zero genetic correlations with current estimates

When the "current" estimates for genetic correlations were used as the "true" parameters, the effect of using "errored" zero genetic correlations was to under-estimate the achieved response in the production index (Figure 7.5) and to under-estimate the response in FEC (Figure 7.6). The amount by which response in the production index was under-estimated increased with increasing REV for FEC and ranged from 1.5%, for a desired gain index of 10%, up to 30.3% for a desired gain index of 90%. For a 50% and 70% desired gain index, two commonly used options in Merino studs selecting for worm resistance, the under-estimate was 8.5% and 14.4%, respectively.

Table 7.3 Genetic (upper triangle) and phenotypic (lower triangle) correlations and heritability estimates (diagonal) used in predictions of genetic gain

Trait	16 GFW	21 GFW	16 CFW	21 CFW	16 FD	21 FD	16 BW	21 BW	10 GFW	10 CFW	10 FD	10 BW	RR
16GFW	**0.40**	0.75	0.80	0.60	0.20	0.25	0.10	0.00	0.75	0.60	0.20	0.10	0.10
21GFW	0.60	**0.45**	0.60	0.80	0.25	0.30	0.00	0.00	0.65	0.55	0.25	0.00	0.10
16CFW	0.85	0.50	**0.38**	0.75	0.20	0.25	0.10	0.00	0.60	0.75	0.20	0.10	0.10
21CFW	0.50	0.85	0.60	**0.42**	0.25	0.30	0.00	0.00	0.55	0.65	0.25	0.00	0.10
16FD	0.25	0.20	0.25	0.20	**0.50**	0.90	0.10	0.10	0.20	0.20	0.90	0.10	0.10
21FD	0.20	0.30	0.20	0.30	0.80	**0.55**	0.10	0.10	0.25	0.25	0.80	0.10	0.10
16BW	0.30	0.25	0.30	0.25	0.20	0.20	**0.45**	0.90	0.10	0.10	0.10	0.90	0.15
21BW	0.25	0.25	0.25	0.25	0.20	0.20	0.80	**0.35**	0.00	0.00	0.10	0.80	0.30
10GFW	0.55	0.40	0.45	0.35	0.15	0.20	0.25	0.25	**0.35**	0.80	0.20	0.10	0.10
10CFW	0.45	0.35	0.55	0.40	0.15	0.20	0.25	0.25	0.85	**0.35**	0.20	0.10	0.10
10FD	0.15	0.20	0.15	0.20	0.70	0.60	0.25	0.25	0.25	0.26	**0.50**	0.10	0.10
10BW	0.25	0.25	0.25	0.25	0.25	0.25	0.70	0.60	0.35	0.35	0.20	**0.30**	0.10
RR	0.10	0.10	0.10	0.10	0.10	0.10	0.20	0.30	0.10	0.10	0.00	0.10	**0.07**

The amount by which the response in FEC was under-estimated also varied, decreasing as FEC REV increased. The "errored" prediction of response in FEC under-estimated the "achieved" response by 151.7%, for a desired gain index of 10%, down to 8.9% for a desired gain index of 90%. For a 50% and 70% desired gain index the under-estimate were 28.0% and 16.2%, respectively.

The ratio of the contribution of each breeding objective trait to the overall index merit was consistent over the range of REVs for FEC when the genetic correlations between FEC and production traits were zero. When the "current" estimates were used (with zero correlations to construct the selection index), the ratio of the contribution of reproductive rate with the other production traits changed, with reproductive rate making a substantially greater contribution (Figure 7.7). This was partly balanced by reductions in the relative contribution of 16CFW, 21CFW and 16FD, traits which were unfavourably correlated with FEC (either directly or through their covariance with other traits). The body weight traits, which were favourably correlated with FEC, increased in contribution with increasing REV for FEC, and the contribution of 21FD remained relatively unchanged reflecting the overall neutral relationship between this trait and FEC.

7.3.3 Effect of reproductive rate correlation on production index

Changing the "true" genetic correlation between FEC and reproductive rate from -0.22 to zero had the effect of substantially reducing the difference between the "errored" prediction and the "achieved" response for both production index and FEC. The amount by which response in the production index now differed (Figure 7.8) was essentially zero across the range of REVs for FEC.

The amount by which the response in FEC was under-estimated (Figure 7.9) was reduced, being 11.7% for a desired gain index of 10%, down to 7.8% for a desired gain index of 90%. For a 50% and 70% desired gain index the under-estimates were 11.5% and 10.0%, respectively.

Once again the ratio of the contribution of each breeding objective trait to the overall index merit was consistent over the range of REVs for FEC when the genetic correlations between FEC and production traits were zero. When the "current" estimates were used, but with the reproductive rate correlation with FEC set to zero, the ratio of the contribution of reproductive rate with the other production traits was much more stable, showing only a small increase in contribution over the range of REVs for FEC (Figure 7.10). The relative contribution of other production traits was also more consistent when the correlation between FEC and reproductive rate was set to zero. Once again these changes reflect the overall relationship between FEC and each trait as defined by both the genetic correlation between FEC and the individual trait as well as the covariance between traits.

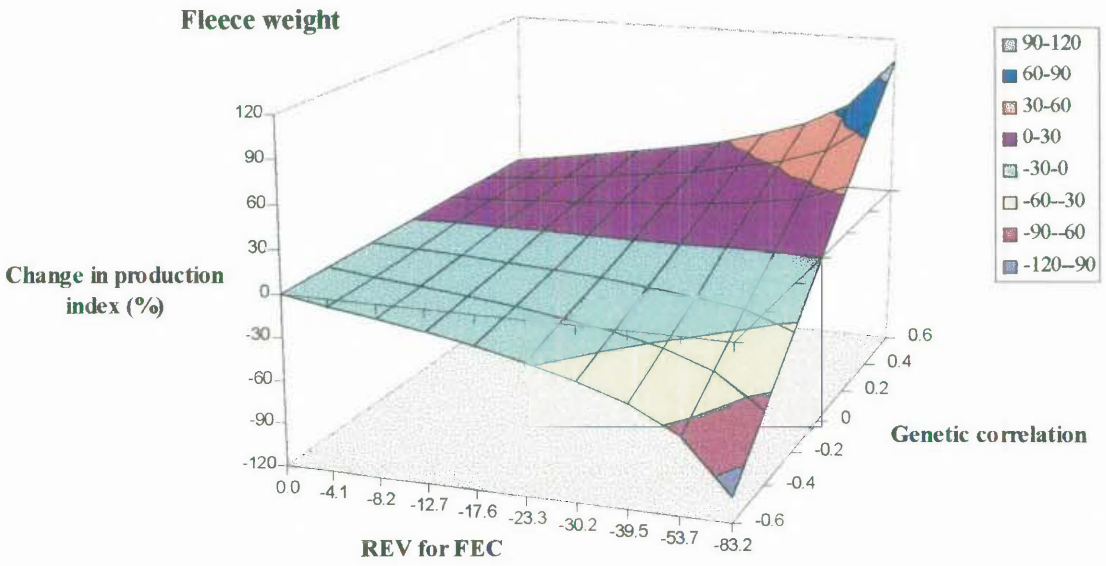

Figure 7.1 Change in production index when the genetic correlation between FEC and fleece weight traits is varied.

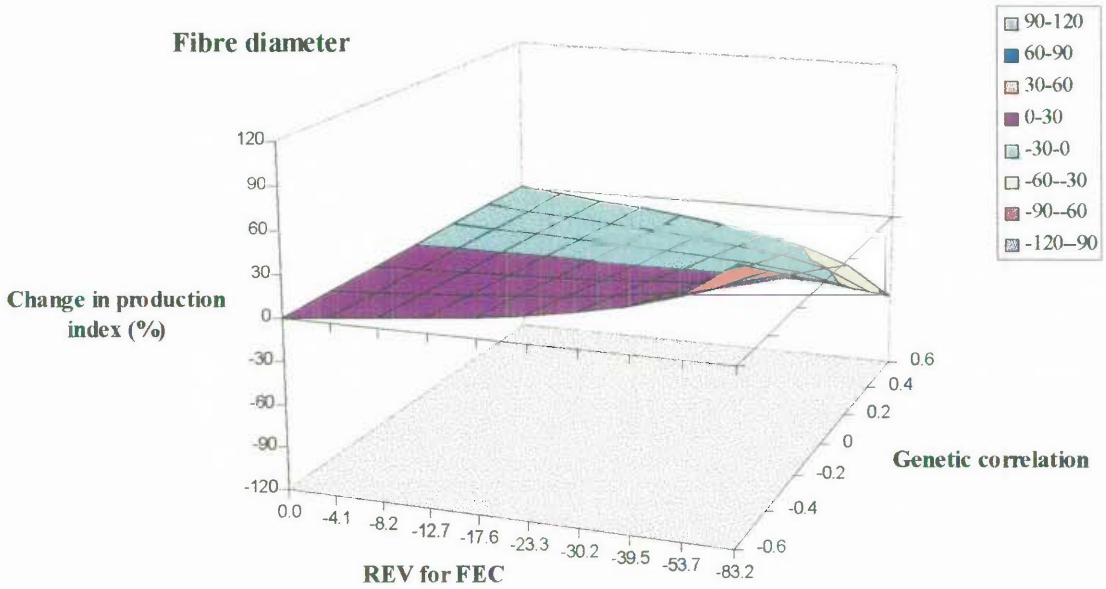

Figure 7.2 Change in production index when the genetic correlation between FEC and fibre diameter traits is varied.

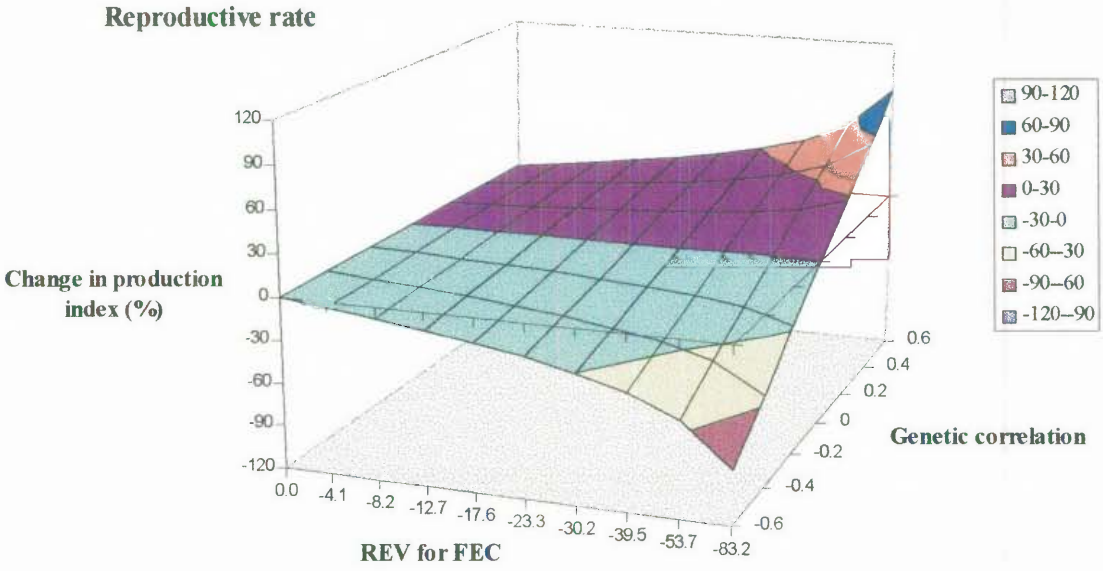

Figure 7.3 Change in production index when the genetic correlation between FEC and reproductive rate is varied.

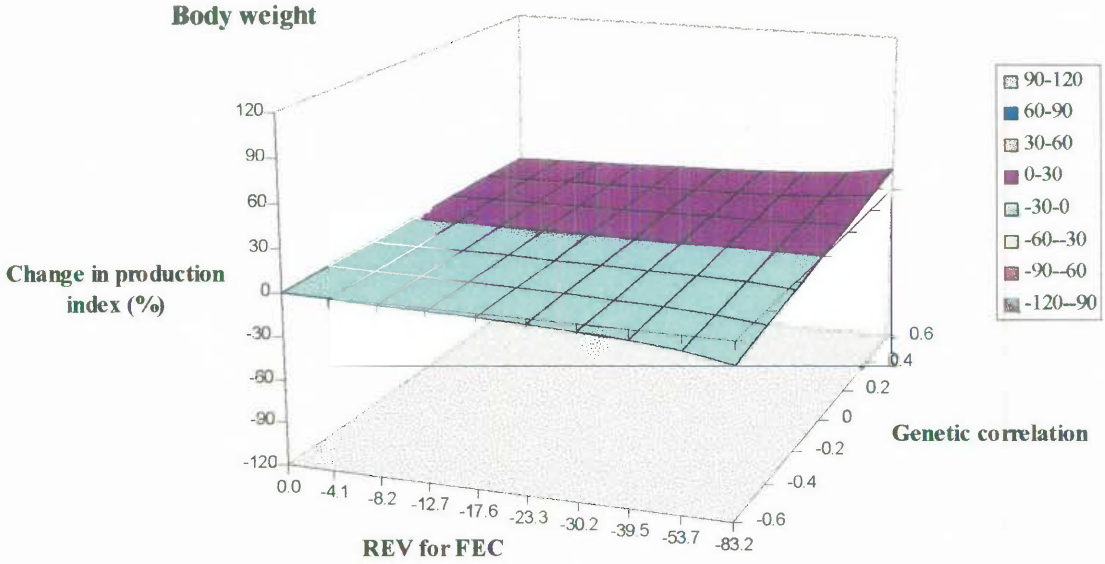

Figure 7.4 Change in production index when the genetic correlation between FEC and body weight traits is varied.

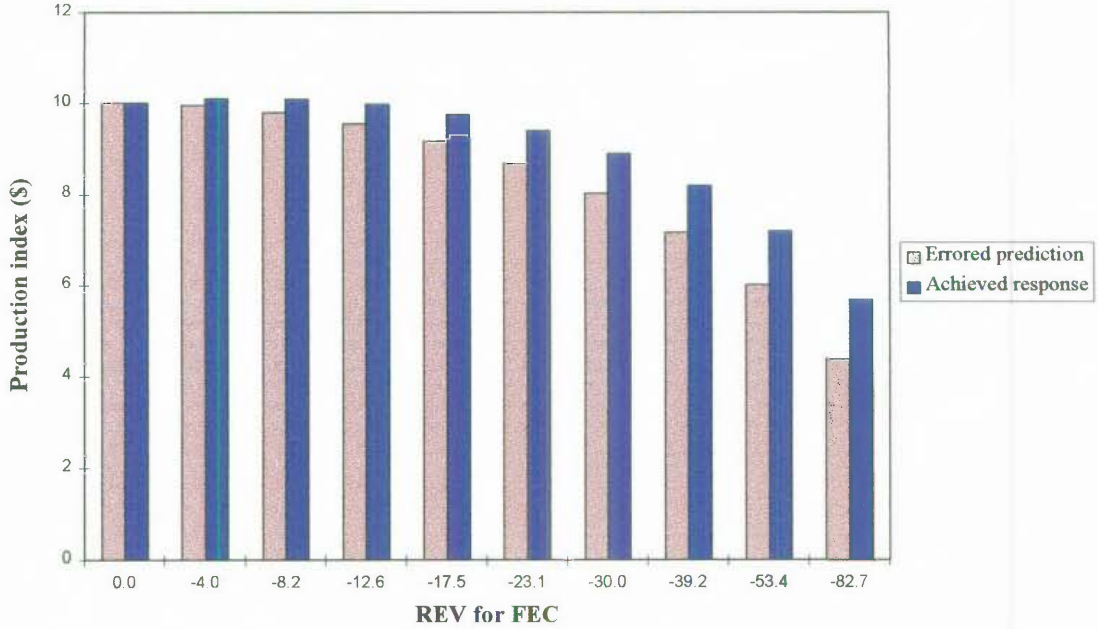

Figure 7.5 Predicted response in production index using zero genetic correlations between FEC and production traits, and actual response achieved when these "errored" parameters are used in a population where the "current" estimates are the "true" parameters.

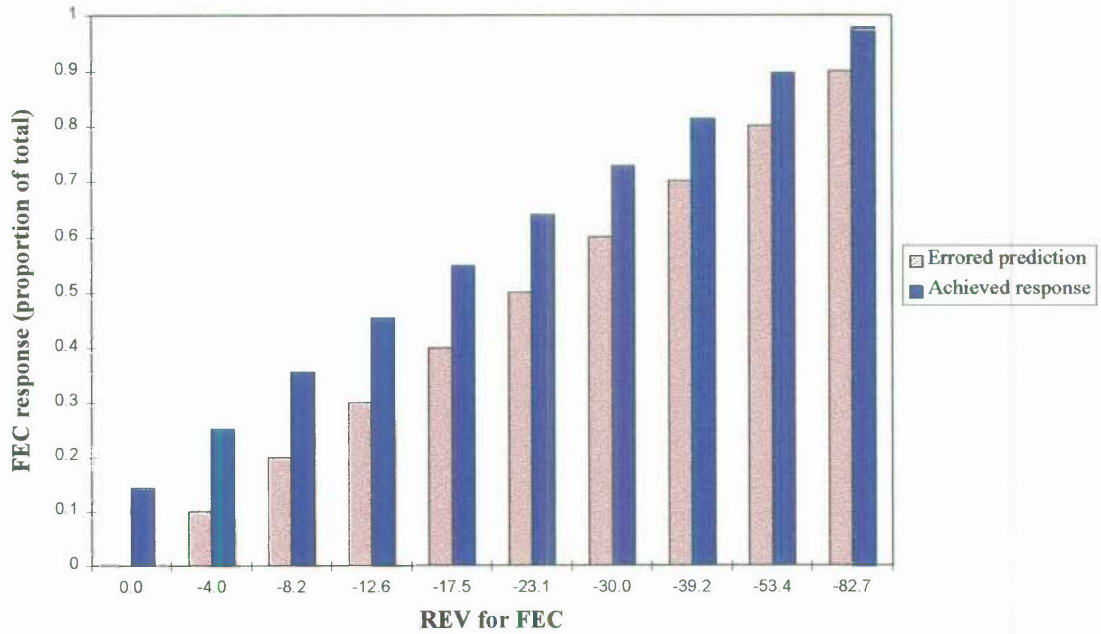

Figure 7.6 Predicted response in FEC using zero genetic correlations between FEC and production traits and actual response achieved when these "errored" parameters are used in a population where the "current" estimates are the "true" parameters.

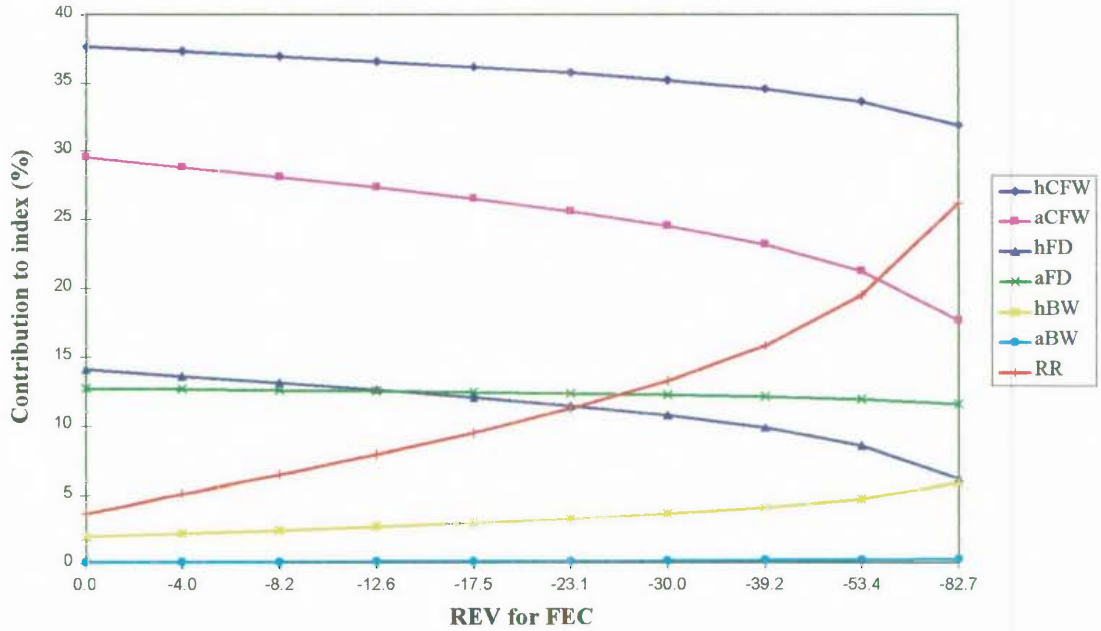

Figure 7.7 Relative contribution of each breeding objective trait to production index merit when the genetic correlations between FEC and production traits are assumed to be the "current" estimates, but with zero correlations used to construct the selection index.

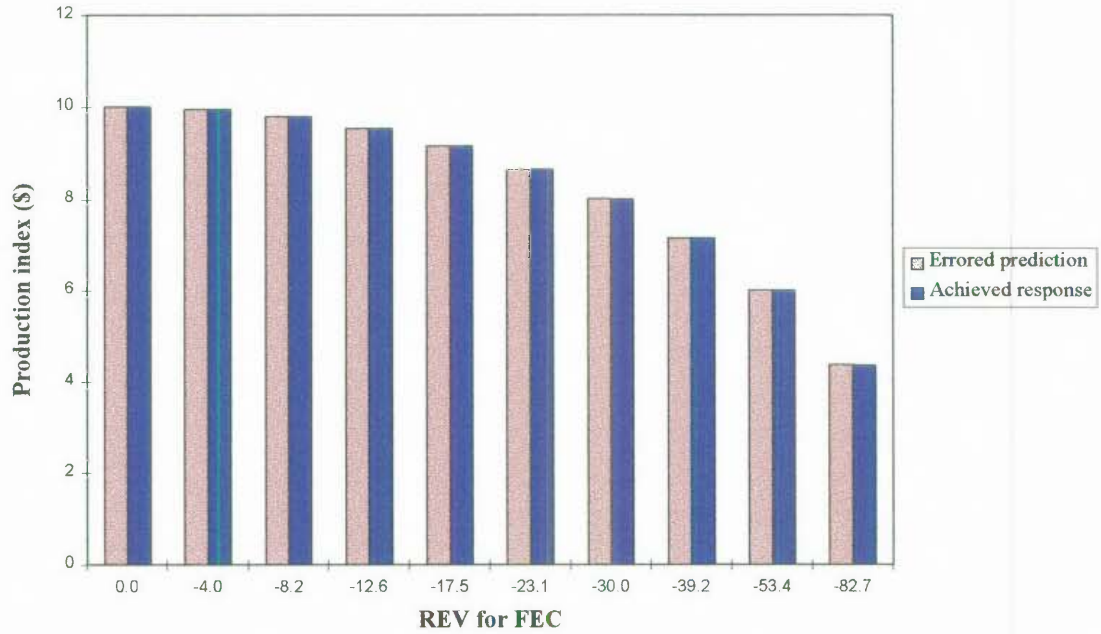

Figure 7.8 Predicted response in production index using zero genetic correlations between FEC and production traits, and actual response achieved when these "errored" parameters are used in a population where the "true" correlations for wool and body weight are the "current" estimates and zero for reproductive rate.

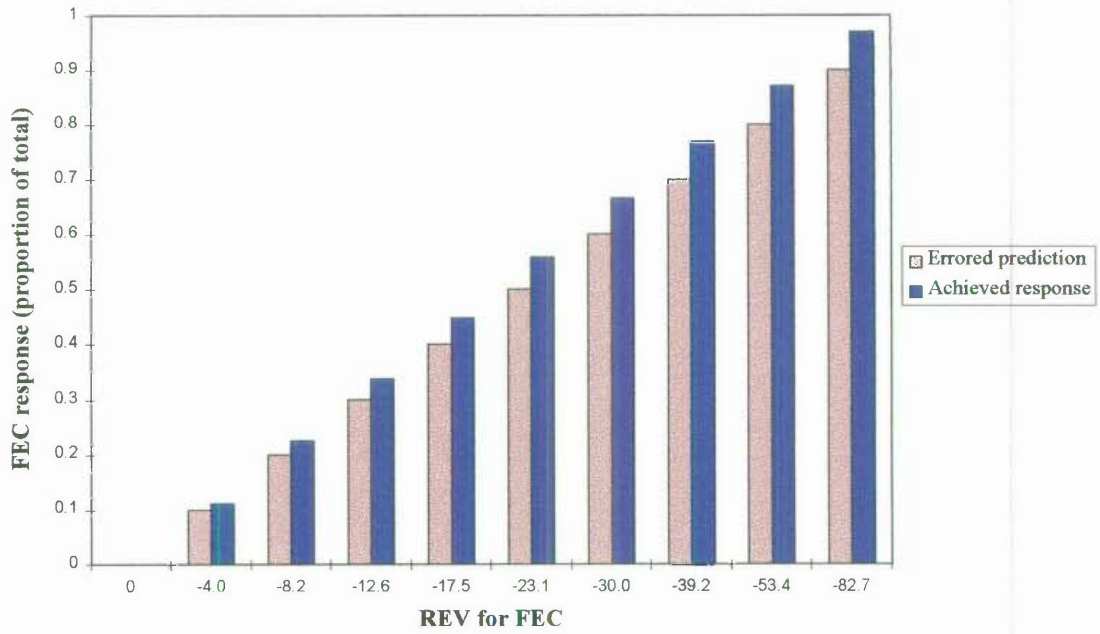

Figure 7.9 Predicted response in FEC using zero genetic correlations between FEC and production traits, and actual response achieved when these "errored" parameters are used in a population where the "true" correlations for wool and body weight are the "current" estimates and zero for reproductive rate.

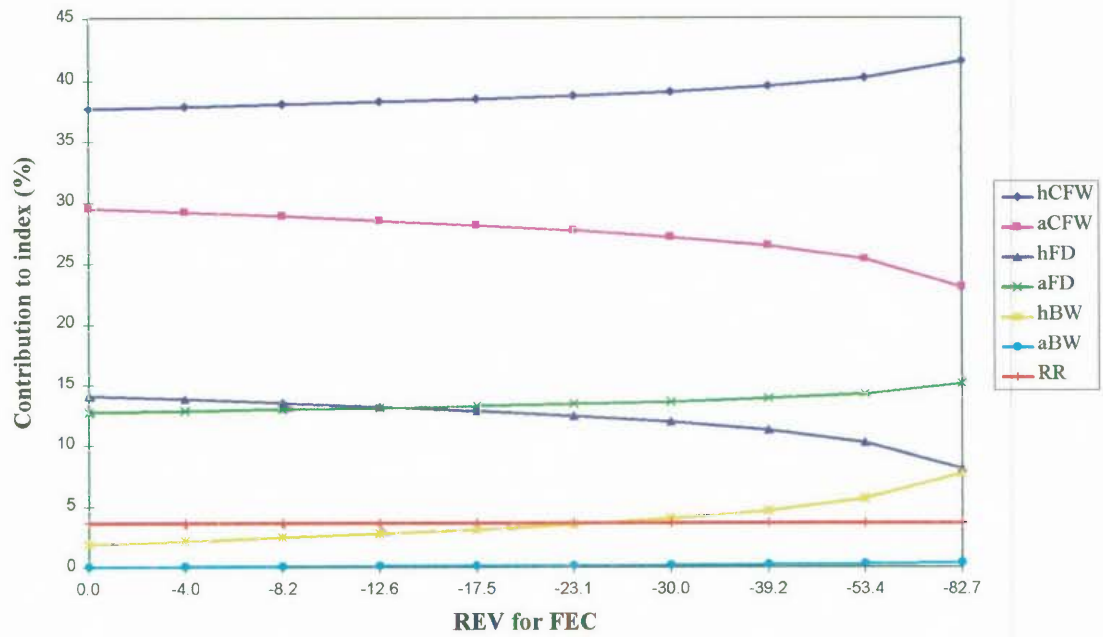

Figure 7.10 Relative contribution of each breeding objective trait to production index merit when using the "current" correlations of FEC with wool and body weight and zero for reproductive rate, but with zero correlations used to construct the selection index.

7.4 Discussion and conclusion

Given the large standard errors for current estimates of genetic correlations between production traits and FEC, it is possible that the "true" parameters in Merino flocks are quite different from the estimates reported in Chapter 6. The sensitivity analysis was undertaken to assess the importance of estimating these parameters with greater precision. Genetic gain in production traits was sensitive to changes in the genetic correlation between FEC and fleece weight traits (Figure 7.1). This result is predictable given the high REV for fleece weight compared to fibre diameter in these analyses (5% micron premium), and this result will vary depending on the relative emphasis on fleece weight and fibre diameter in the breeding objective. As expected, varying the correlation between FEC and liveweight traits (Figure 7.4) had little impact on genetic gain due to the minor importance of these traits in the breeding objective. The interesting result is the relatively large effect on genetic gain of varying the genetic correlation between FEC and reproductive rate (Figure 7.3).

Reproductive rate tends to contribute 3-4% in merit to Merino breeding objectives (Atkins 1987; Ponzoni 1987). The relative contribution of any trait to the index is a combination of the REV for the trait and the ability to achieve genetic selection differential. The latter is a function of the heritability of the trait and its variance (Smith 1983) but also the genetic relationships among traits in the objective. From these results it appears that the relatively minor contribution of reproductive rate in Merino breeding programs is more a function of the inability to change the trait through selection rather than the economic merit ascribed to the trait. The heritability of reproductive rate is low (0.07) and the trait is not strongly correlated with any of the measured index traits. As the genetic correlation between reproductive rate and FEC (which is moderately heritable) increased in the sensitivity analysis, this relationship allowed selection response for reproductive rate that was previously unavailable. The outcome was that increasing the genetic correlation between reproductive rate and FEC resulted in this previously minor trait exerting a large influence on the merit of the aggregate genotype.

This can be contrasted with the minimal effect of varying the genetic correlation between the body weight traits and FEC. Body weight is highly heritable and can be measured directly, allowing it to be included as an index trait. The minor contribution of this trait is due to the low REV assigned to it in the breeding objective rather than the inability to generate a genetic selection differential.

When using a desired gains approach, the outcome of assuming zero genetic correlations between production traits and FEC, in comparison to using the current estimates, was to under-estimate the response in production and the response in FEC. The best estimates available for the genetic correlations between FEC and production traits in Merino sheep are those summarised in Table 7.1. The correlations are low (0 to 0.2 in absolute value) and not significantly different from zero, with the exception of the body weight correlations.

The consequences of using the "errored" parameters (all zero correlations) on first appraisal appear to be relatively minor, given that the result is an under-estimate of response for both production traits and FEC. However, upon closer examination of the contribution of individual objective traits to the index (Figure 7.7 and 7.10), it becomes obvious that a single trait, reproductive rate, is exerting an overwhelming influence on the difference between the "errored" prediction and the "achieved" response (contrast Figure 7.5 with Figure 7.8). When the genetic correlation between reproductive rate and FEC is set to zero in the "true" parameters, the difference between the "errored" prediction and "achieved" response is essentially zero. This result is consistent with the sensitivity analysis, which shows that varying the genetic correlation between reproductive rate and FEC has a disproportionate effect, given the relative contribution of this trait when the REV for FEC is zero.

These results suggest that there will be little bias in predictions for production gain by assuming zero genetic correlations of FEC with wool and body weight traits in preference to the current estimates. However, predictions will under-estimate genetic change in FEC, largely due to the loss in accuracy of selection for this trait by

excluding its covariance with other traits. If there is a danger in using a zero correlation in a population where the "true" correlation is significantly different, it is to substantially under-estimate the changes that will occur in reproductive rate. This situation was demonstrated here when the correlation between FEC and reproductive rate was assumed to be significantly different from zero, but equally would occur if the "true" genetic correlation between reproductive rate and any other objective trait was greater than the assumed value. Unfortunately, reproductive rate is the most difficult trait to obtain precise parameter estimates for, because of the amount of time needed to collect records and the binary nature of the trait. However, additional estimates for this trait are essential to the adoption of a value (other than zero) to be used in breeding programs.

Excluding the favourable correlation between reproductive rate and FEC, the rest of the genetic correlations are close to neutral, in that selection for production alone results in virtually no correlated response in FEC. This reflects a balance of favourable and unfavourable correlations of FEC with fleece weight and fibre diameter at different ages. These correlations were estimated under conditions where the effects of parasitism were probably minimised by management and anthelmintic treatment. Their relevance in a breeding program for disease resistance will be determined by the prevailing environment in which production is measured.

There is a case for arguing that both phenotypic and genetic correlations may become more favourable as anthelmintic efficiency declines. There has been no evidence to date that sheep bred for helminth resistance (low FEC) express a production advantage when managed together with susceptible sheep, receiving routine management for worm control (R.R. Woolaston and R.G. Windon, unpublished data). In an environment where helminth infection is not controlled the anticipated result would be higher production from the resistant sheep, given the effect of helminth challenge and infection on wool production and liveweight in general. However, this assumes alternate strategies will not be employed to ameliorate the effects of the disease, and that sheep will be run under conditions of severe and uncontrolled parasitism. A more

likely scenario will be that alternate control strategies will be employed, but at a considerably higher cost to the sheep enterprise than the current control methods which are largely based on the use of anthelmintics. The cost, in some cases, may be a shift in enterprise mix to alternate livestock species. Under such conditions (with the exception of a change in enterprise), the current or zero estimates for genetic correlations are likely to be the most applicable.

If the environmental conditions are such that the genetic correlations remain neutral, this will have implications for the likely benefits of breeding for resistance. As demonstrated by Piper and Barger (1988), favourable genetic correlations between FEC and production resulted in significant benefits when worm resistance was included in the breeding objective, even when FEC itself had no value. If the correlations are neutral this benefit does not occur. But if the cost of maintaining adequate worm control is high the relative economic value of FEC will be substantial and it becomes an important trait in its own right. In this situation the major emphasis of future research should shift from parameter estimation, with the previously mentioned qualifications for reproductive rate, to an assessment of alternate control strategies including the potential costs of breeding for resistance and the interaction between control strategies, host immunity and the epidemiology of the host-parasite system. This needs to include the assessment of production advantages to resistant sheep when run separately from random-bred and susceptible lines.