REDUCTION IN PREDICTION ERROR VARIANCE UNDER AN ANIMAL MODEL FROM A SELECTION EXPERIMENT IN MERINO SHEEP

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SUMMARY
The reduction in prediction error variance (PEV) achieved through use of pedigree information was investigated in a selection experiment in Merino sheep. Four pairs of up and down lines were selected for Weight, Fleece, Crimp and Folds over 18 years at Trangie NSW. A major reduction in the PEV occurred in the first year and stabilised in subsequent years. The Fleece, Crimp and Folds Minus lines showed a similar pattern of PEV, while the Folds Plus had higher and the Weight lines lower PEV. The higher PEV in the Folds Plus line was due to the effect of natural selection. The PEV declined as number of progeny increased to about 8-12 in different lines and then remained steady. Inclusion of progeny information accounted for 90% to 98% of variation in the PEV in the different lines.

Key Words: selection, sheep, animal model, prediction error variance

INTRODUCTION
Animal model methodology has been increasingly used for the analysis of selection experiments after Sorenson and Kennedy (1983, 1984) showed that inclusion of the numerator relationship matrix accounted for the effects of drift and selection. Breeding values are estimated with higher accuracy using an animal model due to accumulation of information back to the base population. However the animal model is based on several assumptions and is quite sensitive to the assumption of an infinitesimal model. Greater record keeping and cost is also involved in recording for animal model analysis. Ollivier (1999) argued that, while an animal model is valid for the estimation of breeding values, it may not be appropriate for the evaluation of response and genetic variance in selection experiments. However it could be applied for checking the validity of the underlying infinitesimal additive genetic model assumption. The aim of this study was to investigate the validity of the assumption of an infinitesimal model in data from a long term selection experiment. Data from 4 up and down sheep selection lines over 18 years were analysed using an animal model. The criterion used for testing the validity of the infinitesimal assumption was the prediction error variance of the estimated breeding values. The relative effect of using all information under an animal model compared with only progeny information was also examined under a sire model by comparing the prediction error variance of sires.

MATERIALS AND METHODS
Selection lines. Pedigree data were used from 4 pairs of Merino lines selected over 18 years at Trangie, NSW. The lines were subject to up or down (Plus or Minus) single trait selection for clean fleece weight (Fleece), crimp frequency (Crimp), weaning weight (Weight) or skin folds (Folds). Each line was closed and replacement ewes and rams were bred within the line, which comprised 100 ewes with 5 new rams used each year. The general management procedures for the lines were outlined by McGuirk (1973).
**Analysis.** Prediction error variance (PEV) is independent of phenotypic values and comes from the diagonal of the inverse of the right hand side of the mixed model equation and so depends on the heritability and pedigree. The phenotypic value for each animal in each of the selection lines was generated using a random number generator. These phenotypic values were combined with the actual pedigree data of each of the lines. The program Pest (Groeneveld 1990) was used to analyse the data. The data are described in the following linear model:

\[
y_{ijk} = \mu + A_i + T_j + S_k + E_{ijk}
\]

\(y_{ijk}\) is the observation on animal i in year j with sex k, \(\mu\) is the overall mean of the population, \(A_i\) is the random effect of the \(i^{th}\) animal, \(T_j\) is the fixed effect of \(j^{th}\) year, \(S_k\) is the fixed effect of \(k^{th}\) sex.

Heritabilities of 0.27, 0.45, 0.47 and 0.47 were used for weaning weight, fold score, clean fleece weight and crimp frequency respectively.

The accuracy of the progeny testing depends on the number of progeny measured per sire and the heritability of the trait under selection. This accuracy can be expressed mathematically as the correlation between the estimated breeding value and the true breeding value of the animal (\(r_{a'a}\)).

\[
r_{a'a} = \sqrt{\frac{n}{n + \lambda}}
\]

Where n is the effective number of progeny tested and \(\lambda = (4 - h^2)/h^2\) and \(h^2\) is the heritability of the trait under assessment. It was assumed that there is no non-genetic correlation among the progeny.

\[
r_{a'a} = \frac{\text{cov}(a'a')}{\sigma_{a'a}} = \frac{\sigma_{a'a}}{\sigma_a^2} = \frac{\sigma_{a'a}}{\sigma_a^2}
\]

With substitution of \(r_{a'a}\) then

\[
PEV = \sigma_a^2 (1 - \frac{\sigma_{a'a}}{\sigma_a^2}) = \sigma_a^2 (\frac{1}{h^2n})
\]

**RESULTS AND DISCUSSION**

The PEV declined sharply in the first year and then stabilised for the rest of the period in all of the selected lines (Figure 1). The weight lines (Plus and Minus) showed smaller PEV across years compared with the other lines. The Folds Plus line showed a higher PEV after the third year, compared with the other lines. The reduction in the PEV or increase in the accuracy of estimation of breeding values in the first year is due to the inclusion of additional information from both parents compared with the animals selected from the base population which have no parental information. The PEV did not decline further after the first year. Sires were only used in one year so no additional information is available through sire family across years. Accumulation of information for individuals comes mainly through pedigree and for some individuals through dam family. This contribution is small relative to the information provided by individual records due to medium to highheritability of these traits.
The PEV declined as progeny number increased to about 8 to 12 in the different lines, Weight and Folds (Figure 2) and Fleece and Crimp (Figure 3). The observed pattern of PEV in the Fleece, Crimp and Folds Minus lines is consistent with that expected from the theory (eg. Falconer, 1985), but not so the Folds Plus line. The Folds Plus line showed a higher PEV beyond 6 progeny. This discrepancy could be explained by the effect of natural selection against animals with the high folds score (McGuirk 1976; Crook 1992). The consequent smaller effective number of sires in the Folds Plus line led to higher inbreeding (Safari and James, 1995) and greater PEV. Another factor is the smaller average number of offspring in the Folds Plus line compared with the other flocks (61 compared with the average of 80 for the others), which corresponds to a smaller number of relatives and consequently higher PEV. The lower PEV for the Weight Plus and Weight are expected because of the lower heritability used, which means progeny performance has a relatively greater contribution to information.

The observed inbreeding in the Fleece Plus line was lower than that in the other lines (Safari & James 1995). This was expected to result in a higher PEV than in the other lines, but the observed PEV was very similar to the Crimps, Fleece Minus and Folds Minus lines. This discrepancy suggests that the assumption of additivity and an infinitesimal model is not justified in the case of the Fleece Plus line.

The importance of evaluation based on progeny testing was indicated by the ratio of sums of squares for progeny testing to the sums of squares due to progeny testing plus sums of squares due to fitting number of progeny after fitting progeny testing in the model. This ratio ranged between 96.7% and 98% in the group of Fleece, Folds and Crimp lines, while in the Weight lines it was between 89.5% and 93%. This shows that progeny testing is the main factor in increasing accuracy of estimated breeding values. It also highlights that an animal model and accumulation of information does not necessarily lead to a higher accuracy of estimated breeding values.

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REFERENCES
Figure 1. Prediction error variance (PEV) across years in weight selected lines.

Figure 2. Prediction error variance across number of progeny in weight and fleece lines.

Figure 3. Prediction error variance across number of progeny in fleece and crimp lines.