A CONTINUOUS-VARIATE ANALYSIS OF REPEATED MEASURES IN SHEEP

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SUMMARY

Phenotypic and additive genetic covariance functions were estimated from covariance matrices of repeated measures of sheep production traits. The results of these analyses highlight a major shortcoming of traditional estimates of phenotypic variances, namely that they are often substantially overestimated. Analysis of the additive genetic covariance functions indicated that selection for body weight and fleece traits in sheep at any age will result in improvement at all ages.
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INTRODUCTION

Conventional quantitative genetic analyses treat the performance at each age at which measurements are taken as a distinct trait or (with a repeatability model) as distinct repeated performances of the same trait. However, it would be far closer to reality if the full continuous nature of those performances were considered. The 'infinite-dimension' approach, pioneered by Kirkpatrick and Heckman (1989), Kirkpatrick *et al.* (1990), Kirkpatrick and Lofsvold (1992) and Kirkpatrick *et al.* (1994), does just that. It involves estimation of a covariance function from the estimated covariance matrix, and it can be applied to both phenotypic and additive genetic covariances. There are several advantages to this approach. First, it enables the removal of upwards biases in the estimation of variances. These biases (due to measurement and other temporary environmental factors) are inevitable in the traditional estimation of variances, but do not occur in traditional estimation of covariances, thereby introducing a 'ridge' along the diagonal of traditionally-estimated covariance matrices. Estimation of a covariance function enables the removal of this ridge. Second, it enables estimation of the (co)variance between performance at any two ages, even if no animals were measured at either age. Third, it enables the fitting of 'reduced' covariance functions, which provide a smoother covariance surface, described with fewer parameters. Fourth, by studying additive genetic covariance functions, it is possible to draw conclusions about the pattern of additive genetic variation during the lifetime of animals. The initial application of infinite-dimension analysis involved body weight in Chios and synthetic sheep for a limited number and range of ages (birth to 20 weeks of ages) by Kirkpatrick and Lofsvold (1992) and lactation records in dairy data (one to ten months) by Kirkpatrick *et al.* (1994). In this paper, we report the first use of infinite-dimension analysis in Merino sheep.

MATERIALS AND METHODS

Using the REML procedure on data from a flock of Australian Merino sheep (Torshizi 1996), estimates were obtained of additive genetic and phenotypic covariance matrices of performances of body weight (BW) measured at birth, 4, 10, 16 and 22 months of age; greasy fleece production

(GFP) measured at 4, 10, 16 and 22 months of age; and clean fleece production (CFP) and mean fibre diameter (MFD) measured at 10, 16 and 22 months of age. Following Kirkpatrick *et al.* (1990), covariance functions were estimated from these matrices by fitting Legendre polynomials as orthogonal functions. The actual methodology, involving the use of asymmetric coefficients, is described in detail by Kirkpatrick *et al.* (1994). In these initial calculations, the number of polynomials equalled the number of ages actually measured (5 for BW, 4 for GFP, and 3 for CFP and MFD) giving rise to a so-called 'full' fit.

If the 'full-fit' phenotypic covariance surface showed a ridge along the diagonal, indicating upwards biases in the original estimates of variances, a method known as 'extrapolating to the diagonal' was used to re-estimate phenotypic covariance functions using one fewer polynomial, resulting in 'full extrapolated' phenotypic covariance functions (Kirkpatrick *et al.* 1994). In this method, the phenotypic covariance function was estimated after excluding diagonal elements of the original covariance matrix. Excluding the diagonal elements reduces by one the number of polynomials fitted. We then followed Kirkpatrick *et al.* (1990) and re-estimated the phenotypic covariance functions with even fewer polynomials, thereby fitting 'reduced extrapolated' functions. The aim was to obtain phenotypic covariance functions using as few polynomials as possible (to obtain the smoothest possible covariance surface), but which still give phenotypic covariance estimates similar to those in the original matrices. Unfortunately, for phenotypic functions there is no statistical test available for testing the degree of similarity (Kirkpatrick *et al.* 1994). Accordingly, the degree of similarity was assessed subjectively.

For additive genetic covariance functions, extrapolating to the diagonal is not appropriate (Kirkpatrick *et al.* 1994), but the fitting of reduced models is. For additive genetic functions, this task required estimates of the (co)variances of the original genetic (co)variances, which were estimated, following Kirkpatrick *et al.* (1990), by assuming that the original data was obtained from a balanced design, in this case a paternal half-sib design with 157 random sires, each with 25 offspring, and a total of 4260 residual degrees of freedom. Since the sheep measured in this trial came from a breeding programme that had been specifically designed for the estimation of quantitative genetic parameters (Torshizi 1996), the above assumption was not too far from reality. Following Kirkpatrick *et al.* (1990), chi-squared tests were used to compare the additive genetic covariances resulting from reduced models with the covariances in the original matrices. A calculated ^{2} higher than the tabulated value indicates that the difference between the reduced estimate of the covariance function and the original covariance matrix is significant, and thus the reduced estimate should be rejected. The most reduced function that still provided estimates consistent with the original (co)variances is called the preferred function. If none of the reduced functions is satisfactory, the preferred function is the full extrapolated function (in the case of phenotypic functions) and the full function (in the case of additive genetic functions).

The nature of the genetic variation in the population was determined through decomposing the covariance function into its components, *i.e.* eigenfunctions, and eigenvalues, which are analogous to the principal components in a standard multivariate analysis (Kirkpatrick and Heckman 1989). The eigenvalues indicate the relative proportion of additive genetic variance in the population

attributable to the corresponding eigenfunctions. In other words, the relative magnitude of each eigenvalue in relation to the total of all eigenvalues indicates the contribution of that eigenfunction to the total genetic variation. If, for example, the leading eigenvalue is a large proportion of the total of all eigenvalues, then the first eigenfunction explains an equally large proportion of available genetic variation.

RESULTS AND DISCUSSION

Estimates of phenotypic covariance functions. The estimates of the preferred phenotypic covariance functions obtained for body weight and fleece traits, are plotted in Figures 1a to 1d. For BW (plot a) and GFP (plot b), a reduced extrapolated function (with 2 polynomials fitted) resulted in the best fit. The discrepancy between the covariance function and the original variance estimates (i.e., discrepancies along the diagonal) were substantial (up to 64% and 68%, respectively). For CFP (plot c) and MFD (plot d), the full extrapolated function (with 2 polynomials fitted) removed the diagonal upwards biases, which ranged from 29% to 52% and 14% to 26%, respectively. These results clearly show that the phenotypic variances have been overestimated in the original analysis. Similar results were reported by Kirkpatrick *et al.* (1994) for lactation records in dairy cattle. However, the extent of overestimation in the sheep data was substantially higher than in the dairy data (up to 68% compared with 36%).

Estimates of additive genetic covariance functions. The estimates of the preferred additive genetic covariance functions are plotted in Figures 1e to 1h. For BW, none of the reduced models produced a satisfactory additive genetic covariance function. Using a reduced model with 4, 3 and 2 polynomials gave $^{2}_{(DF=5)}$ equal to 19.5, 25.3, and 50.0 ($P < 0.003$ for all cases). Although the shape of the function looked smoother than with a full model (results not shown), there were large discrepancies between these estimates and the original covariance matrix (up to 60%). Consequently, only full-model estimates were consistent with the original covariance matrix. The results for GFP indicate that a reduced function with 3 polynomials (plot f) produces a smoother function than a full model. The goodness-of-fit test for this function gave $^{2}_{(DF=4)} = 5.0$ ($P = 0.288$). The actual differences were less than 15%. For CFP, fitting a reduced model with 2 polynomials gave a smoother function (plot g) compared with full model. However, the goodness-of-fit tests indicated significant differences from the original covariance estimates ($^{2}_{(DF=3)} = 10.9$; $P = 0.012$). However, since the discrepancies were relatively low (a maximum of 13%), a reduced model may be acceptable (Kirkpatrick *et al.* 1994). A similar pattern was observed for MFD (plot h), where the discrepancies between the reduced-model estimate (using 2 polynomials) and the original covariances were relatively low (less than 19%), despite the good-of-fit test indicating significant differences ($^{2}_{(DF=3)} = 21.4$; $P < 0.001$). In this case, again following the philosophy of Kirkpatrick *et al.* (1994), it was decided to prefer the reduced function.

The question whether it is possible to decrease the number of repeated records which are measured for repeatable traits may be answered by considering different performances as infinite-dimensional characters. The analysis of the preferred additive genetic function for BW and GFP indicated that approximately 87% of total additive genetic variance for each of these traits is associated with the first eigenfunction. The proportion of additive genetic variation in CFP and MFD attributable to the

leading eigenfunction was about 98% of total additive genetic variation. These high percentages suggest that there is no tradeoff between early and later measurements for any of these traits, *i.e.*, selection at any age results in improvement at all ages.

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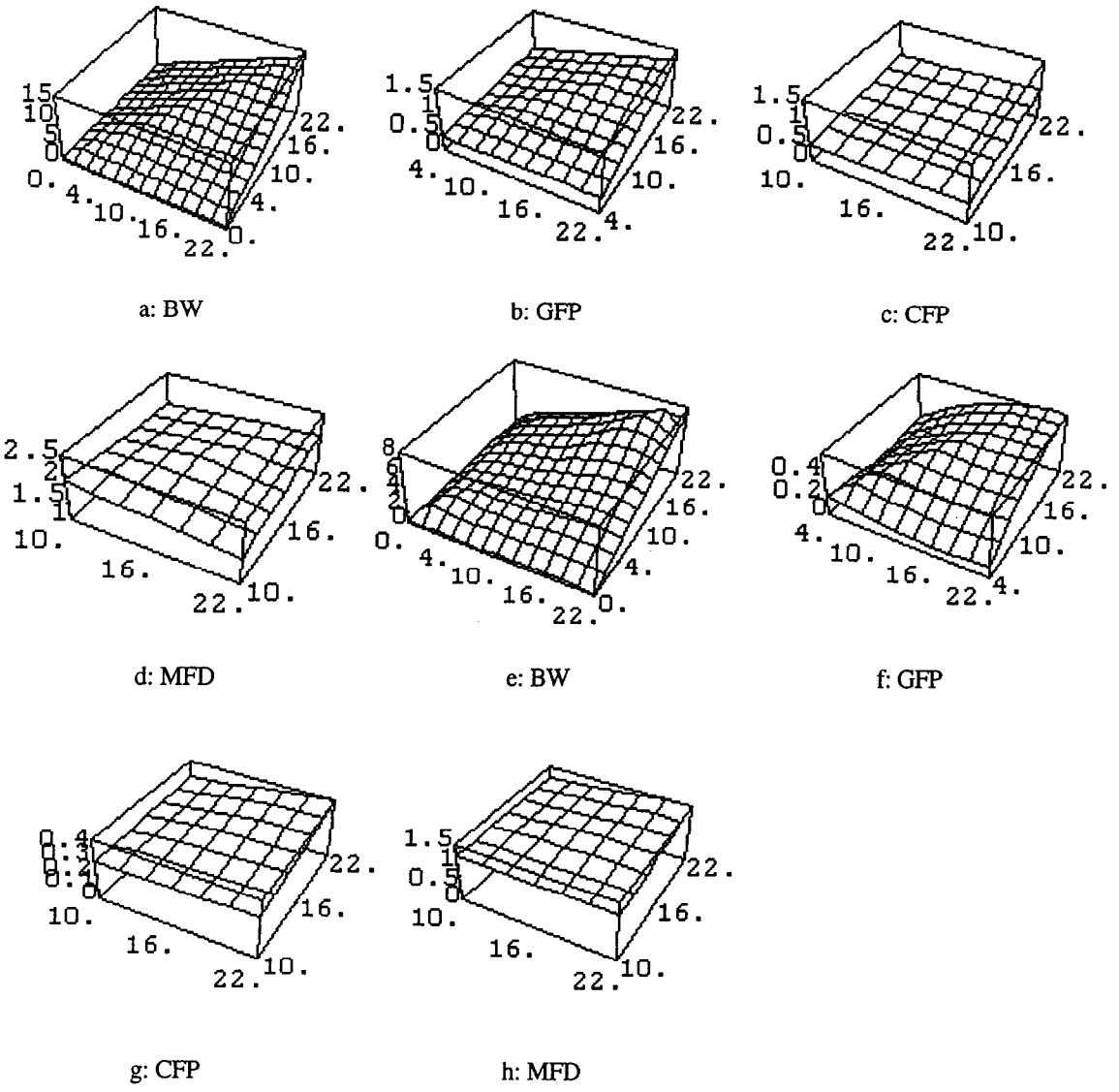

Figure 1. Estimates of the preferred phenotypic and additive genetic covariance functions for production traits in Merino sheep (in each plot, x axis is age in months and y axis is (co)variance).