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Design of multivariate selection experiments to estimate genetic parameters

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Summary. The precision of estimates of genetic variances and covariances obtained from multivariate selection experiments of various designs are discussed. The efficiencies of experimental designs are compared using criteria based on a confidence region of the estimated genetic parameters, with estimation using both responses and selection differentials and offspring-parent regression. A good selection criterion is shown to be to select individuals as parents using an index of the sums of squares and crossproducts of the phenotypic measurements. Formulae are given for the optimum selection proportion when the relative numbers of individuals in the parent and progeny generations are fixed or variable. Although the optimum depends on "a priori" knowledge of the genetic parameters to be estimated, the designs are very robust to poor estimates. For bivariate uncorrelated data, the variance of the estimated genetic parameters can be reduced by approximately 0.4 relative to designs of a more conventional nature when half of the individuals are selected on one trait and half on the other trait. There are larger reductions in variances if the traits are correlated.

Key words: Experimental design – Genetic parameter estimation – Multiple traits – Selection – Canonical variates

Introduction

Precise, unbiased estimates of genetic parameters, such as heritability and genetic correlations, are necessary to optimise breeding programs and to predict rates of change for various selection schemes. These parameters can be estimated from the covariance among collateral relatives or from the regression of the progeny performance on that of their parents. Appropriate equations for the variances of these estimates obtained by such methods are well documented (e.g. Falconer 1981). Equations for calculating the variance of heritability estimates derived from single-trait selection experiments for various designs have been derived by Hill (1971).

One experimental design objective in single-trait selection experiments is to minimise the variance of the heritability estimate which is influenced by factors such as population size, selection intensity, family size, the genetic and phenotypic parameters and the number of generations of selection. Using prior information about the parameters of interest, efficient selection experiments can be designed to obtain precise, unbiased estimates of the parameters using the equations of Hill (1971).

When dealing with two or more traits, the genetic variances and covariances are parameters of interest and, as Thompson (1976) has noted, it is not obvious what the optimal design objective should be. Robertson (1959) and Tallis (1959) discussed the sampling variance of the genetic correlation coefficient and suggested that designs which are efficient for heritability estimation are also efficient for estimation of genetic correlations. For two traits, individuals in the parental generation could be split into two groups, selecting high and low within one group for trait X_1 and selecting high and low within the other group for trait X_2 (Reeve 1955) and studying either the regression of offspring traits on traits of the selected parents or the direct and correlated responses to selection. However, this may not be the most efficient design in an overall sense. Indices using both traits could be used as the selection criteria, rather than selecting directly on the traits measured. However, Gunsett et al. (1984) suggest a strong dependency of the design efficiency on the index weights used. We discuss these techniques for estimating genetic variances and covariances for two traits and compare the efficiencies of different selection designs.

We consider, in detail, two generation selection experiments when parental observations are only taken on one sex. A different experimental design to the classical high-low individual selection method is examined and it is shown to be more efficient and robust.

Optimality criteria

Given a regression problem, $Y = X\beta + e$, where Y is a vector of the dependent variable, X is the design matrix for the independent variables and e is the vector of residuals with variance-covariance matrix V, then the confidence ellipsoid of the generalised least squares estimate $\hat{\beta}$ of β, $\hat{\beta} = (X'V^{-1}X)^{-1}X'V^{-1}Y$, with variance $(X'V^{-1}X)^{-1}$, has the form

$$[\beta\colon (\beta - \hat{\beta})'X'V^{-1}X(\beta - \hat{\beta}) < \text{constant}]$$

for any specified confidence coefficient. The content of the ellipsoid (e.g. volume in three dimensions) is proportional to $|X'V^{-1}X|^{-1/2}$. Therefore one design criterion is to minimise the content of the ellipsoid or to maximise $|X'V^{-1}X|$, the D-optimality criterion (Silvey 1980). The determinant of $X'V^{-1}X$ will be denoted by $\mathrm{DET}(\beta)$. The D-optimality criterion has the useful invariance property that if a design X maximises $\mathrm{DET}(\beta)$, then the same design X also maximises $\mathrm{DET}(T^*\beta)$, where T^* is a full rank transformation matrix. Therefore, a design that is optimal for estimation of β is also optimal for a linear transformation, $T^*\beta$, of β. There are other overall criteria; for example, to maximise the trace of $X'V^{-1}X$ (the sum of the diagonal elements of the matrix) or to maximise the minimum eigenvalue of $X'V^{-1}X$, but these do not have this invariance property.

Standardisation of traits

The genetic and phenotypic variance-covariance matrices for the traits will be denoted by G and P, respectively. We consider cases of standardised traits, with mean zero, when the diagonal elements of the P matrix are equal to one and assume that the traits are normally distributed. The methods and designs considered can be applied to multivariate data but are developed using bivariate data. The genetic variances and covariances of the standardised traits are then heritabilities (h_1^2 and h_2^2) and co-heritabilities ($r_A h_1 h_2$ where r_A is the genetic correlation between the two traits). In the estimation of these parameters, it is convenient to work in terms of the vector $\beta' = 0.5\ [h_1^2\ \ r_A h_1 h_2\ \ h_2^2[$ rather than the (2×2) symmetric matrix of genetic variances and covariances.

There is no loss of generality from standardising the traits, for if the diagonal elements of the P matrix are not equal to one, then the phenotypic variables can be standardised using a transformation, T^*, with the result that the genetic variance-covariance matrix of the transformed variables is $T^*GT^{*\prime}$. The invariance argument for D-optimality shows that a D-optimal design for the parameter β is also D-optimal for the parameters in $T^*GT^{*\prime}$.

Further, we assume that errors in the phenotypic matrix P can be neglected, either because there is adequate previous data or parental data on which to base estimation of P. The emphasis, within this paper, is on comparing estimation procedures and suggesting designs for genetic parameter estimation and so this assumption should have a negligible effect on the conclusions. Certainly, our formulation leads to known results on univariate heritability estimation.

Estimation and design from response to divergent truncation selection

A common method of estimating genetic parameters for two traits, from divergent truncation selection experiments, is to have two selection groups using a different selection index in each group and measure the selection differentials and the correlated responses for the two traits on both selection indices (Falconer 1981). For each of the selection indices, I_m $(m = 1, 2)$, assume a total of M unrelated individuals are measured for both traits and a proportion p with the highest and p with the lowest index values are selected, such that $pM = N$. A total of RM progeny are reared and recorded and with equal family sizes there are $n = R/2p$ progeny per family. Let i and x be the expected selection differential and abscissa on the standardised normal curve corresponding to p and assume equal selection differentials in the two groups. Note that the upper and lower cases of the letter I denote different parameters, however this is standard notation (Falconer 1981).

Initially alternative estimation procedures and designs will be considered for fixed experimental resources. Later, optimisation of the selection proportion, p, family size, n, and the relative proportion of offspring generation measurements to parental generation measurements, R, will be discussed.

It is of interest to consider the possible combinations of selection weights for the two indices. If a selection index $I_m = b_{1m}x_1 + b_{2m}x_2$, then

$$\begin{aligned} I_m &\equiv \left(b_{1m}/\sqrt{b_{1m}^2 + b_{2m}^2}\right)x_1 + \left(b_{2m}/\sqrt{b_{1m}^2 + b_{2m}^2}\right)x_2 \\ &= x_1\cos\theta_m + x_2\sin\theta_m \end{aligned}$$

selects the same individuals, where x_j and b_{jm} are the standardised phenotypic values and index weights of the j^{th} trait for the m^{th} index respectively and $\tan\theta_m = b_{2m}/b_{1m}$. Each selection index is characterised by a single parameter θ_m. By symmetry only the values of θ_m in the range 0° to 180° need consideration. Graphically, the line $x_1 \cos\theta_m + x_2 \sin\theta_m = 0$ makes an angle θ_m with the x_1 axis.

The expected genetic response, ΔG_{jm}, in the progeny for trait j due to selection on index m, is given by the product of the regression of the additive genotype of the j^{th} trait on the phenotype of the m^{th} index and the selection differential (SD_m) of the m^{th} index. Thus $\Delta G_{jm} = 0.5\,(b_{jm}\,\sigma_{jj} + b_{km}\,\sigma_{jk})\,SD_m/\mathrm{var}(I_m)$ where σ_{jj} and σ_{jk} are, respectively, the genetic variance for trait j and genetic covariance for traits j and k ($j = 1, 2$; $k = 3 - j$) and var (I_m) is the variance of the m^{th} index. The selection differential for the m^{th} index is calculated as the difference in mean index value between the high and low parental lines. The response in each trait can be estimated as the difference between the high and low progeny lines. The index weights b_{jm} are usually determined by biological arguments about the traits or the desired direction of the response (Eisen 1977). The responses of trait j in selection group m can be written in the form of a regression model, regressing responses in the two measured traits on selection differentials of the indices.

$$\begin{bmatrix}\Delta G_{1m}\\ \Delta G_{2m}\end{bmatrix} = \begin{bmatrix} b_{1m}\,SD_m/\mathrm{var}(I_m) & b_{2m}\,SD_m/\mathrm{var}(I_m) & 0 \\ 0 & b_{1m}\,SD_m/\mathrm{var}(I_m) & b_{2m}\,SD_m/\mathrm{var}(I_m)\end{bmatrix}\beta + [e]$$

or $Y = X\beta + e$. The model can also be defined in terms of selection differentials for each measured trait (SD_{jm}),

$$\begin{bmatrix}\Delta G_{1m}\\ \Delta G_{2m}\end{bmatrix} = \frac{1}{(1 - r_p^2)}\begin{bmatrix} SD_{1m} - r_p\,SD_{2m} & -r_p\,SD_{1m} + SD_{2m} & 0 \\ & SD_{1m} - r_p\,SD_{2m} & -r_p\,SD_{1m} + SD_{2m}\end{bmatrix}\beta + [e]$$

where r_p is the phenotypic correlation between the two traits. Alternatively, using the expected value of SD_m, the expected value of the design matrix X can be conveniently written using the angles θ_m,

$$\frac{2i}{\sigma_{Im}}\begin{bmatrix}\cos\theta_m & \sin\theta_m & 0\\ 0 & \cos\theta_m & \sin\theta_m\end{bmatrix} \tag{1}$$

for each index, where σ_{Im} is the standard deviation of the m^{th} index.

The residuals within lines are correlated, due to the family structure of the design, but there is no correlation of residuals between lines. The 4×4 variance-covariance matrix (V) of the residuals is therefore symmetric and block diagonal

$$V = f\begin{bmatrix}F & 0\\ 0 & F\end{bmatrix}. \tag{2}$$

The matrix F represents the 2×2 variance-covariance of a family mean after regressing on parental values and the factor f relates the variance of the mean genetic response for one index to the variance of a family mean. With response/selection differential estimation, there are N parents in each of the selected high and low lines, therefore $f = 2/N$.

The structure of F can be derived using the equations of Hill (1971) for the variance of residuals from single-trait selection. The variance for one progeny mean is

$$F = [(r_{oo}\,G - r_{op}\,G\,P^{-1}\,G\,r_{op}) + (P - r_{oo}\,G)/n] \tag{3}$$

where r_{oo} and r_{op} Wright's coefficients of relationship for progeny of the same parent and for progeny with parent respectively. Note that the first term in equation (3) is the variance of a family genotypic mean about the regression (drift variance) and the second term is the variance of measurement error in the family mean value. For example, in single-trait selection on parents of one sex with half-sib families

$$G = h^2, \quad P = 1.0, \quad r_{oo} = 0.25, \quad r_{op} = 0.5$$

and

$$F = [0.25\,h^2(1 - h^2) + (1 - 0.25\,h^2)/n].$$

Gunsett et al. (1982, 1984) gave similar formulae for V, however their genetic drift term does not include any genetic relationship parameters (r_{oo}, r_{op}) and their measurement error term does not have the divisor of the number of parents in each index.

Investigation of DET(β) and calculation of the inverse of V would be simpler if the matrix F was diagonal. As the matrix F is a function of the genetic and phenotypic variance-covariance matrices, transformation to independent traits would diagonalise F. Such a transformation exists and is often called a canonical transformation (Rao 1973). Let S* be the transformation matrix from the original scale to the canonical scale, such that

$$\begin{bmatrix}C_1\\ C_2\end{bmatrix} = S^*\begin{bmatrix}x_1\\ x_2\end{bmatrix}$$

where C_1 and C_2 are the canonical traits which are phenotypically and genetically uncorrelated. Then S^* is such that $S^* P S^{*\prime}$ equals the identity matrix and $S^* G S^{*\prime} = G_C$ where G_C is the diagonal genetic variance-covariance matrix on the canonical scale. For half-sib family data, matrix $F^{-1} = D$ becomes

$$D = \begin{bmatrix} d_1 & 0 \\ 0 & d_2 \end{bmatrix} \tag{4}$$

where $d_j = (0.25\lambda_j(1-\lambda_j) + (1-0.25\lambda_j)/n)^{-1}$ and λ_j denotes the canonical heritability of the j^{th} canonical trait.

If β_C is the vector of genetic parameters on the canonical scale, similar to β, and the indices on the canonical scale are $I_1 = C_1 \cos\theta_{C1} + C_2 \sin\theta_{C1}$ and $I_2 = C_1 \cos\theta_{C2} + C_2 \sin\theta_{C2}$, where θ_{C1} and θ_{C2} are the angles of the canonical selection indices, then $\sigma_{Im} = 1$ and $X'V^{-1}X_C$, the value of $X'V^{-1}X$ for canonical traits, is derived from equations 1 to 4

$$X'V^{-1}X_C = \begin{bmatrix} d_1 B_1 & d_1 B_3 & 0 \\ d_1 B_3 & d_1 B_2 + d_2 B_1 & d_2 B_3 \\ 0 & d_2 B_3 & d_2 B_2 \end{bmatrix}. \tag{5}$$

The expected value of $\mathrm{DET}(\beta_C)$ is

$$\begin{aligned} \mathrm{DET}(\beta_C) &= |X'V^{-1}X_C| \\ &= d_1 d_2 (d_1 B_2 + d_2 B_1)(B_1 B_2 - B_3^2) \end{aligned} \tag{6}$$

where

$$\begin{aligned} B_1 &= 2N i^2 (\cos^2\theta_{C1} + \cos^2\theta_{C2}) \\ B_2 &= 2N i^2 (\sin^2\theta_{C1} + \sin^2\theta_{C2}) = 2N i^2 (2 - B_1) \\ B_3 &= N i^2 (\sin 2\theta_{C1} + \sin 2\theta_{C2}). \end{aligned} \tag{7}$$

It can be shown that $\mathrm{DET}(\beta) = (1-r_p^2)^{-3}\,\mathrm{DET}(\beta_C)$ (see Appendix 1). In order to maximise $\mathrm{DET}(\beta_C)$, it is differentiated with respect to B_2 and B_3, and the maximum occurs when

$$\frac{B_2}{2N i^2} = \frac{-2(d_1 - 2d_2) \pm 2\sqrt{d_1^2 - d_1 d_2 + d_2^2}}{3(d_2 - d_1)} \tag{8}$$

and $B_3 = \sin 2\theta_{C1} + \sin 2\theta_{C2} = 0$, therefore $\theta_{C2} = \theta_{C1} + 90°$ or $\theta_{C1} + \theta_{C2} = 180°$.

There are two cases to consider when maximising $\mathrm{DET}(\beta_C)$. If the canonical heritabilities are equal, d_1 equals d_2, then the maximum value of $\mathrm{DET}(\beta_C)$ occurs when $B_2/2N i^2 = 1$ or $\theta_{C2} = \theta_{C1} + 90°$. The indices on the canonical scale are $I_1 = C_1 \cos\theta_{C1} + C_2 \sin\theta_{C1}$ and $I_2 = C_2 \cos\theta_{C1} - C_1 \sin\theta_{C1}$ and as the this pair of axes are at right angles we call this an orthogonal design. The phenotypic covariance between the indices is zero. There are an infinite number of pairs of indices resulting in the maximum value of $\mathrm{DET}(\beta_C)$.

If the canonical heritabilities are unequal, then $\theta_{C1} + \theta_{C2} = 180°$ and θ_{C1} can be derived using equation (8) as $B_2/2N i^2 = 2\sin^2\theta_{C1}$. The indices on the canonical scale are $I_1 = C_1 \cos\theta_{C1} + C_2 \sin\theta_{C1}$ and $I_2 = C_2 \sin\theta_{C1} - C_1 \cos\theta_{C1}$. The lines $I_1 = 0$ and $I_2 = 0$ are symmetric about the C_1 and C_2 axes and we call this a symmetric design. Note that the angle between I_1 and the C_1 axis is equal to the angle between I_2 and the C_1 axis.

Estimation and design from offspring-parent regression

The heritability of a trait can be estimated from the regression of progeny performance on parent performance, rather than using a summary of parental information and responses to selection. The design of experiments to estimate the heritability of a trait using offspring-parent regression have been discussed by Hill (1970) and Hill and Thompson (1977).

Offspring-parent regression techniques can be used to estimate genetic parameters of more than one trait simultaneously. The standardised observations on two traits for the j^{th} parent and the mean of its offspring are defined as x_{1j}, x_{2j} and $\bar{o}_{x1j}, \bar{o}_{x2j}$, respectively. Then

$$\begin{aligned} \begin{bmatrix} \bar{o}_{x1j} \\ \bar{o}_{x2j} \end{bmatrix} &= 0.5\, G P^{-1} \begin{bmatrix} x_{1j} \\ x_{2j} \end{bmatrix} + [e] \\ &= 0.5\, G \begin{bmatrix} s_{1j} \\ s_{2j} \end{bmatrix} + [e] \\ &= \begin{bmatrix} s_{1j} & s_{2j} & 0 \\ 0 & s_{1j} & s_{2j} \end{bmatrix} \beta + [e] \end{aligned}$$

where s_{1j} and s_{2j} are $(x_{1j} - r_p x_{2j})/(1-r_p^2)$ and $(x_{2j} - r_p x_{1j})/(1-r_p^2)$, respectively.

Combining the information from all 4N offspring-parents pairs, β can be estimated as before. The matrix V is now a $8N \times 8N$ block diagonal matrix with the F matrix repeated 4N times down the diagonal.

The contribution of each family to $X'V^{-1}X$ can be expanded as

$$(X'V^{-1}X)_j = s_{1j}^2 \begin{bmatrix} D_{11} & D_{12} & 0 \\ D_{21} & D_{22} & 0 \\ 0 & 0 & 0 \end{bmatrix} + s_{1j} s_{2j} \begin{bmatrix} 0 & D_{11} & D_{12} \\ D_{11} & D_{12} + D_{21} & D_{22} \\ D_{21} & D_{22} & 0 \end{bmatrix} + s_{2j}^2 \begin{bmatrix} 0 & 0 & 0 \\ 0 & D_{11} & D_{12} \\ 0 & D_{21} & D_{22} \end{bmatrix} \tag{9}$$

where D_{jk} are the elements of F^{-1} (equation (3)). The sums of squares and crossproducts of the parental traits, after selection, are calculated using

$$\begin{aligned}
&\mathrm{cov}\,(x_1, x_2 \mid \text{selection on I}) \\
&\quad = \mathrm{cov}\,(x_1, x_2) - \frac{\mathrm{cov}\,(x_1, I)\,\mathrm{cov}\,(x_2, I)}{\mathrm{var}\,(I)} \\
&\quad\quad + \frac{\mathrm{cov}\,(x_1, I)\,\mathrm{var}\,(I^*)\,\mathrm{cov}\,(x_2, I)}{\mathrm{var}^2(I)} \\
&\quad = \mathrm{cov}\,(x_1, x_2) + \frac{i\,x\,\mathrm{cov}\,(x_1, I)\,\mathrm{cov}\,(x_2, I)}{\mathrm{var}\,(I)} \qquad (10)
\end{aligned}$$

where var (I*) is the variance of the index after selection. The sums of squares and crossproducts of s_{1j} and s_{2j}, after selection, can be determined from

$$\begin{bmatrix} \sum_{j=1}^{4N} s_{1j}^2 & \sum_{j=1}^{4N} s_{1j}\,s_{2j} \\ \sum_{j=1}^{4N} s_{1j}\,s_{2j} & \sum_{j=1}^{4N} s_{2j}^2 \end{bmatrix} = P^{-1} \begin{bmatrix} \sum_{j=1}^{4N} x_{1j}^2 & \sum_{j=1}^{4N} x_{1j}\,x_{2j} \\ \sum_{j=1}^{4N} x_{1j}\,x_{2j} & \sum_{j=1}^{4N} x_{2j}^2 \end{bmatrix} P^{-1}\,. \qquad (11)$$

As before, transformation on to the canonical scale results in the diagonalisation of the F matrix and $X'V^{-1}X_C$ has the same structure as in equation (5), where now

$$B_1 = \sum_{j=1}^{4N} C_{1j}^2,\quad B_2 = \sum_{j=1}^{4N} C_{2j}^2 \quad \text{and} \quad B_3 = \sum_{j=1}^{4N} C_{1j}\,C_{2j} \qquad (12)$$

with C_{1j} and C_{2j} being the observations on the canonical scale of the j^{th} selected parent and a total of 4N selected individuals as before. DET (β_C) becomes

$$\mathrm{DET}\,(\beta_C) = d_1\,d_2\,(d_1\,B_2 + d_2\,B_1)\,(B_1\,B_2 - B_3^2)$$

which is of the same form as equation (6), with B_1, B_2 and B_3 given by equation (12) rather than equation (7). The expected sums of squares and crossproducts of the observations can be rewritten as

$$B_1 = 2N\,[2 + i\,x\,(\cos^2\theta_{C1} + \cos^2\theta_{C2})]$$

$$B_2 = 2N\,[2 + i\,x\,(\sin^2\theta_{C1} + \sin^2\theta_{C2})]$$

$$B_3 = N\,i\,x\,[\sin 2\theta_{C1} + \sin 2\theta_{C2}]\,.$$

Then

$$\begin{aligned}
\mathrm{DET}\,(\beta_C) = {} & (2N)^3\,d_1\,d_2\,[d_1\,(2 + i\,x\,H) \qquad (13) \\
& + d_2\,(2 + i\,x\,(2 - H))]\,[2 + i\,x\,H]\,[2 + i\,x\,(2 - H)]
\end{aligned}$$

with $H = \sin^2\theta_{C1} + \sin^2\theta_{C2}$. In order to maximise DET (β_C), it is differentiated with respect to B_2 and B_3, and the maximum occurs when

$$H = \frac{-2\,[(d_1 - 2\,d_2)\,i\,x - (d_1 + d_2)] \pm 2\,(2 + i\,x)\,\sqrt{d_1^2 - d_1\,d_2 + d_2^2}}{3\,i\,x\,(d_2 - d_1)} \qquad (14)$$

and $B_3 = \sin 2\theta_{C1} + \sin 2\theta_{C2} = 0$, therefore $\theta_{C2} = \theta_{C1} + 90°$ or $\theta_{C1} + \theta_{C2} = 180°$.

If the canonical heritabilities are equal, d_1 equals d_2, then H equals one and DET (β_C) is maximised when $\theta_{C2} = \theta_{C1} + 90°$. This corresponds to a ridge of points where DET (β_C) is of constant value (the previously mentioned orthogonal design). If the canonical heritabilities are not equal a symmetric design with $2\sin^2\theta_{C1} = H$, found from equation (14), is again optimal.

The ratio of values of DET (β_C) from the orthogonal design using the offspring-parent regression and response/selection differential estimation is $((2 + i\,x)/i^2)^3 > 1.0$. For example, when p equals 0.10 and 0.20, the ratio equals $(1.38)^3$ and $(1.62)^3$, respectively. The proportional gain in precision $(2 + i\,x)$ from the offspring-parent regression designs comes from two sources. For example, if $I_1 = C_1$ and $I_2 = C_2$, then $(1 + i\,x)$ is proportional to the sums of squares for C_1 from selection on I_1 compared to i^2 used in response/selection differential estimation. The remainder $((2 + i\,x) - (1 + i\,x))$ is proportional to the sums of squares for C_1 with selection on I_2, which is information not used in response/selection differential estimation.

Canonical traits have been used to simplify the development of the variance formulae and interpretation of the designs. When the experiment is being designed, G and hence the canonical transformation are not known precisely, therefore the specification of the optimal design is difficult. However, the class of orthogonal designs includes all pairs of indices that are phenotypically uncorrelated. On the standardised scale, an index $I_2 = x_1 \cos\theta_{C2} + x_2 \sin\theta_{C2}$ can be found phenotypically uncorrelated to $I_1 = x_1 \cos\theta_{C1} + x_2 \sin\theta_{C1}$, if $\tan\theta_{C2} = -(1 + r_p \tan\theta_{C1})/(r_p + \tan\theta_{C1})$. This gives some flexability in the choice of designs. For example, the three pairs of indices $I_1 = x_1$ and $I_2 = x_2 - r_p x_1$, $I_1 = x_2$ and $I_2 = x_1 - r_p x_2$ and also $I_1 = x_1 + x_2$ and $I_2 = x_1 - x_2$ are members of the class of orthogonal designs. This choice of indices can be made without "a priori" knowledge of G and is optimal if the canonical heritabilities are equal.

Manipulation of equations (13) and (14) shows that the ratio of DET (β_C) using the optimal symmetric design compared with using one pair from the above three indices is $(1 + \eta\,\delta)/(1 - \eta^2)$ with

$$\eta = (-1 \pm \sqrt{1 + 3\delta^2})/3 = i\,x\,(H - 1)/(2 + i\,x)$$

and $\delta = (d_1 - d_2)/(d_1 + d_2)$. For a range of canonical heritabilities, the ratio was generally less than 1.05.

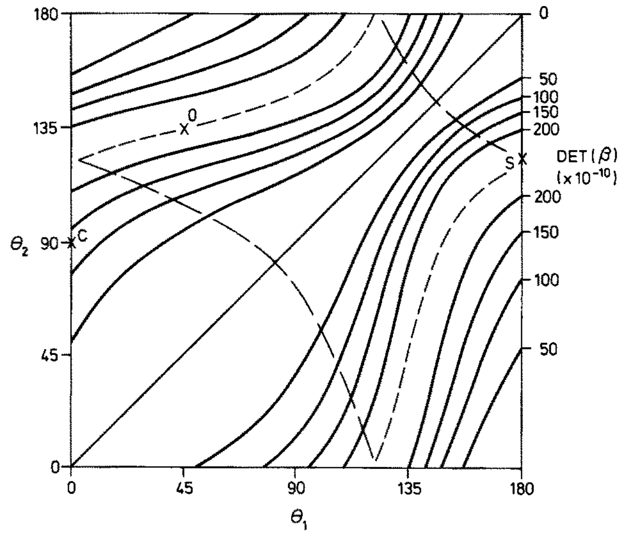

Fig. 1. Contours for DET(β) (divided by 10^{10}) for various linear indices of the traits defined by angles θ_1 and θ_2 with β estimated by response/selection differential. The classes of orthogonal designs (---), symmetric designs (——), the orthogonal design $I_1 = x_1 + x_2$, $I_2 = x_1 - x_2$ (O), the optimal symmetric design (S) and the classical design $I_1 = x_1$, $I_2 = x_2$ (C) are included

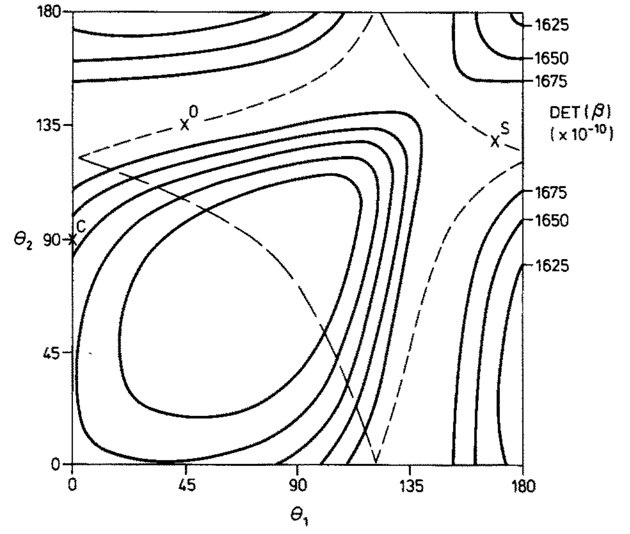

Fig. 2. Contours for DET(β) (divided by 10^{10}) for various linear indices of the traits defined by angles θ_1 and θ_2 with β estimated by offspring-parent regression. Classes of designs and individual designs are denoted as in Fig. 1

This suggests that the proportional increase in precision of a genetic variance or covariance estimate will be at most 0.02 ($= (1.05)^{1/3} - 1$), from using the symmetric design compared with using the orthogonal design. Therefore efficient selection indices can be constructed without estimates of the genetic parameters being available.

To illustrate these results, Figs. 1 and 2 show the contours for DET(β) estimated by response/selection differential (Fig. 1) and offspring-parent regression (Fig. 2). The heritabilities are 0.6 and 0.9 and the genetic and phenotypic correlations are 0.8 and 0.6, respectively, with 600 sires selected per index and a family size of 10 and selection proportion of 0.3, as used by Gunsett et al. (1984). Included are lines indicating the orthogonal designs with the same value of DET(β) (the orthogonal design $I_1 = x_1 + x_2$, $I_2 = x_1 - x_2$ is denoted by 0) and the symmetric designs (the optimal symmetric design is denoted by S). The classical design $I_1 = x_1$, $I_2 = x_2$ is denoted by C ($\theta_1 = 0°$, $\theta_2 = 90°$). The contour for the orthogonal designs in Fig. 1 corresponds to the ridge noted by Gunsett et al. (1984). When $\theta_1 = \theta_2$ in Fig. 1, then DET(β) = 0 because only two parameters can be estimated. The orthogonal, symmetric and classical designs have values of DET(β) (divided by 10^{10}) of 233, 235 and 136 in Fig. 1 and 1,702, 1,719 and 1,635 in Fig. 2, respectively. The ratio $1{,}702/233 = ((2 + \mathrm{i}\,\mathrm{x})/\mathrm{i}^2)^3 = 1.94^3$ shows the advantage of using offspring-parent regression with orthogonal designs.

When two linear indices are used to select parents, we have shown how to improve the precision of parameter estimates using offspring-parent regression. We have also shown how to choose the linear indices in an efficient way (viz. pairs of orthogonal indices on the canonical scale). We now consider an alternative selection criteria on which to select individuals.

Elliptical selection experimental design

When using offspring-parent regression to estimate genetic parameters, the variance of the genetic parameters depends on the sum of squares of the observations on the parents. When only one trait is of interest, the sum of squares is maximised by selecting individuals with high and low values of the trait to be parents (i.e. selection of individuals with extreme values). By analogy, in the two dimensional case, this suggests selecting a proportion p_E (if the same experimental resources are used as in the divergent selection schemes, then p_E equals 2p) of the 2M individuals measured which are as far from the origin is possible. Invariance arguments suggest using a quadratic index of the form $(x_{1j}\, x_{2j})'\, P^{-1}\, (x_{1j}\, x_{2j})$ for the jth individual. Geometrically, this can be thought of as selecting individuals outside an ellipse given by the formula $(x_1 + x_2)^2/2(1 + r_p) + (x_1 - x_2)^2/2(1 - r_p) = w^2$, where w is chosen such that a proportion p_E of the individuals are outside the ellipse and, because this depends on P, we call the ellipse a phenotypic selection ellipse.

Tallis (1963) considered this type of selection in a different context and showed that the proportion p_E and the variance-covariance matrix of the observations after elliptical selection, P^*, can be derived as $p_E = F_2(w^2)$ and $P^* = [F_4(w^2)/F_2(w^2)]\,P$ where $F_k(w^2)$ is the probability that a χ^2 variable with k d.f. is greater than w^2. The recursive procedure of Hill and Pike (1966) gives the relationship between $F_2(w^2)$ and $F_4(w^2)$, viz. $F_4(w^2) = F_2(w^2) + (w^2/2)\exp(-w^2/2)$, where $F_2(w^2) = \exp(-w^2/2) = p_E$. Therefore $P^* = (1 - \log p_E)\,P$.

As before, transformation onto the canonical scale results in the diagonalisation of the F matrix and $\mathrm{DET}(\beta_C)$ can be written as

$$\mathrm{DET}(\beta_C) = (2\,M\,p_E)^3\,d_1\,d_2\,(d_1+d_2)\,(1-\log p_E)^3 . \quad (15)$$

The ratio of the determinants from elliptical selection and the orthogonal index design is $(2\,(1-\log p_E)/(2+i\,x))^3 > 1.0$. For example, when p_E equals 0.2 and 0.4, the ratio equals $(1.23)^3$ and $(1.21)^3$, respectively, which shows the advantage of using the phenotypic selection ellipse rather than selecting on orthogonal canonical indices. Obviously, if no phenotypic selection is performed then $p_E = 1.0$ and $p = 0.5$ and the ratio of the two determinants is one.

The selection criteria $(x_1\,x_2)'\,P^{-1}\,(x_1\,x_2) = w^2$ can be thought as $(x_1+x_2)^2/2(1+r_p)+(x_1-x_2)^2/2(1-r_p)^2 = w^2$ and x_1+x_2, x_1-x_2 are the axes of the ellipse. For canonical traits the selection ellipse reduces to a canonical circle which is generated by the orthogonal axes $C_1\cos\theta_{C1} + C_2\sin\theta_{C1}$ and $C_2\cos\theta_{C1} - C_1\sin\theta_{C1}$, for all values of θ_{C1}. These axes are precisely those of the orthogonal indices suggested in the previous section. This naturally leads to the question if a canonical ellipse generated by the symmetric axes $C_1\cos\theta_{C1} + C_2\sin\theta_{C1}$ and $C_1\sin\theta_{C1} - C_2\cos\theta_{C1}$ can give a more efficient design. The calculation of the sums of squares and crossproducts for the parental values is more difficult and requires numerical integration (see Appendix 2 for calculation of DET (β_C)). The maximum value of $\mathrm{DET}(\beta_C)$ occured when the canonical ellipse was rotated by an angle ϕ with values 0° and 90°, for $0° \leq \phi \leq 180°$. When $\phi = 90°$, this correspounds to reparameterising C_1 as C_2 and vica versa. Therefore, the canonical ellipse generated by the symmetric axes gives the most efficient design.

Again there is the difficulty that these axes require estimates of G and we could not find an analytic formula for the optimal angle. The ratio of values of $\mathrm{DET}(\beta_C)$ from using the optimal symmetric and orthogonal axes depends on the proportion of individuals selected as parents. For combinations of canonical heritabilities in the range of 0.1 to 0.9 and a range of selection proportions $(0.05 < p_E < 0.30)$, the maximum value of the ratio was 1.01. The ratio decreased as the selection proportion increased and as the magnitude of the difference between $\lambda_1(1-\lambda_1)$ and $\lambda_2(1-\lambda_2)$ decreased. Therefore, there is a negligible loss of efficiency when using the phenotypic elliptical selection scheme compared with using the optimal elliptical scheme.

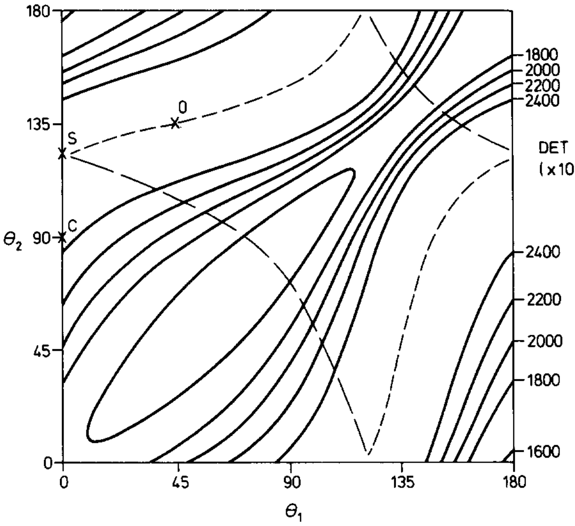

Fig. 3. Contours for $\mathrm{DET}(\beta)$ (divided by 10^{10}) for various quadratic indices of the traits defined by angles θ_1 and θ_2 with β estimated by offspring-parent regression. Classes of designs and individual designs are denoted as in Fig. 1

Figure 3 shows $\mathrm{DET}(\beta)$ using ellipses generated by axes $I_1 = x_1\cos\theta_1 + x_2\sin\theta_1$ and $I_2 = x_1\cos\theta_2 + x_2\sin\theta_2$ using the same G and P matrices and experimental facilities as in Figs. 1 and 2. The values (divided by 10^{10}) of $\mathrm{DET}(\beta)$ for the orthogonal (O), symmetric (S) and classical (C) axes are 2,650, 2,652 and 2,454, respectively, showing a marked increase over the corresponding values in Fig. 2, with

$$2{,}650/1{,}702 = (2\,(1-\log p_E)/(2+i\,x))^3 = (1.16)^3 ,$$

for the phenotypic selection ellipse.

Optimising the selection proportion, the family size and the ratio of individuals measured in the two generations

If the canonical heritabilities are equal, say to λ, the optimum proportion to select for maximising $\mathrm{DET}(\beta)$ with different estimation methods and selection designs can be found. For example, if β is estimated by response/selection differential the optimal p is found by differentiation of equation (6) with respect to p. The solution is given by

$$\frac{(1 - r_{oo}\lambda)}{R\,\lambda\,(r_{oo} - r_{op}^2\lambda)} = \frac{2x - i}{4\,(i - x)\,p}$$

which suggests that p must be at least 0.27, that is when $2x > i$.

When estimating genetic parameters using offspring-parent regression, the optimal proportion p is obtained by differentiating equation 12 with respect to p, which satisfies

$$\frac{(1-r_{oo}\lambda)}{R\lambda(r_{oo}-r_{op}^2\lambda)}=\frac{1+x^2}{2p(1+ix-x^2)}=W(2,p) \qquad (16)$$

which is similar to that of Hill and Thompson (1977), derived in a univariate context,

$$\frac{(1-r_{oo}\lambda)}{R\lambda(r_{oo}-r_{op}^2\lambda)}=\frac{x^2}{2p(1+ix-x^2)}=W(1,p)\,.$$

The minimum value of the right hand side of $W(2,p)$ is one when $p = 0.5$, and all individuals are then used as parents. When using a phenotypic selection ellipse, differentiating equation (15) with respect to p_E, gives the result

$$\frac{(1-r_{oo}\lambda)}{R\lambda(r_{oo}-r_{op}^2\lambda)}=\frac{-\log p_E}{p_E}=W(3,p_E)\,. \qquad (17)$$

These equations give an optimal design for fixed numbers of individuals in the parental, 2M, and offspring, 2MR, generations. If the balance of individuals in the two generations can be adjusted, R, then the optimal value of $\mathrm{DET}(\beta_C)/(2M(1+R))^3$, a measure of the efficiency of the design on a per individual measured basis, can be determined. When divergent selection lines are used, the optimum value of p satisfies

$$\frac{(1-r_{oo}\lambda)}{\lambda(r_{oo}-r_{op}^2\lambda)}=\left[\frac{1+x^2}{1+ix-x^2}\right]^2\frac{1}{2p}=W(4,p)$$

and $R=(1+x^2)/(1+ix-x^2)$. When the phenotypic selection ellipse is used, the optimum value of p_E satisfies

$$\frac{(1-r_{oo}\lambda)}{\lambda(r_{oo}-r_{op}^2\lambda)}=(\log p_E)^2/p_E=W(5,p_E) \qquad (18)$$

and $R = -\log p_E$. Figure 4 has been constructed to aid in the solution of the above equations, giving values of $W(s,q)$ against the total proportion selected, p_T, where $q = p_{T/2}$ for $s = 1, 2$ and 4 and $q = p_T$ for $s = 3$ and 5.

Since the genetic parameters are not known "a priori", designs should be robust to poor estimates of these parameters. The $\mathrm{DET}(\beta_C)$ values using elliptical selection were calculated for a range of equal canonical heritabilities, with fixed values of R, at fixed and optimum values of p_E and were then compared with $\mathrm{DET}(\beta_C)$ values when both the p_E and R are optimised (Fig. 5). The efficiency of designs when both p_E and R are optimised are shown as 100 and $\mathrm{DET}(\beta_C)$ values of other designs are shown relative to this base. Figure 5 indicates that for a wide range of canonical heritabilities, with $R = 2$, $p_E = 0.20$ is efficient. For example, with λ values in the ranges (0.18, 0.87) and (0.13, 0.90) designs using $p_E = 0.20$ are at least 0.90 and 0.95 as efficient as the optimal design. When $R = 10$, designs are generally less than 0.40 as efficient as when R is optimised, although $p_E = 0.30$ is close to the optimal value of p, for $R = 10$.

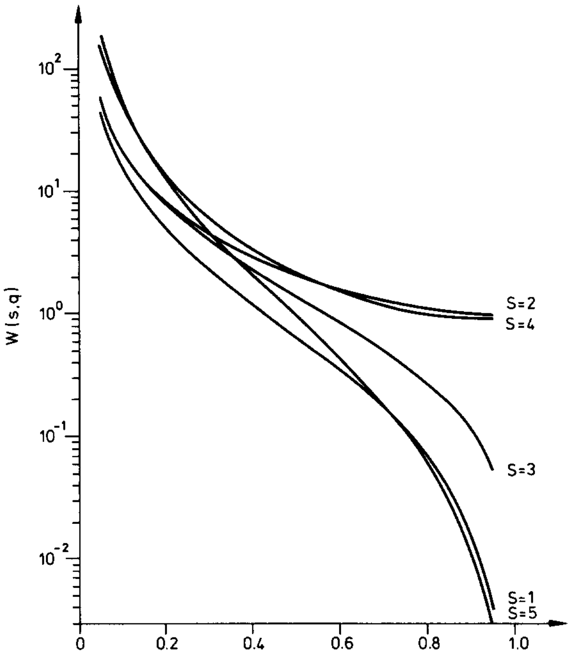

Fig. 4. Values of $W(s,q)$ plotted against the total proportion selected, p_T

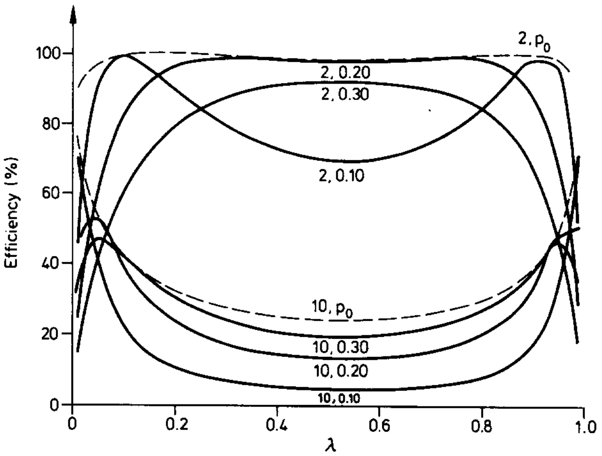

Fig. 5. Efficiency of alternative elliptical designs expressed as $\mathrm{DET}(\beta)$ for a fixed total number recorded relative to that when both p_E and R are optimised. Results are given for specified R and p_E, with p_E fixed or optimal (p_O)

The optimum proportion of individuals to select as parents has been determined, but only when the canonical heritabilities are equal. When the canonical heritabilities are unequal, one suggestion is to use a pooled value of λ in equations (16) to (18), with λ chosen such that the resulting d satisfies

$$2d^3 = d_1 d_2 (d_1 + d_2) . \tag{19}$$

As there are two solutions to the quadratic equation for λ, we suggest using the λ value that lies between λ_1 and λ_2. Due to some symmetry in the d value (i.e. $\lambda(1-\lambda)$), the value of λ is less than 0.5 when $\lambda_1 + \lambda_2 < 1$ and λ is greater than 0.5 otherwise. The value of λ satisfying equation (19) is essentially independent of the value of n, the number of progeny per parent, when n is moderate (> 15). When no "a priori" estimates of the genetic parameters are available, $n = 25$ seems a reasonable value to estimate λ with. The values of $\mathrm{DET}(\beta)$ calculated with the optimum p_E were regressed on the $\mathrm{DET}(\beta)$ values calculated using p_E derived from equation (17), for combinations of canonical heritabilities in the range 0.1 to 0.9 with various R and n values. If the methods of choosing p_E were identical, then the pooled regression coefficient and intercept are expected to have values 1.0 and 0.0 and the actual values were 0.980 and 0.003, respectively. Therefore, the use of equation (19) to generate a pooled λ value seems reasonable, for estimation of the optimum selection proportion, p_E.

Extensions

The gains from using assortative mating when selection is practiced on both male and female parents in one dimensional problems have been demonstrated (Reeve 1955; Hill and Thompson 1977). The same results apply directly to multivariate designs with selection of mates being based on minimising the "phenotypic distance" between mates.

Selection over several generations can also be effective in increasing the precision. However, the distribution of the progeny measurements, the next parental generation, would not be normal which introduces further complications in the estimation of the variance of the parameters.

Estimation of genetic parameters with a selection ellipsoid is not just limited to two traits. For v (> 2) traits the phenotypic selection ellipsoid and transformation onto the canonical scale can be used as before. When the traits have equal canonical heritabilities, the determinant of the inverse of the variance-covariance matrix of the genetic parameter estimates, on the canonical scale, can be written as

$$\mathrm{DET}(\beta_C) = (v\, M\, p_E\, d\, [F_{v+2}(w^2)/F_v(w^2)])^{v(v+1)/2}\, 2^{v(v-1)/2} .$$

The optimum proportion of individuals to select can be determined by differentiating $v\, M\, p_E\, d\, F_{v+2}(w^2)/F_v(w^2) = v\, M\, p_E\, d\, K$ with respect to p_E in order to maximise the value of $\mathrm{DET}(\beta_C)$, where $K = F_{v+2}(w^2)/F_v(w^2)$. However by defining the function $W(p_E)$, the optimal proportion is determined by solving

$$\frac{(1 - r_{oo}\lambda)}{R\lambda(r_{oo} - r_{op}^2\lambda)} = \frac{-1}{p_E}\left[\frac{K}{p_E\,\partial K/\partial p_E} + 1\right] = W(p_E)$$

where $v M p_E$ is the total number of individuals selected for the ellipsoidal design. The mean parental sums of squares decreases as the number of traits increases and obviously as the proportion selected decreases. However marked gains for increasing the precision of estimates of genetic parameters can be made with at least 5 traits.

An example

An example of a design using elliptical selection is taken from an ABRO sheep experiment to estimate genetic parameters for growth rate and carcass leanness in lambs slaughtered at fixed age. A total of 100 rams are measured and 750 progeny are expected, giving a R value of 7.5. The "a priori" estimates of the heritabilities are 0.20 and 0.40 and the genetic and phenotypic correlations are 0.25 and 0.15, respectively. The canonical traits are $1.010\,x_1 - 0.203\,x_2$ and $0.052\,x_1 + 0.991\,x_2$, which are phenotypically uncorrelated and have phenotypic variance of 1.0. The canonical heritabilities are 0.192 (derived from $1.010^2 h_1 + 2(1.010)(-0.203)\, r_A h_1 h_2 + (-0.203)^2 h_2^2$) and 0.401, and using $n = 25$ to estimate λ, the value of 0.262 is derived from equation (19). Given the R value of 7.5, the optimum proportion of rams to select, p_E, is 0.378 from solving $W(3, p_E) = (-\log p_E)/p_E = 2.57$ (equation (17)) or using Fig. 4, and so each selected ram has an expected 20 progeny. Therefore 38 rams are selected such that $x_1^2 + 2(-0.15)\, x_1 x_2 + x_2^2 > 1.94(1 - 0.15^2)$ where x_j are the standardised measurements of growth rate and carcass leanness. The value of $w^2 = 1.94$ is derived from $p_E = \exp(-w^2/2)$.

The matrix $X'V^{-1}X_C$ on the canonical scale can be derived using equations (5) and (12) and is diagonal with elements 866, 1,578 and 712 using $d_1 = 11.58$ and $d_2 = 9.52$ with $B_1 = B_2 = 38(1 - \log 0.38)$ and $B_3 = 0$. Appendix 1 derives the matrix R^* such $R^*\beta = \beta_C$, and in this case

$$R^* = \begin{bmatrix} 0.102 & -0.411 & 0.041 \\ 0.053 & 0.990 & -0.202 \\ -0.003 & 0.104 & 0.982 \end{bmatrix} .$$

The variance-covariance matrix of the genetic parameter estimates is then
$4(R^*)^{-1}(X'V^{-1}X_C)^{-1}((R^*)^{-1})' = 4\,\mathrm{var}(\beta)$

$$= \begin{bmatrix} 46.4 & 7.8 & 1.3 \\ 7.8 & 26.0 & 8.7 \\ 1.3 & 8.7 & 56.0 \end{bmatrix} \times 10^{-4} .$$

The expected standard errors for the heritabilities of 0.20 and 0.40 are 0.068 and 0.075, respectively and for the genetic covariance of 0.064 the standard error is 0.051.

If the rams were split into two groups and selected high and low in each group, using an orthogonal design, then the variances of the genetic parameter estimates are proportionately increased by 1.21 (derived from $2(1-\log p_E)/(2+ix)$) compared to using elliptical selection. If only information on the parental selection traits is used, then the proportional increase is larger, 1.75 from $2(1-\log p_E)/(1+ix)$.

If the classical design is used to estimate the genetic parameters, then the matrix $X'V^{-1}X$, determined from equations (9) and (10), equals

$$\begin{bmatrix} 743 & -187 & 11 \\ -187 & 1{,}381 & -175 \\ 11 & -175 & 616 \end{bmatrix}$$

using $D_{11} = 11.85$, $D_{22} = 9.83$ and $D_{12} = D_{21} = -1.88$ with

$$\sum_{j=1}^{38} x_{1j}^2 = \sum_{j=1}^{38} x_{2j}^2 = 19\,(1 + i\,x) + 19\,(1 + i\,x\,(0.15)^2) = 62.36$$

and

$$\sum_{j=1}^{38} x_{1j}\,x_{2j} = 12.84\,.$$

Then

$$\sum_{j=1}^{38} s_{1j}^2 = \sum_{j=1}^{38} s_{2j}^2 = 62.7 \quad \text{and} \quad \sum_{j=1}^{38} s_{1j}\,s_{2j} = -5.83$$

from equation (11). The variance-covariance matrix of the genetic parameters is then $4\,\mathrm{var}(\beta)$, as before, and equals

$$\begin{bmatrix} 55.8 & 7.7 & 1.2 \\ 7.7 & 31.1 & 8.7 \\ 1.2 & 8.7 & 67.4 \end{bmatrix} \times 10^{-4}.$$

Therefore, the proportional increase in the variance of the genetic parameter estimates using the classical design compared to the elliptical design is $1 \cdot 22$.

Note that the matrix of weights on the original scale contributing to the selection indices (B) can be determined from the matrix of weights on the canonical scale ($\mathrm{ANG_C}$). If selection is on the orthogonal canonical indices $I_1 = C_1 + C_2$ and $I_2 = C_1 - C_2$, such that $\theta_{C1} = 45°$ and $\theta_{C2} = 135°$, then

$$\mathrm{ANG_C} = \begin{bmatrix} \cos\theta_{C1} & \sin\theta_{C1} \\ \cos\theta_{C2} & \sin\theta_{C2} \end{bmatrix} = \begin{bmatrix} 0.707 & 0.707 \\ -0.707 & 0.707 \end{bmatrix}$$

and

$$B = \mathrm{ANG_C}\,S^* = \begin{bmatrix} 0.751 & 0.557 \\ -0.677 & 0.844 \end{bmatrix}$$

Equivalent indices are

$$\begin{bmatrix} \cos\theta_1 & \sin\theta_1 \\ \cos\theta_2 & \sin\theta_2 \end{bmatrix} = \begin{bmatrix} 0.803 & 0.596 \\ -0.626 & 0.780 \end{bmatrix}$$

and the angles of the indices on the original scale are 36.6° and 128.8°.

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Appendix 1

The value of $\mathrm{DET}(\beta)$ can be determined from $\mathrm{DET}(\beta_C)$. Since $G_C = S^*\,G\,S^{*\prime}$, then

$$\beta_C = 0.5 \begin{bmatrix} G_{C11} \\ G_{C12} \\ G_{C22} \end{bmatrix} = \begin{bmatrix} S_{11}^{*2} & 2S_{11}^*\,S_{12}^* & S_{12}^{*2} \\ S_{11}^*\,S_{21}^* & S_{11}^*\,S_{22}^* + S_{21}^*\,S_{12}^* & S_{12}^*\,S_{22}^* \\ S_{21}^{*2} & 2\,S_{21}^*\,S_{22}^* & S_{22}^{*2} \end{bmatrix}.$$

Let the above 3×3 matrix be denoted R^*, then

$$\beta_C = R^*_\beta \quad \text{and} \quad \beta = (R^*)^{-1}\,\beta_C$$

$$\mathrm{var}(\beta) = (R^*)^{-1}\,\mathrm{var}(\beta_C)\,((R^*)^{-1})'$$

$$\mathrm{var}(\beta)^{-1} = R^*\,\mathrm{var}(\beta_C)^{-1}\,R^{*\prime}$$

$$|X'V^{-1}X| = |R^*|^2\,|X'V^{-1}X|_C\,.$$

As $S^*\,P\,S^{*\prime} = I$, then $|S^*|^{-2} = |P| = (1 - r_p^2)$. The determinant of R^* can be shown to equal $|S^*|^3$, therefore

$$\mathrm{DET}(\beta) = (1 - r_p^2)^{-3}\,\mathrm{DET}(\beta_C)\,.$$

Appendix 2

In this appendix the calculation of p_E and the mean sums of squares and crossproducts after elliptical truncation selection is illustrated. The selection ellipse based on symmetric axes is $C_1\cos\theta + C_2\sin\theta$ and $C_1\cos\theta - C_2\sin\theta$ is $a^2\,C_1^2 + b^2\,C_2^2 = w^2$, where C_1, C_2 are the canonical variates and $a^2 = 2\cos^2\theta$, $b^2 = 2\sin^2\theta$. Given the proportion to be selected, p_E, the "size" of the ellipse, w, satisfies

$$p_E = 1 - \frac{4}{\sqrt{2\pi}} \int_0^{\sqrt{a w^2}} \exp(-C_1^2/2) \int_0^{C_2(C_1)} \frac{1}{\sqrt{2\pi}} \cdot \exp(-C_2^2/2)\, dC_2\, dC_1$$

where $C_2(C_1) = \sqrt{(w^2 - a^2 C_1^2)/b^2}$. Likewise the mean sum of squares and crossproducts of the canonical variates after elliptical selection are given by $S S_1(\theta)$, $S S_2(\theta)$ and $C P(\theta)$

$$p_E\, S S_1(\theta_1) = 4 \left[\frac{1}{\sqrt{2\pi}} \int_0^{\sqrt{a w^2}} C_1^2 \exp(-C_1^2/2) \int_{C_2(C_1)}^{\infty} \frac{1}{\sqrt{2\pi}} \cdot \exp(-C_2^2/2)\, dC_2\, dC_1 + \frac{1}{\sqrt{2\pi}} \int_{a w^2}^{\infty} C_1^2 \exp(-C_1^2/2)\, 0.5\, dC_1 \right]$$

with $S S_2(\theta_1) = S S_1(90° - \theta_1)$ and by symmetry $C P(\theta) = 0$. By integrating by parts,

$$p_E\, S S_1(\theta_1) = 4 \left[\frac{1}{2} \int_0^{\sqrt{a w^2}} C_1^2 \exp(-C_1^2/2)\, p_2\, dC_1 + x z + p_1 \right] \quad \text{(A1)}$$

where

$$p_1 = \frac{1}{2\sqrt{2\pi}} \int_0^{\sqrt{a w^2}} \exp(-C_1^2/2)\, dC_1 \quad \text{and}$$

$$p_2 = \frac{1}{\sqrt{2\pi}} \int_{C_2(C_1)}^{\infty} \exp(-C_2^2/2)\, dC_2$$

and z is the height of the ordinate at truncation point x. If the indices of the selection ellipse are defined by angles θ_{C1} and θ_{C2}, the ellipse can be written as:

$$w^2 = (C_1 \cos\theta_{C1} + C_2 \sin\theta_{C1})^2 + (C_1 \cos\theta_{C2} + C_2 \sin\theta_{C2})^2$$

or

$$w^2 = 2 u^2 \cos^2((\theta_{C1} - \theta_{C2})/2) + 2 v^2 \sin^2((\theta_{C1} - \theta_{C2})/2)$$

where

$$u = C_1 \cos((\theta_{C1} + \theta_{C2})/2) + C_2 \sin((\theta_{C1} + \theta_{C2})/2)$$
$$v = C_1 \cos((\theta_{C1} + \theta_{C2} + 180°)/2) + C_2 \sin((\theta_{C1} + \theta_{C2} + 180°)/2)$$

which is the equation of an ellipse on a scale with orthogonal axes u and v. The sums of squares of u and v ($S S_u$ and $S S_v$) can therefore be calculated using equation (A1). By transforming back to the canonical scale, the mean sums of squares and crossproducts of the canonical variates are

$$S S_1 = S S_u \cos^2((\theta_{C1} + \theta_{C2})/2) + S S_v \sin^2((\theta_{C1} + \theta_{C2})/2)$$
$$S S_2 = S S_u \sin^2((\theta_{C1} + \theta_{C2})/2) + S S_v \cos^2((\theta_{C1} + \theta_{C2})/2)$$
$$C P = (S S_u - S S_v)(\sin(\theta_{C1} + \theta_{C2}))/2 .$$