Theor Appl Genet (1996) 93: 287–294

F. Phocas · J. J. Colleau

Genetic steady-state under BLUP selection for an infinite and homogeneous population with discrete generations

Received: 6 June 1995 / Accepted: 15 December 1995

Abstract A matrix derivation is proposed to analytically calculate the asymptotic genetic variance-covariance matrix under BLUP selection according to the initial genetic parameters in a large population with discrete generations. The asymptotic genetic evolution of a homogeneous population with discrete generations is calculated for a selection operating on an index including all information (pedigree and records) from a non-inbred and unselected base population (BLUP selection) or on an index restricted to records of a few ancestral generations. Under the first hypothesis, the prediction error variance of the selection index is independent of selection and is calculated from the genetic parameters of the base population. Under the second hypothesis, the prediction error variance depends on selection. Furthermore, records of several generations of ancestors of the candidates for selection must be used to maintain a constant prediction error variance over time. The number of ancestral generations needed depends on the population structure and on the occurrence of fixed effects. Without fixed effects to estimate, accounting for two generations of ancestors is sufficient to estimate the asymptotic prediction error variance. The amassing of information from an unselected base population proves to be important in order not to overestimate the asymptotic genetic gains and not to underestimate the asymptotic genetic variances.

Key words Linkage disequilibrium · Discrete generations · BLUP selection · Infinite population

Introduction

The evolution of genetic parameters due to selection must be accounted for when predicting the efficiency of breeding schemes. As genetic variances decrease under selection, selection response is reduced after several cycles of selection. Under the usual assumptions of an infinitesimal genetic model and a population of infinite size, genetic parameters are only modified by the linkage disequilibrium induced by selection (Bulmer 1971). For discrete generations and closed homogeneous populations, several formulae of asymptotic values of genetic parameters have been derived as a function of the base population parameters. Bulmer (1971) derived the asymptotic genetic variance for mass selection. Fimland (1979) extended this to the genetic covariance between two traits under indirect selection, or between traits under direct selection and traits under indirect selection. Gomez-Raya and Burnside (1990) proposed a method to deal with index selection, but it quickly becomes tedious when the amount of information included in the index increases or when males and females are evaluated with different accuracies. Dekkers (1992) derived asymptotic genetic variance for a four-selection-path breeding scheme when selection is on breeding values estimated by the method of Best Linear Unbiased Predictor (BLUP) under an animal model and when information on performance and pedigree has already been accumulated before the start of selection. Villanueva et al. (1993) and Andersen (1994) extended Dekkers' (1992) result to genetic covariances between a trait under direct selection and traits under indirect selection. A matrix and synthetic expression of the same result is presented in this paper. Since the basic assumption underlying this derivation is a constant prediction error variance matrix (PEV), the aim of the paper is to numerically examine the consequences of using a wrong PEV because of either considering too small a number of pedigree records to get the limiting value of PEV or to selecting a base population.

Communicated by E. J. Eisen

F. Phocas (✉) · J. J. Colleau
Institut National de la Recherche Agronomique,
Station de Génétique Quantitative et Appliquée,
78 352 Jouy-en-Josas, Cedex, France

Matrix derivation of asymptotic genetic variances and covariances under multi-trait BLUP selection

As underlined by Andersen (1994), "BLUP evaluation" is a misleading term in deterministic breeding plan modelling because generally no attention is paid to the estimation of fixed effects. Thus, a more correct specification would be evaluation on index selection principles with complete information. However, the term BLUP will be used since it is the reputed term in pioneering studies (Meuwissen 1989; Wray and Hill 1989; Dekkers 1992). Moreover, the existence of fixed effects is accounted for in our paper.

The PEV matrix

A BLUP-Animal Model is considered for one trait: $\mathbf{y} = \mathbf{Xb} + \mathbf{Zu} + \mathbf{e}$, where $\mathbf{y}$, $\mathbf{b}$, $\mathbf{u}$ and $\mathbf{e}$ are the vectors of the *n* performances, fixed effects, breeding values and residuals respectively; $\mathbf{X}$ and $\mathbf{Z}$ are the incidence matrices.

The inverse of the mixed model equations is the PEV matrix (Henderson 1973). A diagonal element of PEV is var(u-û), and the reliability of the corresponding estimated breeding value û is CD = 1-var(u-û)/var(u).

$$\mathbf{PEV} = \begin{pmatrix} \frac{1}{\sigma_e^2}\mathbf{X'X} & \frac{1}{\sigma_e^2}\mathbf{X'Z} \\ \frac{1}{\sigma_e^2}\mathbf{Z'X} & \frac{1}{\sigma_e^2}\mathbf{Z'Z} + \frac{1}{\sigma_u^2}\mathbf{A}^{-1} \end{pmatrix}^{-1} \tag{1}$$

where σ_u^2 and σ_e^2 are the genetic and residual variances and $\mathbf{A}^{-1}$ is the inverse of the relationship matrix. The above equation is easily extended to a multi-trait evaluation by considering the residual and genetic variance-covariance matrices between all traits. We consider such a multi-trait evaluation when each animal is recorded for each trait ($\mathbf{Z} = \mathbf{I}_n$ for each trait) and when there are no fixed effects ($\mathbf{X} = \mathbf{0}$) or only an overall mean per trait ($\mathbf{X} = \mathbf{1}_n$).

As mentioned by Dekkers (1992), in deterministic breeding plan modelling, the assumption of a constant PEV matrix over the generations of BLUP selection is correct for one candidate for selection only if pedigrees and performance records on ancestors go back well before the start of selection. Such a condition is related to the two following points:

1) Henderson (1982) shows that the PEV is not affected by selection if BLUP evaluation accounts for all information (performance and pedigrees) from the unselected and non-inbred base population. At a given time, the PEV matrix associated with a population undergoing BLUP selection would be the same as the PEV matrix of the equivalent unselected population.
2) In a practical situation, the PEV matrix would be modified over time due to the increase in records and animals, even if condition (1) is fulfilled. However, in deterministic modelling of a breeding plan, this is not the PEV matrix of the whole population that is considered but the PEV matrix of a candidate for selection. The PEV matrix of this candidate reaches a limiting value when ancestral information has sufficiently accumulated. Consequently, the PEV matrix of the candidate for selection can be considered as constant over time.

The asymptotic genetic variance-covariance matrix for four selection paths

By extension of Bulmer's (1971) approach, the additive genetic covariance between traits j and k for progeny of sex y, born at year t+1, is:

$$\sigma_{jk}(y,t+1) = \frac{1}{2}\sigma_{jk}(0) + \frac{1}{4}\sum_{x=1}^{2} Vs_{jk}(x,y,t) \tag{2}$$

where

$\sigma_{jk}(0)$ is the additive genetic covariance in the base population (prior to selection);

$1/2\ \sigma_{jk}(0)$ is the segregation covariance; for traits j and k governed by an infinite number of unlinked loci with small additive effects, the segregation covariance remains unchanged under selection when inbreeding does not accumulate, i.e. when population is of infinite size;

$Vs_{jk}(x,y,t)$ is the covariance among parents of sex x selected at time t to produce progeny of sex y.

Under constant selection over time, the genetic (co)variances tend towards asymptotic values. When the subscript t is dropped, the asymptotic additive genetic covariance between traits j and k for progeny of sex y is:

$$\sigma_{jk}(y) = \frac{1}{2}\sigma_{jk}(0) + \frac{1}{4}\sum_{x=1}^{2}\left(\sigma_{jk}(x) - k_{xy}\frac{\sigma_{Ij}(x,y)\,\sigma_{Ik}(x,y)}{\sigma_I^2(x,y)}\right) \tag{3}$$

where

k_{xy} is the factor of variance reduction due to selection on the xy path;

$\sigma_{Ik}(x,y)$ is the covariance between the selection index I and the breeding value on trait k for animals of sex x selected to produce progeny of sex y;

$\sigma_I(x,y)$ is the corresponding standard deviation of the selection index I.

Let us define:

$\mathbf{G_0}$ and $\mathbf{G_x}$, the initial and asymptotic genetic variance-covariance matrices for sex x.

$I_{xy} = \mathbf{a'\hat{u}_{xy}}$ the index used to select animals of sex x to produce progeny of sex y.

$\mathbf{C_{xy}} = \mathrm{Cov}(\mathbf{u},\mathbf{\hat{u}'_{xy}}) = \mathrm{Var}(\mathbf{\hat{u}_{xy}})$ is the asymptotic variance-covariance matrix between true and estimated breeding values, which is equal to:

$\mathbf{C_{xy}} = \mathbf{G_x} - \mathbf{PEV_{xy}}$

$\mathbf{W_{xy}} = \mathbf{C_{xy}}\,\mathbf{a}$

$\mathbf{a'W_{xy}}$ is a scalar and corresponds to the variance of the selection index I_{xy}.

In matrix notation, Eq. 3 becomes:

$$\mathbf{G_y} = \frac{1}{2}\mathbf{G}_0 + \frac{1}{4}\sum_{x=1}^{2}\left(\mathbf{G_x} - k_{xy}(\mathbf{a'W_{xy}})^{-1}\mathbf{W_{xy}}\,\mathbf{W'_{xy}}\right) \tag{4}$$

This gives

$$\begin{cases} 3\mathbf{G_1} = 2\mathbf{G_0} + \mathbf{G_2} & (4a) \\ \qquad -\left[k_{11}(\mathbf{a'W_{11}})^{-1}\mathbf{W_{11}}\,\mathbf{W'_{11}} + k_{21}(\mathbf{a'W_{21}})^{-1}\mathbf{W_{21}}\,\mathbf{W'_{21}}\right] & \\ 3\mathbf{G_2} = 2\mathbf{G_0} + \mathbf{G_1} & (4b) \\ \qquad -\left[k_{12}(\mathbf{a'W_{12}})^{-1}\mathbf{W_{12}}\,\mathbf{W'_{12}} + k_{22}(\mathbf{a'W_{22}})^{-1}\mathbf{W_{22}}\,\mathbf{W'_{22}}\right] & \end{cases}$$

Multiplying Eq. 4a by 3 and replacing $3\mathbf{G_2}$ by Eq. 4b, Eq. 4a becomes:

$$\begin{aligned} 8\mathbf{G_1} = 8\mathbf{G_0} \\ &-3\left[k_{11}(\mathbf{a'W_{11}})^{-1}\mathbf{W_{11}}\,\mathbf{W'_{11}} + k_{21}(\mathbf{a'W_{21}})^{-1}\mathbf{W_{21}}\,\mathbf{W'_{21}}\right] \\ &-\left[k_{12}(\mathbf{a'W_{12}})^{-1}\mathbf{W_{12}}\,\mathbf{W'_{12}} + k_{22}(\mathbf{a'W_{22}})^{-1}\mathbf{W_{22}}\,\mathbf{W'_{22}}\right] \end{aligned}$$

The equivalent equation can be derived for $8\mathbf{G_2}$, and then the following system of equations is established:

$$\begin{bmatrix}\mathbf{G_1}\\ \mathbf{G_2}\end{bmatrix} = \begin{bmatrix}\mathbf{G_0}\\ \mathbf{G_0}\end{bmatrix} - \frac{1}{8}\begin{bmatrix}3 & 1\\ 1 & 3\end{bmatrix}\begin{bmatrix} k_{11}(\mathbf{a'W_{11}})^{-1}\mathbf{W_{11}}\,\mathbf{W'_{11}} + k_{21}(\mathbf{a'W_{21}})^{-1}\mathbf{W_{21}}\,\mathbf{W'_{21}} \\ k_{12}(\mathbf{a'W_{12}})^{-1}\mathbf{W_{12}}\,\mathbf{W'_{12}} + k_{22}(\mathbf{a'W_{22}})^{-1}\mathbf{W_{22}}\,\mathbf{W'_{22}} \end{bmatrix} \tag{5}$$

Under the assumptions of constant $\mathbf{PEV_{xy}}$, the asymptotic vectors $\mathbf{W_{xy}}$ can be expressed as:

$$\mathbf{W_{xy}} = \mathbf{W^0_{xy}} + (\mathbf{G_x} - \mathbf{G}_0)\,\mathbf{a} \tag{6}$$

Subtracting $\mathbf{G_0}$ and postmultiplying Eq. 5 by $\mathbf{a}$, the following equation is obtained:

$$\begin{bmatrix} (\mathbf{G_1}-\mathbf{G_0})\,\mathbf{a} \\ (\mathbf{G_2}-\mathbf{G_0})\,\mathbf{a} \end{bmatrix} = -\frac{1}{8}\begin{bmatrix} 3 & 1 \\ 1 & 3 \end{bmatrix}\begin{bmatrix} k_{11}\,\mathbf{W_{11}} + k_{21}\,\mathbf{W_{21}} \\ k_{12}\,\mathbf{W_{12}} + k_{22}\,\mathbf{W_{22}} \end{bmatrix} \tag{7}$$

Pooling Eqs. 6 and 7, the asymptotic vectors $\mathbf{W_{xy}}$ of size n can be expressed as a linear function of their values $\mathbf{W^0_{xy}}$ in the base population:

$$\begin{bmatrix} \mathbf{W_{11}} \\ \mathbf{W_{21}} \\ \mathbf{W_{12}} \\ \mathbf{W_{22}} \end{bmatrix} = \left(\begin{bmatrix} 1+\frac{3}{8}k_{11} & \frac{3}{8}k_{21} & \frac{1}{8}k_{12} & \frac{1}{8}k_{22} \\ \frac{1}{8}k_{11} & 1+\frac{1}{8}k_{21} & \frac{3}{8}k_{12} & \frac{3}{8}k_{22} \\ \frac{3}{8}k_{11} & \frac{3}{8}k_{21} & 1+\frac{1}{8}k_{12} & \frac{1}{8}k_{22} \\ \frac{1}{8}k_{11} & \frac{1}{8}k_{21} & \frac{3}{8}k_{12} & 1+\frac{3}{8}k_{22} \end{bmatrix}^{-1} \otimes \mathbf{I}_n \right) \begin{bmatrix} \mathbf{W^0_{11}} \\ \mathbf{W^0_{21}} \\ \mathbf{W^0_{12}} \\ \mathbf{W^0_{22}} \end{bmatrix} \tag{8}$$

Equations 5 and 8 give a matrix formulation of the asymptotic genetic variance-covariance matrix for a n-trait BLUP evaluation. This result was first obtained by scalar algebra (Villanueva et al. 1993).

The asymptotic genetic variance-covariance matrix for two selection paths

For two selection paths, the expression of the asymptotic genetic variance-covariance matrix can be simplified when equal accuracy of selection is assumed for both sexes.

Equation 4 corresponds to:

$$\mathbf{G} = \mathbf{G_0} + b\,(\mathbf{a'Ca})^{-1}\,\mathbf{Caa'C'} \tag{9}$$

where

$\mathbf{G} = \mathbf{G_1} = \mathbf{G_2}$ is the asymptotic genetic variance-covariance matrix;

$b = -\frac{k_1 + k_2}{2}$; $k_1 = k_{11} = k_{12}$ and $k_2 = k_{21} = k_{22}$;

$\mathbf{C}$ is the asymptotic variance-covariance matrix between true and estimated breeding values: $\mathbf{C} = \mathbf{C}_{11} = \mathbf{C}_{12} = \mathbf{C}_{21} = \mathbf{C}_{22}$.

Under the assumption of constant **PEV** ($\mathbf{PEV} = \mathbf{PEV_0}$), $\mathbf{C} = \mathbf{G} - \mathbf{PEV}$ is written as a function of $\mathbf{C_0} = \mathbf{G_0} - \mathbf{PEV_0}$, the initial variance-covariance matrix between true and estimated breeding values:

$$\mathbf{C} = \mathbf{C_0} + b\,(\mathbf{a'Ca})^{-1}\,\mathbf{Caa'C'} \tag{10}$$

Postmultiplying Eq. 10 by $\mathbf{a}$ and premultiplying by $\mathbf{a'}$, the following equations are obtained:

$$\mathbf{Ca} = \frac{1}{1-b}\,\mathbf{C_0\,a}$$

$$\mathbf{a'Ca} = \frac{1}{1-b}\,\mathbf{a'C_0\,a}$$

Consequently, Eq. 9 is equal to:

$$\mathbf{G} = \mathbf{G_0} + \frac{b}{1-b}\,(\mathbf{a'C_0a})^{-1}\,\mathbf{C_0\,aa'C_0'} \tag{11}$$

The results of Villanueva et al. (1993) and Andersen (1994) are retrieved from formula 11. In particular, the ratio of response for the first selection cycle to the asymptotic response is equal to $(1-b)^{-0.5}$ for any trait considered in the BLUP evaluation with all ancestral information used. Furthermore, Eq. 11 allows one to compare initial and asymptotic genetic correlations for BLUP selection and two selection paths with equal accuracy.

Under phenotypic selection on a single trait and discrete generations, genetic correlation between any trait and the trait under direct selection tends towards 0, whatever its initial sign, but the genetic correlation between two traits indirectly selected can either decrease or increase in absolute value (Villanueva and Kennedy 1990). Stranden et al. (1993) showed by simulation that these results do not hold when the evaluation of animals is carried out by the BLUP method under a multi-trait animal model. If selection is on a single trait, genetic correlation between the trait under direct selection and another trait (used in the evaluation) can increase in absolute value when the initial genetic correlation is low and the environmental correlation is high and has the same sign. The discrepancy with phenotypic selection is due to the use of selection index weights that account for all traits considered in the evaluation. Formula 11 for asymptotic genetic (co)variances under BLUP selection confirms the results observed by Stranden et al. (1993). Any asymptotic genetic correlation r_{jk} between two traits included in a BLUP evaluation under a multi-trait animal model can be written from Eq. 11 as:

$$r_{jk} = \frac{r^0_{jk} + \varepsilon\beta\sqrt{CD^0_j\,CD^0_k}}{\sqrt{\left(1-\beta\,CD^0_j\right)}\sqrt{\left(1-\beta\,CD^0_k\right)}} \tag{12}$$

where

$\beta = \frac{-b}{1-b}$ $(\beta > 0)$;

$\varepsilon = 1$ for $\sigma^0_{Ij}\,\sigma^0_{Ik} < 0$ and $\varepsilon = -1$ for $\sigma^0_{Ij}\,\sigma^0_{Ik} > 0$;

CD^0_j and CD^0_k are the reliabilities in the base population of estimated breeding value I with trait j and k, respectively; $CD^0_k = \left(\frac{\sigma^0_{Ik}}{\sigma^0_I\,\sigma^0_k}\right)^2$.

The genetic correlation between one trait positively correlated with the selection index and another trait negatively correlated with the selection index increases under selection. Such a case occurs frequently for high environmental correlation and low genetic correlation of the same sign, i.e. the situation described by Stranden et al. (1993). For two traits correlated with the selection index in the same direction, a negative initial genetic correlation gets even more negative under selection. However, there are no generalized general results for two traits correlated with the selection index in the same direction and a positive initial genetic correlation between both traits: here the genetic correlation can either decrease or increase under selection, depending on the initial value, BLUP reliabilities and selection intensity.

If, for instance, $CD^0_k = 0$ $(\sigma^0_{Ij}\,\sigma^0_{Ik} = 0)$, then $r_{jk} = \frac{r^0_{jk}}{\sqrt{\left(1-\beta\,CD^0_j\right)}}$

Consequently, initial restriction of genetic change in trait k to zero leads under selection to the increase in absolute value of the genetic correlation among trait k and another trait j included in the multi-trait BLUP evaluation because selection does not change genetic covariances but decreases the genetic variance of trait j. Equation 11 clearly shows that the genetic covariances and the variance of the restricted trait remain unaltered due to the weightings of a restricted selection index $\mathbf{a} = \mathbf{C_0^{-1}k}$ (Itoh and Yamada 1987). For instance, $\mathbf{k} = \begin{pmatrix} 1 \\ 0 \end{pmatrix}$ when considering a two-trait selection index with the second trait maintained constant under selection, and Eq. 11 becomes:

$$\mathbf{G} = \mathbf{G_0} + \frac{b}{1-b}\,(\mathbf{a'C_0a})^{-1}\begin{bmatrix} 1 & 0 \\ 0 & 0 \end{bmatrix}$$

Consequences of using approximate values of the PEV matrix

The above asymptotic matrix derivation of genetic parameters under the constant PEV assumption was used to predict asymptotic genetic gain using the Rendel and Robertson (1950) formula for a closed and homogeneous population under BLUP selection. Numerical investigations were conducted in order to:

1) establish how many ancestral generations should be considered to reach the asymptotic value of the PEV matrix of a candidate for selection. The direct inclusion of this number of ancestral generations in the evaluation of the candidate overcomes the need for iterations without selection described by Dekkers' (1992) deterministic prediction model.

2) measure the bias occurring in the prediction of genetic gain when available information does not go back to the unselected base population and when selection index theory is used in selection and prediction. BLUP maximizes the response to one generation of selection. Actually, a general question concerns the long-term selection response. Stochastic simulations showed that a higher long-term response can be reached by phenotypic selection than by BLUP selection in small-sized populations (Verrier et al. 1993). Some deterministic comparisons for large-sized populations were also attempted and always resulted in a better response for BLUP despite a larger reduction in the genetic variance for BLUP selection. However, the validity of such deterministic comparision is uncertain. By both a deterministic comparison and a stochastic comparison of BLUP and selection index asymptotic responses, we want to demonstrate that selection index theory cannot be used to predict the true response to index selection.

Parameters used for numerical investigations

Deterministic predictions were carried out assuming a two-path selection scheme and equal accuracy of selection for males and females. Selection rates were 50% for females and 10% for males. One or two traits were simultaneously considered. Phenotypic standard deviation was set to 1.0 in the base population for each trait. Investigations concerned traits with initial heritabilities of 0.1, 0.3 and 0.5; initial genetic correlation between traits of –0.8, –0.4, 0.4 and 0.8; and an environmental correlation of –0.8, 0 and 0.8.

Selection was applied on an index that uses records at the least from the individual, its *n* paternal half-sibs, its sire and its dam. This index was called the two-generation index. Other indexes with more complete pedigrees were considered. In the three-generation index, records from the four grandparents and the *n* paternal half-sibs of each parent were included. In the four-generation index, records from the eight great-grandparents and the *n* paternal half-sibs of each grandparent were also added. Finally, in the six-generation index, the 32 great-great-great-grandparents and the *n* paternal half-sibs of each great-great-grandparent were included. At each ancestral generation, ancestors were assumed to be unrelated. Table 1 shows corresponding reliabilities and PEV in the base population for different heritabilities.

Table 1 Reliability of selection (CD) and variance of prediction errors (PEV) for a three-generation index

Estimated mean	h^2	$n=10^a$		$n=100$		$n=1000$	
		CD	PEV	CD	PEV	CD	PEV
No	0.1	0.20	0.08	0.31	0.07	0.37	0.06
	0.3	0.43	0.17	0.49	0.15	0.50	0.15
	0.5	0.60	0.20	0.62	0.19	0.63	0.19
Yes	0.1	0.09	0.09	0.13	0.09	0.15	0.09
	0.3	0.27	0.22	0.31	0.21	0.32	0.21
	0.5	0.44	0.28	0.48	0.26	0.49	0.26

[a] *n* is the number of paternal half-sibs recorded

Impact of the number of ancestral generations on PEV convergence

If it is assumed that genetic parameters of the unselected base population are known, we show in Table 2 the successive ratios of PEVs for a x-generation index as compared to a x+1-generation index (x equal to 2, 3 or 4) for a single-trait selection according to heritability values, the number of paternal half-sibs and the estimation of an overall mean over the performances of the candidate for selection and its relatives. Convergence of PEV is faster for a small number of paternal half-sibs. The estimated breeding value of the sire is well-assessed for a two-generation index since the paternal half-sibs of the candidate are recorded. More ancestral generations are needed to estimate the breeding value of the dam accurately since dam's progenies do not generally play a significant role on accuracy due to their low number (compared to the number of paternal half-sibs) in most domestic species. For that reason, the maternal half-sibs were ignored in our modelling. However, it was verified that convergence of PEV was the same for a few maternal half-sibs (below 10) as for none. When a large number of the paternal half-sibs of the dam are known, the estimated breeding value of the dam is better assessed and thus plays a greater role in the accuracy of the estimated breeding value of its progeny; consequently, the PEV of the candidate converges slowly. When only a small number of paternal half-sibs of the dam and of the dam's ancestors are known, the PEV of the candidate is not significantly modified by the small increase in the accuracy of its dam's estimated breeding value.

Convergence of PEV is greatly delayed by the estimation of a mean. Whereas a three-generation index is sufficient to get the asymptotic value of PEV without estimation of fixed effects, a five-generation index is insufficient to get the asymptotic PEV when an overall mean is estimated. The PEV for a five-generation index is still 3% to 6% larger than that for a six-generation index. However, such an error for the asymptotic value of PEV does not significantly modify the prediction of asymptotic genetic gain. The corresponding error for asymptotic genetic gain is inferior to 2%. In practice, the impact of the estimation of the overall mean would be significantly decreased since it will concern the whole population and not only a candidate and its nearest relatives. However, the numbers of fixed effects and levels of fixed effects are really important. Hence, the asymptotic PEV in practical situations is likely to be obtained only after considering a greater number of ancestral generations than is shown in Table 2. If

Table 2 Successive ratios of PEV according to the number of ancestral generations

h^2	Ratio of PEVs[b]	$n=10$[a]		$n=100$		$n=1000$	
		No fixed effects	Mean	No fixed effects	Mean	No fixed effects	Mean
0.1	PEV_2/PEV_3	1.033	1.039	1.058	1.067	1.075	1.093
	PEV_3/PEV_4	1.012	1.040	1.014	1.083	1.017	1.117
	PEV_4/PEV_5	1.004	1.035	1.003	1.070	1.004	1.092
	PEV_5/PEV_6	1.001	1.027	1.001	1.048	1.001	1.057
0.3	PEV_2/PEV_3	1.040	1.119	1.048	1.138	1.053	1.149
	PEV_3/PEV_4	1.009	1.102	1.008	1.127	1.008	1.139
	PEV_4/PEV_5	1.002	1.074	1.001	1.087	1.001	1.093
	PEV_5/PEV_6	1.000	1.047	1.000	1.051	1.000	1.053
0.5	PEV_2/PEV_3	1.027	1.218	1.028	1.212	1.029	1.214
	PEV_3/PEV_4	1.003	1.154	1.003	1.150	1.003	1.153
	PEV_4/PEV_5	1.001	1.095	1.001	1.089	1.001	1.089
	PEV_5/PEV_6	1.000	1.054	1.000	1.048	1.000	1.047

[a] n is the number of paternal half-sibs recorded

[b] PEV_x/PEV_{x+1} is the ratio of the x-generation index PEV to the x+1-generation index PEV

Table 3 Ratio of PEVs for a three-generation index to a four-generation index (1000 paternal-halfsibs considered) for a two-traits BLUP evaluation without fixed effects

Heritabilities	Genetic correlation						Environmental correlation
	+0.4			+0.8			
	R_{11}[a]	R_{22}	R_{12}	R_{11}	R_{22}	R_{12}	
0.1 & 0.1	1.010	1.010	0.969	1.006	1.006	0.999	−0.8
	1.016	1.016	1.012	1.014	1.014	1.013	0
	1.016	1.016	1.021	1.017	1.017	1.017	+0.8
0.3 & 0.3	1.009	1.009	1.078	1.006	1.006	0.987	−0.8
	1.008	1.008	0.999	1.006	1.006	1.002	0
	1.008	1.008	1.013	1.008	1.008	1.008	+0.8
0.5 & 0.5	1.007	1.007	1.020	1.007	1.007	0.949	−0.8
	1.003	1.003	0.995	1.003	1.003	0.997	0
	1.004	1.004	1.005	1.003	1.003	1.003	+0.8
0.1 & 0.3	1.014	1.005	0.861	1.008	1.002	0.994	−0.8
	1.015	1.008	1.005	1.011	1.007	1.006	0
	1.017	1.006	1.017	1.014	1.007	1.010	+0.8
0.3 & 0.5	1.008	1.004	1.010	1.021	1.004	0.978	−0.8
	1.008	1.003	0.996	1.007	1.003	0.999	0
	1.010	1.006	1.036	1.008	1.003	1.006	+0.8
0.1 & 0.5	1.016	1.003	1.184	1.010	1.002	0.991	−0.8
	1.016	1.003	1.000	1.010	1.003	1.001	0
	1.017	1.003	1.014	1.014	1.002	1.006	+0.8

[a] R_{ij} is the ratio of the covariances of prediction errors between trait i and trait j

fixed effects are ignored, as often occurs in deterministic modelling, then two generations of ancestors are sufficient to validate the assumption of constant PEV.

Table 3 gives the ratio of PEVs of a three-generation index to a four-generation index for a two-trait selection according to the number of paternal half-sibs and genetic and environmental parameters. If two traits are considered in the evaluation, the variances of the prediction errors for both traits converge at the same speed as for a single-trait evaluation, whatever the genetic and phenotypic parameters. However, the covariance between prediction errors does not necessarily converge at the same speed as the variances. Convergence for covariance is slower if genetic and environmental correlations have opposite signs. In any case, the variance of prediction error for the sum of both breeding values converges quickly. Hence, a limited number of ancestral generations included in the pedigree does not greatly influence the prediction of asymptotic genetic gain for a global breeding objective.

Comparison of selection index theory versus BLUP theory on the prediction of asymptotic genetic gains and variances

In the following section, it is assumed that sufficient information has been accumulated so that the PEV of the candidate for selection has reached its limiting value for a given genetic variance-covariance matrix. A three-generation index is considered without estimation of fixed effects. In an alternative index, the average progeny performance of 50 animals is added to the previously described three-generation index with 100 paternal half-sibs. In order to derive asymptotic selection index response, it is assumed that the population has already reached its steady-state under index selection. Thus, asymptotic genetic variance-covariance matrix and PEV are predicted by successive iterations of Eqs. 9 and 1 until convergence. Such a procedure corresponds to an index selection theory's approach. Results are compared to results obtained when PEV corresponds to a BLUP evaluation accounting for all information (performances and pedigree) from the unselected base population.

We also simulate a population with 400 males and 400 females born each generation. In order to compare the stochastic and the deterministic results (assuming an infinite population size), breeding values were generated and evaluation was performed ignoring inbreeding. The first two generations have undergone random selection. Subsequently, four generations of selection are considered by selecting the best 200 females and the best 40 males based on their estimated breeding value according to BLUP or selection index theory. Because preliminary results show that the population size was too small to avoid sampling problems for small heritabilities (0.1), it was doubled.

Table 4 Asymptotic genetic evolution: BLUP versus selection index theory for a single-trait selection

h^2		$n=10$[a]	$n=100$	$n=1000$	$n=100$ & 50 progeny
0.1	$\Delta G^*_\infty/\Delta G_\infty$	0.85	0.87	0.87	0.96
	$\sigma^{2*}_\infty/\sigma^2_\infty$	1.04	1.05	1.06	1.04
	σ_e^{2*}/σ_e^2	1.11	1.18	1.23	1.19
0.3	$\Delta G^*_\infty/\Delta G_\infty$	0.91	0.91	0.91	0.98
	$\sigma^{2*}_\infty/\sigma^2_\infty$	1.05	1.05	1.06	1.02
	σ_e^{2*}/σ_e^2	1.18	1.23	1.25	1.19
0.5	$\Delta G^*_\infty/\Delta G_\infty$	0.95	0.95	0.95	0.99
	$\sigma^{2*}_\infty/\sigma^2_\infty$	1.04	1.04	1.04	1.01
	σ_e^{2*}/σ_e^2	1.20	1.23	1.24	1.24

[a] n is the number of paternal half-sibs recorded when the selection index includes only ancestral and individual performance

$\Delta G^*_\infty/\Delta G_\infty$ is the ratio of asymptotic genetic gains for BLUP selection versus index selection; $\sigma^{2*}_\infty/\sigma^2_\infty$ is the ratio of asymptotic genetic variances for BLUP selection versus index selection; σ_e^{2*}/σ_e^2 is the ratio of initial variance of prediction error (constant under BLUP selection) versus the asymptotic value under index selection

Selection on a single trait

Table 4 presents ratios of asymptotic genetic gains and variances derived under both assumptions on PEV. Asymptotic genetic gain under BLUP selection theory is smaller than the genetic gain derived with the selection index theory, but higher asymptotic genetic variance is found. With the selection index theory, calculated PEV is smaller because it uses a smaller genetic variance (affected by selection). This decrease could be considered an artifact due to the fact that prior selection is inadequately considered in the selection index evaluation. Thus, accuracy of selection appears to be higher and, consequently, asymptotic genetic gains are predicted to be superior to those predicted under BLUP selection theory. The magnitude of the bias for variance is smaller (1–6%) than for genetic gain (1–15%). These biases seem to be nearly independent of selection rates but highly dependent on initial heritabilities and selection accuracies. Larger values of these parameters lead to better agreement between selection index theory and BLUP selection theory. When candidates for selection are evaluated without their own progeny performance, correct estimation of genetic gain and variance is difficult to obtain by selection index theory unless very high heritability (over 0.5) is concerned. Thus, selection index theory overestimates real genetic progress when a large pedigree is considered unless very accurate selection indexes are considered; if initial PEV is small, its reduction due to selection has no impact on asymptotic results.

The fact that selection index theory overestimates the asymptotic genetic gain and underestimates the asymptotic genetic variance is confirmed by the stochastic results presented in Tables 5 and 6, respectively. The overestimation

Table 5 BLUP versus selection index theory for a single-trait selection: simulation results and asymptotic prediction of genetic gain per generation

Heritability	Methodology	First-generation observed genetic gain	Second-generation observed genetic gain	Third-generation observed genetic gain	Fourth-generation observed genetic gain	Asymptotic predicted genetic gain
0.1[a]	BLUP	0.149 (0.015)	0.149 (0.021)	0.149 (0.025)	0.151 (0.023)	0.147
	selection index	0.149 (0.015)	0.139 (0.020)	0.145 (0.023)	0.141 (0.021)	0.172
0.3[b]	BLUP	0.397 (0.039)	0.354 (0.042)	0.350 (0.045)	0.356 (0.045)	0.357
	selection index	0.399 (0.037)	0.356 (0.043)	0.347 (0.044)	0.346 (0.045)	0.390
0.5[b]	BLUP	0.634 (0.042)	0.534 (0.051)	0.524 (0.045)	0.515 (0.048)	0.534
	selection index	0.628 (0.045)	0.529 (0.048)	0.520 (0.046)	0.519 (0.049)	0.562

[a] Expectation and standard deviation (given in brackets) correspond to 100 replicates for 400 females and 80 males selected among 800 candidates per sex each generation

[b] Expectation and standard deviation (given in brackets) correspond to 200 replicates for 200 females and 40 males selected among 400 candidates per sex each generation

Table 6 BLUP versus selection index theory for a single-trait selection: simulation results and asymptotic prediction of genetic variance

Heritability	Methodology	First-generation realized genetic variance	Fourth-generation realized genetic variance	Asymptotic predicted genetic variance
0.1[a]	BLUP	0.089 (0.004)	0.088 (0.005)	0.090
	selection index	0.089 (0.004)	0.088 (0.005)	0.087
0.3[b]	BLUP	0.243 (0.016)	0.238 (0.015)	0.243
	selection index	0.244 (0.016)	0.240 (0.016)	0.232
0.5[b]	BLUP	0.378 (0.023)	0.367 (0.024)	0.372
	selection index	0.379 (0.025)	0.370 (0.025)	0.358

[a] Expectation and standard deviation (given in brackets) correspond to 100 replicates for 400 females and 80 males selected among 800 candidates per sex each generation

[b] Expectation and standard deviation (given in brackets) correspond to 200 replicates for 200 females and 40 males selected among 400 candidates per sex each generation

of the asymptotic genetic gain under selection index is statistically highly significant and large: 22%, 13% and 8% for heritability 0.1, 0.3 and 0.5, respectively. The underestimation of the asymptotic genetic variance is small (below 3%), but statistically significant.

The stochastic results show that the asymptotic response under BLUP selection is fairly well predicted. Differences between the predicted asymptotic genetic gain and the observed genetic gain at the fourth generation of selection are below 4%. There is a slight underestimation (3%) at a small heritability, which is not statistically significant. To the contrary, a slight overestimation (4%) is found at a high heritability, which is statistically significant. This overestimation is probably related to sampling problems linked to a insufficient population size when comparing the stochastic results to the deterministic prediction derived for an infinite population size. Asymptotic genetic variances are well-predicted (errors below 3%), although the differences between the observed and the predicted asymptotic genetic gain are statistically significant. Asymptotic responses to BLUP selection are observed to be larger than selection index responses, while the predictions lead to the reverse conclusion. This illustrates the inability of selection index theory to correctly predict asymptotic genetic response.

Selection on equally important two traits

Results (Table 7) are presented for a three-generation index with 100 paternal half-sibs and no fixed effects. When both traits have the same heritability, all the factors that increase accuracy of the selection index (high heritability, highly positive genetic correlation, highly negative environmental correlation) favour the similarity between results from index and BLUP selection theories. Selection index theory is inadequate to predict asymptotic genetic gain for situations with small to medium heritabilities, negative genetic correlation and positive environmental correlation.

Table 7 Ratio (in %) of asymptotic genetic gain on the sum of two traits for BLUP versus selection index

Heritabilies	Genetic correlation				Environmental correlation
	−0.8	−0.4	+0.4	+0.8	
0.1 & 0.1	87	90	94	95	−0.8
	82	85	88	89	0
	80	84	86	87	+0.8
0.3 & 0.3	91	96	98	99	−0.8
	86	89	93	94	0
	84	87	90	91	+0.8
0.5 & 0.5	95	98	99	100	−0.8
	89	93	96	97	0
	87	90	94	95	+0.8
0.1 & 0.3	93	95	97	97	−0.8
	91	90	91	92	0
	96	93	92	92	+0.8
0.3 & 0.5	95	97	99	99	−0.8
	91	92	95	96	0
	92	91	94	95	+0.8
0.1 & 0.5	97	97	98	99	−0.8
	94	94	95	95	0
	98	97	96	96	+0.8

Implications

In a deterministic prediction of asymptotic genetic gain under BLUP selection, PEV must be considered as being constant over time. For that purpose, it seems sufficient to consider a three-generation index when no fixed effects are estimated. One must be aware that if fixed effects are considered, a much larger number of ancestral generations are necessary to reach the asymptotic value of PEV.

According to Dekkers' (1992) results, losses of variance are larger for selection on BLUP than for mass selection, but asymptotic response to selection on BLUP remains larger than the response to mass selection. Here, response to index selection with pedigree and information from three generations is larger than response on BLUP with the same amount of information considered. Such a result must be considered as an artifact, which demonstrates the inefficiency of the selection index theory to consider prior selection and thus to predict proper genetic gains and variances.

In applied "BLUP evaluation", the return to an unselected base population with sufficient pedigree information is only a theoretical framework. The evaluation and selection of animals are realized with a finite pedigree. Base genetic parameters are estimated from a limited pedigree involving selected animals and are therefore biased, which in turn biases PEV estimates. Thus, the question, which is not addressed here, is whether applied "BLUP estimation" of genetic gain is likely to overestimate real genetic gains, since genetic parameters and PEV are estimated from a selected base population.

References

Andersen S (1994) Calculation of response and variance reduction due to multi-stage and multiple-trait selection. Anim Prod 58:1–9

Bulmer MG (1971) The effect of selection on genetic variability. Am Nat 105:201–211

Dekkers JCM (1992) Asymptotic response to selection on best linear unbiased predictors of breeding values. Anim Prod 54:351–360

Fimland E (1979) The effect of selection on additive genetic parameters. Z Tierz Zuechtungsbiol 96:120–134

Gomez-Raya L, Burnside EB (1990) The effect of repeated cycles of selection on genetic variance, heritability and response. Theor Appl Genet 79:568–574

Henderson CR (1973) Sire evaluation and genetic trends. In: Proc Anim Breed Genet Symp in honor of Dr JL Lush, ADSA and ASAS, Champaign, Illinois, pp 10–41

Henderson CR (1982) Best linear unbiased prediction in populations that have undergone selection. In: Barton RA, Smith WC (eds) World Cong Sheep Beef Cattle, Vol 1. Dunmore Press, Palmerston North, New Zealand, pp 191–200

Itoh Y, Yamada Y (1987) Comparisons of selection indices achieving predetermined proportional gains. Génét Sél Evol 19:69–82

Meuwissen THE (1989) A deterministic model for the optimization of dairy cattle breeding based on BLUP breeding value estimates. Anim Prod 49:193–202

Rendel JM, Robertson A (1950) Estimation of genetic gain in milk yield by selection in a close herd of dairy cattle. J Genet 50:1–8

Stranden I, Mäntysaari EA, Mäki-Tanila A (1993) Change in genetic correlation due to selection using animal model evaluation. J Anim Breed Genet 110:412–422

Verrier E, Colleau JJ, Foulley JL (1993) Long-term effects of selection based on the animal model BLUP in a finite population. Theor Appl Genet 87:446–454

Villanueva B, Kennedy BW (1990) Effect of selection on genetic parameters of correlated traits. Theor Appl Genet 80:746–752

Villanueva B, Wray NR, Thompson R (1993) Prediction of asymptotic rates of response from selection on multiple traits using univariate and multivariate best linear unbiased predictors. Anim Prod 57:1–13

Wray NR, Hill WG (1989) Asymptotic rates of response from index selection. Anim Prod 49:217–227