Prediction of Rates of Inbreeding in Populations Selected on Best Linear Unbiased Prediction of Breeding Value

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Manuscript received August 5, 1999
Accepted for publication May 8, 2000

ABSTRACT

Predictions for the rate of inbreeding (ΔF) in populations with discrete generations undergoing selection on best linear unbiased prediction (BLUP) of breeding value were developed. Predictions were based on the concept of long-term genetic contributions using a recently established relationship between expected contributions and rates of inbreeding and a known procedure for predicting expected contributions. Expected contributions of individuals were predicted using a linear model, $u_{i(x)} = \alpha + \beta s_i$, where s_i denotes the selective advantage as a deviation from the contemporaries, which was the sum of the breeding values of the individual and the breeding values of its mates. The accuracy of predictions was evaluated for a wide range of population and genetic parameters. Accurate predictions were obtained for populations of 5–20 sires. For 20–80 sires, systematic underprediction of on average 11% was found, which was shown to be related to the goodness of fit of the linear model. Using simulation, it was shown that a quadratic model would give accurate predictions for those schemes. Furthermore, it was shown that, contrary to random selection, ΔF less than halved when the number of parents was doubled and that in specific cases ΔF may increase with the number of dams.

IN genetic evaluation of individuals, best linear unbiased prediction (BLUP; Henderson 1963, 1975) of additive genetic merit is an increasingly applied procedure in a variety of fields. Though developed in the context of livestock breeding programs, BLUP is now becoming an integral component of tree breeding (Kerr 1998), is being used in selection experiments, and has recently been introduced into fish breeding (Gjøen and Gjerde 1998). The BLUP procedure utilizes information of all relatives in an optimal way to give the most accurate prediction of additive genetic merit. BLUP, therefore, has become the method of choice for estimating breeding values of individuals from field records of large and complex pedigrees (Lynch and Walsh 1998). Selection on breeding values estimated using BLUP allows for increased genetic selection differentials and gives the highest response from a single cycle of selection (Goffinet 1983). For this reason, truncation selection on BLUP of additive genetic merit has often been regarded as the optimal selection procedure.

In most selection schemes, however, a balance needs to be found between short-term and long-term selection response. Selection schemes that maximize short-term response by utilizing all available information generally lead to increased rates of inbreeding (*e.g.*, Robertson 1961; Belonsky and Kennedy 1988; Toro *et al.* 1988). High rates of inbreeding (*i.e.*, small effective population size) cause a decrease in genetic variation and a decreased accumulation of mutational variance (*e.g.*, Lynch and Hill 1986; Keightley and Hill 1987; Wei *et al.* 1996), resulting in a reduction of long-term selection response and fitness. To safeguard the genetic variation of the population in the long term, the rate of inbreeding needs to be restricted to an acceptable level. Therefore, besides the expected selection response, one needs to know the expected rate of inbreeding before being able to choose among breeding schemes. This requires a method for predicting rates of inbreeding in populations undergoing BLUP selection, which is currently lacking.

The rate of inbreeding (ΔF) is proportional to the sum of squared longterm genetic contributions (Wray and Thompson 1990). Using genetic contributions, Wray and Thompson (1990) obtained accurate predictions of ΔF for populations undergoing mass selection. However, their method was complicated due to the recursive nature of the prediction procedure and the need for predicting the variance of long-term genetic contributions.

Recently, on the basis of the concept of long-term genetic contributions, a general procedure to predict rates of inbreeding in selected populations was presented by Woolliams *et al.* (1999) and Woolliams and Bijma (2000), simplifying and generalizing the approach of Wray and Thompson (1990). Using that pro-

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TABLE 1

Notations used

N_{m}, N_{f}, d	Number of sires, number of dams, mating ratio $d = N_{\mathrm{f}}/N_{\mathrm{m}}$
n_{o}, T	Number of offspring born per dam, total number of candidates
p_x, t_x	Selected proportion and standardized truncation point for sex x
i_x, k_x	Selection intensity, variance reduction coefficient for sex x
x	Subscript, $x = m$ or f denoting males or females
P, A, $\hat{A}$	Phenotype, breeding value, estimated breeding value (EBV)
$\mathbf{b}$, $\mathbf{x}_i$	6×1 vector of index weights, 6×1 vector of index information sources
σ^2_A, $\sigma^2_{\hat{A}}$	Additive genetic variance, variance of $\hat{A}$
ρ, h^2	Accuracy of selection, heritability
$\bar{\rho}_{\mathrm{FS}}$, $\bar{\rho}_{\mathrm{HS}}$	Sample correlation between EBVs of full sibs, and between EBVs of half sibs
ΔF, $r_{i(x)}$	Rate of inbreeding, long-term genetic contribution of individual i of sex x
$s_{i(x)}$, $\sigma^2_{s(x)}$	Selective advantage of individual i of sex x, variance of $s_{i(x)}$
$u_{i(x)}$	Expectation of $r_{i(x)}$ conditional on $s_{i(x)}$
α_x, β_x	Linear model for $u_{i(x)} = \alpha_x + \beta_x s_{i(x)}$
Π, π_{xy}	2×2 matrix of regression coefficients of $s_{\mathrm{offspring}}$ on s_{parent}, element of Π
Λ	2×2 matrix of regression coefficients of the number of selected offspring on s_{parent}
λ_{xy}, $\mu_x(y)$	Element of Λ, expected number of offspring of sex y selected from parent of sex x
$\mathbf{V}_{n(x)}$, $\Delta\mathbf{V}_{n(x)}$	2×2 matrix of variance of family size, deviation of $\mathbf{V}_{n(x)}$ from Poisson variance
δ_x	Correction term needed when $\Delta\mathbf{V}_{n(x)} \neq 0$, see Equations 1 and 9

cedure, Bijma *et al.* (2000) developed predictions of ΔF for populations with discrete or overlapping generations and mass selection. Woolliams and Bijma (2000) developed predictions for populations with discrete generations and sib-index selection.

The current article extends the procedure for predicting ΔF to populations with discrete generations that are selected on BLUP of additive genetic merit, using the general approach of Woolliams *et al.* (1999) and Woolliams and Bijma (2000). The accuracy of predictions is evaluated by comparing predictions to rates of inbreeding observed in simulated data. Furthermore, it is shown that with BLUP selection the relationship between ΔF and the size of the breeding scheme and between ΔF and the mating ratio differs qualitatively from those relationships with random selection. Finally, in discussion, the current prediction method is compared to an extension of the method of Burrows (1984a,b).

DERIVATION OF EXPRESSIONS

Population structure: This section describes the trait and the population structure for which rates of inbreeding were predicted. The model described in this section was also used in the stochastic simulations (see also Bijma *et al.* 2000 for details on the simulation procedure). Table 1 shows the notation used. The infinitesimal model was assumed. Phenotypic values were the sum of additive genetic values (breeding values) and environmental values, $P = A + E$. Heritability was $h^2 = \sigma^2_A/\sigma^2_P$, where σ^2_A is the additive genetic variance and σ^2_P is the phenotypic variance.

A population with discrete generations was modeled. Every generation, $\frac{1}{2}T$ male selection candidates and $\frac{1}{2}T$ female selection candidates were ranked on the BLUP of their breeding value (*i.e.*, the estimated breeding value, denoted as $\hat{A}$), and the highest ranking N_{m} males and N_{f} females were selected to become sires and dams of the next generation. Each sire was mated at random to $d = N_{\mathrm{f}}/N_{\mathrm{m}}$ dams and each dam produced n_{o} offspring ($\frac{1}{2}n_{\mathrm{o}}$ of each sex). The total number of offspring born per generation equaled, therefore, $T = n_{\mathrm{o}}N_{\mathrm{f}}$, so that selected proportions were $p_{\mathrm{m}} = 1/(\frac{1}{2}n_{\mathrm{o}}d)$ and $p_{\mathrm{f}} = 1/(\frac{1}{2}n_{\mathrm{o}})$. Selection and mating were iterated until equilibrium genetic variances (Bulmer 1971) were reached (see appendix a). The current prediction uses those equilibrium genetic variances.

Pseudo-BLUP selection index: To allow deterministic prediction of ΔF, BLUP selection was approximated by the pseudo-BLUP selection index of Wray and Hill (1989). As shown by Wray and Hill (1989), this selection index analogy of BLUP very closely approximates true BLUP selection. The Wray and Hill (1989) index was simplified by using an orthogonal reparameterization of the information sources, so that most information sources are independent. (The reparameterized index is a BLUP analogy of the Wray *et al.* 1994 sib index.) The advantage is that the (co)variance matrix of the information sources contains only a few nonzero elements. The reparameterized index for the *i*th candidate was $\hat{A} = \mathbf{b}^{\mathrm{T}}\mathbf{x}_i$, where T denotes the transpose, $\hat{A}_i$ is the estimated breeding value (EBV), $\mathbf{b}$ is a (6×1) vector of weights, and $\mathbf{x}_i$ is a 6×1 vector of information sources for the *i*th candidate. Information sources in $\mathbf{x}_i$ were as follows: (1) $\hat{A}_{\mathrm{m}}$, the EBV of the sire of i; (2) $(\hat{A}_{\mathrm{f}} - \bar{\hat{A}}_{\mathrm{f}})$, the EBV of the dam of i measured as a deviation from the average EBV of the d dams mated to the sire; (3) $\bar{\hat{A}}_f$; (4) $\bar{P}_{\mathrm{HS}}$, the phenotypic average of the $n_{\mathrm{o}}d$ half sibs of i (including i and its full sibs); (5) $(\bar{P}_{\mathrm{FS}} -$

$\bar{P}_{\mathrm{HS}}$), the phenotypic average of the n_{o} full sibs of i (including i) measured as a deviation from the half sibs; and (6) ($P_i - \bar{P}_{\mathrm{FS}}$), the phenotype of candidate i measured as a deviation from its full sibs. Information sources 1 and 4, 3 and 4, and 2 and 5 are correlated; the others are mutually independent. Iterative equations for calculating index weights, the accuracy of selection (ρ), the correlation between estimated breeding values of full sibs and of half sibs (intraclass correlation, $\bar{\rho}_{\mathrm{FS}}$ and $\bar{\rho}_{\mathrm{HS}}$, where the bars denote the finite sample mean), and equilibrium variances (Bulmer 1971) are given in appendix a.

Prediction of rates of inbreeding

General: The prediction method is based on the concept of long-term genetic contributions. The long-term genetic contribution (r_i) of ancestor i in generation t_1 is defined as the proportion of genes from i that are present in individuals in generation t_2 deriving by descent from i, where $(t_2 - t_1) \rightarrow \infty$ (Woolliams *et al.* 1993). In the remainder of this article, long-term genetic contributions are referred to as "genetic contributions," or just "contributions."

Rates of inbreeding were predicted from

$$E(\Delta F) = \tfrac{1}{2}[N_{\mathrm{m}}E_s(u^2_{i(m)}) + N_{\mathrm{f}}E_s(u^2_{i(f)})] + \tfrac{1}{8}[N_{\mathrm{m}}\delta_{\mathrm{m}} + N_{\mathrm{f}}\delta_{\mathrm{f}}] \quad (1)$$

(assuming random mating; Woolliams and Bijma 2000), where E_s denotes the expectation with respect to the selective advantage, $u_{i(x)}$ is the expected genetic contribution of a parent of sex x conditional on its selective advantage $s_{i(x)}$ (*i.e.*, $u_{i(x)} = E[r_{i(x)}|s_{i(x)}]$), and δ_x is a term to correct the prediction of ΔF for deviations of the variance of family size ($\mathbf{V}_{n(x)}$, where $x = m$ or f), conditional on the selective advantage from independent Poisson variances. (The second term of Equation 1 is referred to as "term for deviations from Poisson.") Throughout this article, family size refers to the number of selected offspring of a parent, not to the number of selection candidates. The selective advantage may consist of any term that affects the long-term genetic contribution of an ancestor (*i.e.*, by affecting selection of its offspring or of more distant descendants); *e.g.*, it can be the breeding value.

To compute Equation 1, one needs to decide which elements should be included in the selective advantage. In the current prediction, the selective advantage of an individual is the sum of its breeding value and the breeding values of its mate(s) (although other choices are possible; see discussion). With mass selection, a selective advantage consisting of linear terms of the breeding value is sufficient for accurately predicting ΔF (Bijma *et al.* 2000). However, when more emphasis is placed on family information, higher-order terms may be required, as observed by Woolliams and Bijma (2000) for selection on a sib index. Therefore, two models are evaluated. First, the long-term genetic contribution is a linear function of the breeding value, denoted "linear model." Second, the long-term genetic contribution is a quadratic function of the breeding value, denoted "quadratic model." For the quadratic model, components of Equation 1 are estimated from simulated data; *i.e.*, no fully deterministic prediction is presented for the quadratic model.

Rates of inbreeding are predicted in three steps. First, expected genetic contributions [$u_{i(x)}$] are predicted using the method of Woolliams *et al.* (1999). Second, $E_{\mathrm{s}}(u^2_{i(x)})$ is derived, which enables calculation of the first term of Equation 1. Finally, δ_{m} and δ_{f} are derived, giving the term for deviations from Poisson. These steps are described in detail for the linear model, and modifications for the quadratic model are noted afterward.

Linear model: In the linear model, the selective advantage of sires was

$$s_{i(m)} = (A_{i(m)} + \bar{A}_{\mathrm{f}}) - \overline{(A_{\mathrm{m}} + \bar{A}_{\mathrm{f}})}, \quad (2)$$

where $A_{i(m)}$ is the breeding value of sire i, $\bar{A}_{\mathrm{f}}$ is the average breeding value of the d dams mated to sire i, and the second term represents subtraction of the average. For dams, the selective was

$$s_{i(f)} = [(A_{i(f)} + A_{\mathrm{m}}) - \overline{(A_{\mathrm{f}} + A_{\mathrm{m}})}], \quad (3)$$

where A_{m} is the breeding value of the sire (*i.e.*, the mate of dam i). Note that $s_{i(m)}$ and $s_{i(f)}$ are zero on average.

Step 1, prediction of expected contributions: Expected contributions ($u_{i(x)}$) were predicted by linear regression on the selective advantage. For both sexes, the model was

$$u_{i(x)} = E(r_{i(x)}|s_{i(x)}) = \alpha_x + \beta_x s_{i(x)}. \quad (4)$$

With discrete generations, $\alpha_{\mathrm{m}} = 1/(2N_{\mathrm{m}})$ and $\alpha_{\mathrm{f}} = 1/(2N_{\mathrm{f}})$ always. Solutions for β_{m} and β_{f} were obtained from a simplified form of Equations 7b and 8 of Woolliams *et al.* (1999),

$$\begin{bmatrix} N_{\mathrm{m}}\beta_{\mathrm{m}} \\ N_{\mathrm{f}}\beta_{\mathrm{f}} \end{bmatrix} = (\mathbf{I}_2 - \tfrac{1}{2}\Pi^{\mathrm{T}})^{-1}(\tfrac{1}{2}\Lambda^{\mathrm{T}}) \begin{bmatrix} N_{\mathrm{m}}\alpha_{\mathrm{m}} \\ N_{\mathrm{f}}\alpha_{\mathrm{f}} \end{bmatrix} \quad (5)$$

(since with discrete generations the gene-flow matrix can be replaced by 1/2), where $\mathbf{I}_2$ is the 2×2 identity matrix, Π is a 2×2 matrix of regression coefficients π_{xy}, being the regression coefficient of $s_{i(x)}$ of a selected offspring of sex x on $s_{j(y)}$ of its parent of sex y [*e.g.*, π_{12} is the regression coefficient of $s_{i(m)}$ of a selected male offspring on $s_{j(f)}$ of its dam], Λ is a 2×2 matrix of regression coefficients, λ_{xy} being the regression coefficient of the number of selected offspring of sex x on $s_{j,y}$ of the parent of sex y [*e.g.*, λ_{21} is the regression of the number of selected female offspring on $s_{i(m)}$ of its sire]. Matrices Π and Λ are calculated using the method of Woolliams *et al.* (1999) as outlined in appendix b of the current article.

Step 2, derivation of $E_s(u^2_{i(x)})$*:* Since all terms of the selective advantage are expressed as a deviation from their mean, expectations of squares are equal to variances, so that $E(s^2_{i(x)}) = \sigma^2_{s(x)}$. Therefore, squaring Equation 4 and taking expectations gives

$$E_s(u^2_{i(x)}) = \alpha^2_x + \beta^2_x\sigma^2_{s(x)}, \qquad (6)$$

and from Equations 2 and 3,

$$\sigma^2_{s(m)} = \sigma^2_{\mathrm{A}}[(1 - k_{\mathrm{m}}\rho^2) + (1 - k_{\mathrm{f}}\rho^2)/d](1 - 1/N_{\mathrm{m}}) \qquad (7)$$

$$\sigma^2_{s(f)} = \sigma^2_{\mathrm{A}}[(1 - k_{\mathrm{m}}\rho^2)(1 - 1/N_{\mathrm{m}}) + (1 - k_{\mathrm{f}}\rho^2)(1 - 1/N_{\mathrm{f}})], \qquad (8)$$

where k_x is Pearson's (1903) variance reduction coefficient (Falconer and Mackay 1996, p. 201).

Step 3, calculation of δ_m *and* δ_f: The term for deviations from Poisson (*i.e.*, the second term of Equation 1) requires the calculation of δ_x. As an approximation, Woolliams and Bijma (2000) and Bijma *et al.* (2000) used $\delta_x = \boldsymbol{\alpha}^{\mathrm{T}}\Delta\mathbf{V}_{n(x)}\boldsymbol{\alpha}$, where $\boldsymbol{\alpha}^{\mathrm{T}} = (\alpha_{\mathrm{m}}\ \alpha_{\mathrm{f}})$ and $\Delta\mathbf{V}_{n(x)}$ is the 2 × 2 matrix of deviations of the variance of family size from independent Poisson variances. For example, $\Delta\mathbf{V}_{n(m)}(1, 1)$ is the deviation of the variance of the number of selected male offspring of a sire from the Poisson variance, and $\Delta\mathbf{V}_{n(m)}(1, 2)$ is the full covariance between the number of selected male and female offspring, since independent Poisson variances would result in no covariances. When calculating δ_x, the approximation $\delta_x = \boldsymbol{\alpha}^{\mathrm{T}}\Delta\mathbf{V}_{n(x)}\boldsymbol{\alpha}$ accounts only for the average contribution of an offspring (*i.e.*, α), whereas the effect of the selective advantage of the parent on the contribution of its offspring is ignored. This effect can be included by using

$$\delta_x = E_s[\mathbf{u}^{*\mathrm{T}}_{i(x)}\Delta\mathbf{V}_{n(x),i}\mathbf{u}^*_{i(x)}] \qquad (9)$$

(see Equations 25–27 of Woolliams and Bijma 2000), where $\mathbf{u}^{*\mathrm{T}}_{i(x)} = (u^*_{j(m)}, u^*_{j(f)})_x$, with $u^*_{j(y)} = E(r_{j(y)}|s_{i(x)}, j$ is offspring of $i)$, which is the expected contribution of selected offspring j of sex y given the selective advantage $s_{i(x)}$ of its parent i of sex x. The terms $\mathbf{u}^*_{i(x)}$ and $\Delta\mathbf{V}_{n(x),i}$ are assumed independent and $\mathbf{u}^*_{i(x)}$ is calculated from

$$\mathbf{u}^*_x = \begin{bmatrix} \alpha_{\mathrm{m}} + \beta_{\mathrm{m}}\pi_{mx}s_{i(x)} \\ \alpha_{\mathrm{f}} + \beta_{\mathrm{f}}\pi_{fx}s_{i(x)} \end{bmatrix}, \qquad (10)$$

where π, as defined in Equation 5, represents the transfer of the selective advantage from the parent to the offspring.

Equation 9 requires the calculation of $\Delta\mathbf{V}_{n(x)}$. With fixed n_{o}, family size follows a correlated hypergeometric distribution and the variance of family size can be approximated using a result of Burrows (1984a,b), as described in detail in appendix d of Woolliams and Bijma (2000). Here we outline only the concept for a single sex, without giving the derivation. Detailed equations are given in appendix b.

In general, variance of family size equals $\mathrm{Var}(n_i) = E[n_i^2] - E[n_i]^2$, where n_i denotes family size after selection, conditional on the selective advantage. Diagonal elements of $\mathbf{V}_{n(x)}$ represent the variance of the number of selected offspring of a particular sex, and, with $n_i \sim$ Poisson, $\mathrm{Var}(n_i) = E(n_i)$, so that for diagonal elements deviations from Poisson variances are

$$\begin{aligned} \Delta\mathbf{V}_{n(x)} &= E_s\{E[n_i^2] - E[n_i]^2 - E[n_i]\} \\ &= E_s\{E[n_i(n_i - 1)]\} - E_s\{E[n_i]^2\}. \end{aligned} \qquad (11)$$

Off-diagonal elements of $\mathbf{V}_{n(x)}$ represent the covariance between the number of selected male and female offspring and are obtained following the same approach as for the diagonal elements (appendix b).

From Burrows (1984a),

$$\begin{aligned} &E_s\{E[n_i(n_i - 1)]\} \\ &\quad\approx [n(n-1)N(N-1)]/[T(T-1)R(p, \bar{\rho}_{\mathrm{fam}})], \end{aligned} \qquad (12)$$

where n is the number of candidates per family, N is the total number selected, T is the total number of candidates, and $R(p, \bar{\rho}_{\mathrm{fam}})$ is the ratio of the probability of selecting two arbitrary candidates over the probability of selecting two family members, where p is the selected proportion and $\bar{\rho}_{\mathrm{fam}}$ is the intraclass correlation between family members. The probability of selecting two family members can be approximated using a result of Mendel and Elston (1974; see appendix b). Wray *et al.* (1990) observed that Equation 12 gives substantial bias in cases where the number of parents is small compared to the number of offspring per parent and suggested an adjustment to the selected proportion,

$$p_{x,\mathrm{adj}} = (1 - \bar{\rho}_{\mathrm{fam}})p_x + \bar{\rho}_{\mathrm{fam}}\max(p_x, 1/N_{\mathrm{m}}). \qquad (13)$$

In Equation 13, $p_{x,\mathrm{adj}}$ is a weighted sum of the original selected proportion and the selected proportion when selecting between families. Thus Equation 13 accounts for the fact that, with large $\bar{\rho}_{\mathrm{fam}}$, selection moves toward between-family selection. This is particularly important when there are few families with a large number of candidates per family, so that selection needs to involve only one or two families. For schemes with few parents ($N_{\mathrm{m}} = 5$ or 10), selection intensities and variance reduction coefficients were recalculated using $p_{x,\mathrm{adj}}$ and used in the calculation of $R(p_x, p_y, \bar{\rho}_{\mathrm{fam}})$.

In Equation 11, the term $E_s\{E[n_i]^2\}$ denotes the expectation of the square of the expected number of selected offspring conditional on the selective advantage (denoted μ). This term can be obtained from $E\{E[n_i]^2\} = E_s\{\mu^2\} = E_s\{[\bar{\bar{n}}(1 + \lambda s)]^2\}$, where $\bar{\bar{n}}$ is the overall expected number of offspring selected per parent (*e.g.*, $\bar{\bar{n}} = 1$ male offspring per sire and $\bar{\bar{n}} = d$ female offspring per sire, since population size is constant over time) and λs represents the change of the expected number of selected offspring due to the selective advantage of the parent. The extension to two sexes and a hierarchical mating structure is described in detail in Appendix D of Woolliams and Bijma (2000). The resulting equations for calculating $\Delta\mathbf{V}_{n(x)}$ used in the current prediction and more details on the calculation of Equations 9 and 10 are in appendix b. An example of computation is in Bijma and Woolliams (2000).

Quadratic model: With the quadratic model, the selective advantage consists of two terms. For sires, $\mathbf{s}_{i(m)}^{\mathrm{T}} = (s_{i,1},\ s_{i,2})$, where

$$s_{i,1} = (A_{i(m)} + \bar{A}_{\mathrm{f}}) - \overline{(A_{\mathrm{m}} + \bar{A}_{\mathrm{f}})} \tag{14}$$

$$s_{i,2} = s_{i,1}^2 - \overline{s_{i,1}^2}. \tag{15}$$

For dams, $\mathbf{s}_{i(f)}^{\mathrm{T}} = (s_{i,3},\ s_{i,4})$, where

$$s_{i,3} = (A_{\mathrm{m}} + A_{i(f)}) - \overline{(A_{\mathrm{m}} + A_{\mathrm{f}})} \tag{16}$$

$$s_{i,4} = s_{i,3}^2 - \overline{s_{i,3}^2}. \tag{17}$$

For the quadratic model, components needed to compute Equation 1 were estimated from simulated data. For step one, β was estimated as the multiple regression of the long-term contribution of ancestors on their selective advantage (*e.g.*, for sires, $\beta_{(\mathrm{m})}^{T} = (\beta_1,\ \beta_2)$ was the multiple regression of the long-term contribution of sires on $s_{i,1}$ and $s_{i,2}$). For step two, the (co)variance matrix of $s_{i,1}$ through $s_{i,4}$ was estimated from the simulated data and the first term of Equation 1 was calculated analogous to Equation 6. For step three, $\mathbf{V}_{n(x)}$ and Λ were estimated from simulated data and the term for deviations from Poisson was calculated analogous to Equations 9 and 10.

RESULTS

Accuracy of predictions

Linear model: For the linear model, the accuracy of predictions was tested over a wide range of values: all combinations of N_{m} = 5, 10, 20, 40, 60, or 80; d = 1, 2, 3, 5, or 10; n_{o} = 4, 8, or 16; and h^2 = 0.1, 0.2, 0.4, or 0.6 were evaluated (due to computational restrictions, N_{f} was restricted to be ≤200; *e.g.*, for N_{m} = 80 only d = 1 and d = 2 were evaluated).

Three different ranges of results could be identified, exemplified in Tables 2 to 4. First, despite very large rates of inbreeding (up to 12.5%), accurate predictions were obtained for schemes with N_{m} = 5 or 10 (Table 2). For those schemes, the term for deviations from Poisson was calculated using adjusted selected proportions according to Equation 13. The maximum relative error encountered for schemes with N_{m} = 5 or 10 was 12%, which occurred with N_{m} = 5, d = 2, h^2 = 0.1, and n_{o} = 16. For schemes with N_{m} = 5 or 10, the average relative error was −2% and the standard deviation of the relative error was 5%.

Second, a range with accurate predictions was found for N_{m} = 20 (Table 3). For the schemes in Table 3, most errors were negative, with a maximum of −9%. For N_{m} = 20, d = 10, n_{o} = 16, and h^2 = 0.1 (data not shown), an overprediction of 37% was encountered, which was due to bias in Equation 12, and was reduced to −13% when $p_{x,\mathrm{adj}}$ (Equation 13) was used. Note that this is an extreme scheme (*i.e.*, $\bar{i}_{\mathrm{m}}$ = 2.59, $\bar{\rho}_{\mathrm{FS}}$ = 0.86, $\bar{\rho}_{\mathrm{HS}}$= 0.59, ΔF_{sim} = 0.0495).

TABLE 2

Rates of inbreeding from simulation (ΔF_{sim}) and corresponding prediction errors for a population with 10 sires

		n_{o} = 4		n_{o} = 16	
N_{f}	h^2	ΔF_{sim}[a]	Error (%)	ΔF_{sim}[a]	Error (%)
20	0.1	0.0347	−8	0.0917	+11
	0.2	0.0323	−4	0.0794	+8
	0.4	0.0289	−5	0.0623	+0
	0.6	0.0253	−5	0.0474	−4
100	0.1	0.0378	−4	0.0700	−1
	0.2	0.0333	−4	0.0609	−9
	0.4	0.0269	−5	0.0452	−10
	0.6	0.0224	−5	0.0341	−10

Predictions were obtained using $p_{x,\mathrm{corr}}$ (Equation 13). N_{f}, number of dams; h^2, initial heritability; n_{o}, number of offspring per dam; error (%), 100% × $(\Delta F_{\mathrm{pred}} - \Delta F_{\mathrm{sim}})/\Delta F_{\mathrm{sim}}$; ΔF_{pred}, predicted rate of inbreeding from Equation 1 with linear model.

[a] Standard errors of ΔF_{sim} were ≤1% of the estimate.

Third, underpredictions were found for schemes with many sires and n_{o} = 8 or 16. Table 4 shows the prediction errors for N_{m} = 80, d = 2, and n_{o} = 16, where errors up to −19% were found. These were the largest errors encountered throughout the whole range evaluated. To

TABLE 3

Simulated (ΔF_{sim}) rates of inbreeding and corresponding prediction errors for a population with 20 sires

		n_{o} = 4		n_{o} = 8	
N_{f}	h^2	ΔF_{sim}[a]	Error (%)	ΔF_{sim}[a]	Error (%)
20	0.1	0.0182	−5	0.0393	−2
	0.2	0.0174	−2	0.0359	−3
	0.4	0.0158	−1	0.0295	−4
	0.6	0.0143	−2	0.0239	−6
40	0.1	0.0184	−9	0.0361	−3
	0.2	0.0171	−5	0.0314	−3
	0.4	0.0151	−5	0.0251	−6
	0.6	0.0130	−5	0.0201	−9
60	0.1	0.0188	−9	0.0350	−2
	0.2	0.0172	−6	0.0305	−4
	0.4	0.0146	−5	0.0230	−5
	0.6	0.0123	−4	0.0181	−7
100	0.1	0.0199	−7	0.0347	3
	0.2	0.0178	−6	0.0294	−2
	0.4	0.0145	−6	0.0220	−5
	0.6	0.0121	−6	0.0168	−7

N_{f}, number of dams; h^2, initial heritability; n_{o}, number of offspring per dam; error (%), 100% × $(\Delta F_{\mathrm{pred}} - \Delta F_{\mathrm{sim}})/\Delta F_{\mathrm{sim}}$; ΔF_{pred}, predicted rate of inbreeding from Equation 1 with linear model.

[a] Standard errors of ΔF_{sim} were ≤1% of the estimate.

TABLE 4

Simulated rates of inbreeding (ΔF_{sim}) and corresponding prediction errors for a population with 80 sires, 160 dams, and 16 offspring per dam

h^2	ΔF_{sim}[a]	Error (%)[b]	Error (%)[c]	Error (%)[d]
0.1	0.0210	−17	−19	−7
0.2	0.0171	−19	−19	−6
0.4	0.0114	−17	−16	−5
0.6	0.0079	−15	−12	−4

h^2, initial heritability.

[a] Standard errors of ΔF_{sim} were ≤1% of the estimate.

[b] Error from full prediction with linear model.

[c] Error from linear model with components of Equation 1 estimated from simulation.

[d] Error from quadratic model with components of Equation 1 estimated from simulation; error (%), 100% × ($\Delta F_{\mathrm{pred}} - \Delta F_{\mathrm{sim}})/\Delta F_{\mathrm{sim}}$; ΔF_{pred}, predicted rate of inbreeding from Equation 1.

TABLE 5

Simulated (ΔF_{sim}) and predicted rate of inbreeding with (ΔF_{pred}) or without (ΔF_{pred}) the term for deviations from Poisson

n_o	h^2	ΔF_{sim}[a]	ΔF_{pred}[b]	ΔF_{pred}[c]
4	0.1	0.0184	−9	−25
	0.2	0.0171	−6	−14
	0.4	0.0151	−6	−4
	0.6	0.0130	−5	+5
16	0.1	0.0602	+9	−52
	0.2	0.0511	+2	−42
	0.4	0.0374	−4	−32
	0.6	0.0280	−9	−24

For $N_m = 20$, $N_f = 40$; h^2, initial heritability; n_o, number of offspring per dam.

[a] Standard errors of ΔF_{sim} were ≤1% of the estimate.

[b] Predicted rate of inbreeding with the term for deviations from Poisson.

[c] Predicted rate of inbreeding without the term for deviations from Poisson.

identify the origin of the underprediction, components of Equation 1 were estimated from simulated data (for the linear model) and ΔF was predicted from Equation 1 using those estimates (Table 4). However, this did not remove the underprediction, which indicates that components of Equation 1 were predicted accurately for the linear model, but the linear model is insufficient for predicting ΔF when the number of parents is large, irrespective of ΔF.

The accuracy of predictions for schemes that are not included in Tables 2, 3, or 4 showed values in the range of the schemes presented in the tables. For example, for $N_m = 40$, $d = 2$, and $n_o = 4$, prediction errors were −9, −7, −3, and −5% for $h^2 = 0.1$, 0.2, 0.4, and 0.6, respectively. The average error for schemes with $N_m \geq 40$ was −10%.

Contribution of the term for deviations from Poisson to E[ΔF]: The prediction procedure would be simplified considerably if the term for deviations from Poisson could be ignored or simplified. Therefore, ΔF was predicted omitting this term. Prediction errors in Table 5 reveal that the term for deviations from Poisson showed positive values in most cases and became very large for schemes with large n_o and low h^2. For the schemes in Table 5, the term for deviations from Poisson contributed up to 55% of the total value. For $N_m > 20$, $n_o = 16$, and $h^2 = 0.1$ (data not shown), even larger contributions were found. These large values of the term for deviations from Poisson are due to remaining correlations between selection probabilities of sibs after conditioning on the linear effect of the selective advantage (see DISCUSSION).

We investigated whether the term for deviations from Poisson can be simplified by ignoring any terms due to β, in which case Equations B32 and B33 can be omitted. However, this increased the underprediction for schemes with $N_m > 20$, $n_o = 16$, and $h^2 = 0.1$ or 0.2 by ~8 and 4%, respectively. For example, for the schemes in Table 4, prediction errors became −25, −23, −18, and −16%. For schemes with $n_o = 4$ or schemes with $h^2 > 0.2$, prediction errors were only slightly affected. Therefore, Equations B32 and B33 are required only for schemes with $n_o > 4$, $N_m > 20$, and $h^2 \leq 0.2$.

Quadratic model: For schemes where the linear model showed underprediction, ΔF was predicted using the quadratic model with components of Equation 1 estimated from simulation. Table 4 shows that the prediction error reduces from a maximum of −19% for the linear model to a maximum of −7% for the quadratic model. For schemes with $N_m \geq 40$, the average relative error was only −2% with a standard deviation of 3% for the quadratic model, whereas for the linear model the average relative error was −11% with a standard deviation of 5%.

Goodness of fit: Figures 1 and 2 show the relationship between the selective advantage [$s_{i(m)}$] and the genetic contribution for sires from the linear model, the quadratic model, and the relationship observed in the simulated data for $N_m = 80$, $d = 2$, $h^2 = 0.4$, and $n_o = 4$ or 16. For the linear model, predicted β was almost identical to β estimated from the simulations and, therefore, only the predicted relationship is presented. For $n_o = 4$ (Figure 1), there is a relatively small difference between the linear and the quadratic fit, and the linear model showed only −3% error. (Approximately 95% of the individuals were within ± 2 SD, so deviations outside this range have limited impact.) For $n_o = 16$ (Figure 2), there is substantial nonlinearity, and the quadratic fit is better than the linear fit (*e.g.*, the linear model assigned negative contributions to all individuals below −0.8 SD). For this scheme, the linear prediction showed −17% error *vs.* −6% for the quadratic model.

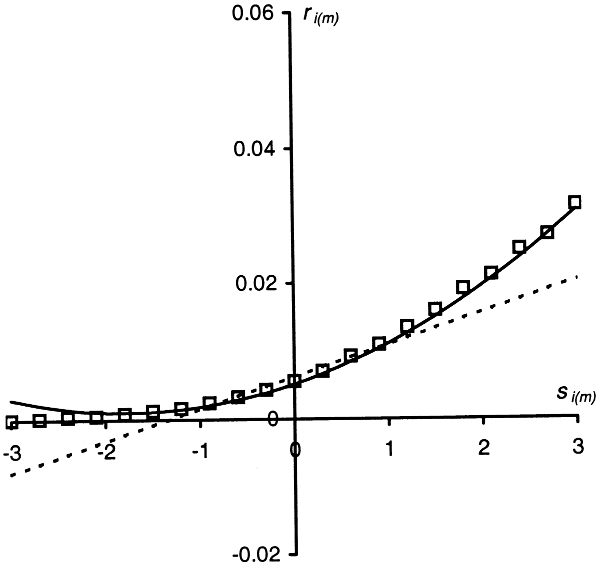

FIGURE 1.—Relation between the genetic contribution ($r_{i(m)}$) and the selective advantage ($s_{i(m)}$) for sires, with N_m = 80, d = 2, h^2 = 0.4, and n_o = 4. (···) Linear model; (—) quadratic model; (□) observed in simulated data. Note that $s_{i(m)}$ is in SD.

TABLE 6

Relation between the rate of inbreeding and the number of parents

	$h^2 = 0.1$, $n_o = 16$		$h^2 = 0.6$, $n_o = 4$	
N_m	ΔF_{sim}[a]	Reduction[b]	ΔF_{sim}[a]	Reduction[b]
5	0.1252	—	0.0483	—
10	0.0917	0.27	0.0253	0.48
20	0.0602	0.34	0.0130	0.49
40	0.0364	0.40	0.0066	0.49
80	0.0210	0.42	0.0033	0.50

For a mating ratio of 2; N_m, number of sires; h^2, initial heritability; n_o, number of offspring per dam.

[a] Standard errors of ΔF_{sim} were $\leq$1% of the estimate.

[b] Reduction, *e.g.*, (0.1252 − 0.0917)/0.1252 = 0.27.

Comparing Figures 1 and 2 shows that with increasing selection intensity, the contributions are increasingly affected by the selective advantage (*i.e.*, the slope of the linear fit increases) and that for positive values of the selective advantage the slope becomes steeper, whereas for negative values the slope becomes flatter. For example, for n_o = 16, all individuals with a negative selective advantage are expected to make the same (*i.e.*, almost zero) genetic contribution, whereas for individuals with a positive selective advantage, the genetic contribution increases rapidly with the selective advantage. For the schemes in Figures 1 and 2, respectively, 31 and 68% of the selected sires made no long-term contribution at all. For low heritabilities, the nonlinearity was even more extreme, *e.g.*, for N_m = 80, N_f = 160, n_o = 16, and h^2 = 0.1, 83% of the sires had zero long-term contribution. (The linear model predicted negative contributions for ~20% of the sires.) Not surprisingly, this scheme gives an extremely large rate of inbreeding, ΔF_{sim} = 0.0210 (Table 4), almost 10 times that with random selection and 6.6 times that with mass selection.

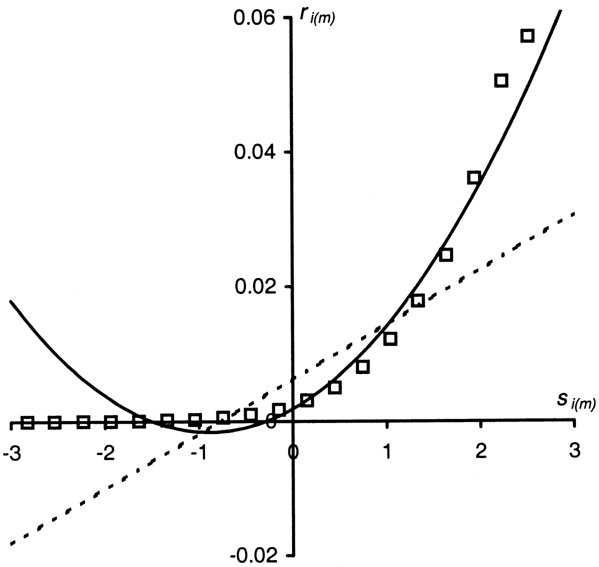

FIGURE 2.—Relation between the genetic contribution ($r_{i(m)}$) and the selective advantage ($s_{i(m)}$) for sires, with N_m = 80, d = 2, h^2 = 0.4, and n_o = 16. (···) Linear model; (—) quadratic model; (□) observed in simulated data. Note that $s_{i(m)}$ is in SD.

Relationship between ΔF and population parameters

Relationship between ΔF and the number of parents: Table 6 shows the relationship between ΔF and the number of parents for d = 2. In the absence of selection, $E(\Delta F) \approx 1/(8N_m) + 1/(8N_f)$ (FALCONER and MACKAY 1996), showing that with random selection the rate of inbreeding halves when the number of parents is doubled. However, for BLUP selection with h^2 = 0.2 and n_o = 16, the rate of inbreeding less than halves when doubling the number of parents. For example, when N_m increased from 5 to 10, ΔF reduced by only 27%. For h^2 = 0.6 and n_o = 4, the reduction was closer to 50%. SANTIAGO and CABALLERO (1995) observed a similar pattern for mass selection, but here the effect is much larger.

The difference in the effect of doubling the number of parents with and without selection is due to the effect of a finite number of families on the intraclass correlation between sibs and on the variance of family size. For example, when N_m decreased from 80 to 5, the intraclass correlations between sibs decreased from $\bar{\rho}_{FS} = 0.86$ and $\bar{\rho}_{HS} = 0.55$ to $\bar{\rho}_{FS} = 0.78$ and $\bar{\rho}_{HS} = 0.40$ for schemes with h^2 = 0.1 and n_o = 16. This reduction of the intraclass correlation was accurately predicted using the current method (see APPENDIX A). Additionally, for schemes with N_m = 5 or 10, the correction of

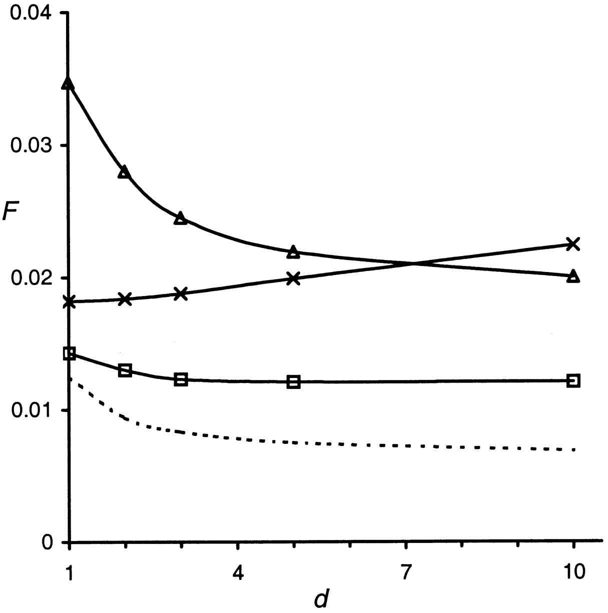

FIGURE 3.—Relation between the rate of inbreeding (ΔF) and the mating ratio (d) for $N_m = 20$. (···) Random selection; (□) $n_o = 4$, $h^2 = 0.6$; (×) $n_o = 4$, $h^2 = 0.1$; (Δ) $n_o = 16$, $h^2 = 0.6$.

the selected proportions (Equation 13) further reduces $\mathbf{V}_{n(x)}$ and this reduction is greater with higher intraclass correlation, which reduces ΔF proportionally more for schemes with large emphasis on family information (*i.e.*, large n_o and low h^2). For such schemes, increasing the number of parents is an inefficient way of reducing ΔF.

Relationship between ΔF and mating ratio: With random selection, ΔF decreases when the number of sires is kept constant and the number of dams is increased. BIJMA *et al.* (2000) found a similar pattern for mass selection. Figure 3 shows the relationship between ΔF and the mating ratio for BLUP selection with $N_m = 20$. (Note that n_o remains constant.) The dotted line represents random selection, for which $\Delta F = 1/(8N_m) + 1/(8N_f)$, and serves as a reference. Surprisingly, for $n_o = 4$ and $h^2 = 0.1$, Figure 3 shows an increase of ΔF when N_f increases. This increase is due to an increased male selection intensity when d increases, *i.e.*, for $d = 1$, $p_m = 20/(20 \times 1 \times 4 \times 1/2) = 0.5 \rightarrow i_m = 0.798$, whereas for $d = 10$, $p_m = 0.05 \rightarrow i_m = 2.063$. An increased selection intensity results in an increased Λ (see Equations B1 and B2), which increases the term $E(u^2_{i(m)})$ in Equation 1. Additionally, decreased selected proportions result in an increased variance of family size, increasing δ_m. Together, both effects more than compensate for the reduction of the term due to dams (*i.e.*, $N_f E[u^2_{i(f)}]$ and $N_f\delta_f$, which are approximately proportional to $1/N_f$) for schemes with low h^2 and low n_o. For high h^2, the effect of selection intensity on the rate of inbreeding is smaller, and consequently there was only a small effect of d on ΔF for $n_o = 4$ and $h^2 = 0.6$. For $n_o = 16$ and $h^2 = 0.6$, the relationship was similar to random selection. For schemes with high n_o, selection intensity among males is already reasonably large, so that the increase of i_m with d is limited. Therefore, those schemes showed a decrease of ΔF with increasing d (*e.g.*, this was found for $N_m = 20$, $n_o = 16$, and $h^2 = 0.1$, data not shown). When instead of n_o, the total number of offspring was kept constant [*i.e.*, by using $n_o = T/(N_m d)$], the rate of inbreeding always decreased with increasing d.

DISCUSSION

This article has presented a method to predict the rate of inbreeding in populations with discrete generations undergoing BLUP selection, which has not been possible until now. The method is based on the concept of long-term genetic contributions (WRAY and THOMPSON 1990), using the recently established relationship between rates of inbreeding and expected genetic contributions (WOOLLIAMS and BIJMA 2000) and the method of WOOLLIAMS *et al.* (1999) for predicting expected genetic contributions.

Quantitative genetics theory: The results have verified the theory developed by WOOLLIAMS and BIJMA (2000), showing that the simple form of the relationship between ΔF and expected contributions derived in that article can be applied to challenging selection indices. Examination of the results showed that this relation (*i.e.*, Equation 1) was accurate over a range of ΔF from 0.3 to 12.5%. Even where significant errors were encountered, further examination using a nonlinear model, where expected contributions were derived from stochastic simulation, showed that Equation 1 remained accurate and that the inaccuracies were due to inadequacy of the linear model used to implement Equation 1. The issues surrounding the parameterization are addressed in *Execution of the methods.*

Other methods, for example, the method of BURROWS (1984a,b), have accounted for only a single generation of inheritance of selective advantage and, therefore, systematically underpredict ΔF (WRAY *et al.* 1990). This can be illustrated by extending the method of BURROWS (1984a,b) to BLUP selection and two sexes (APPENDIX C), which shows a systematic underprediction of on average −16% for $N_m = 20$ (Table 7) to −28% for $N_m = 80$ (not shown). WRAY *et al.* (1990) investigated methods accounting for two generations' inheritance of selective advantage. Those methods, however, still rely on simulation to calculate the variance of family size. Further discussion on the relation between the present approach and other approaches to predict ΔF, in particular those based on the drift of gene frequency (*e.g.*, SANTIAGO and CABALLERO 1995), is in BIJMA *et al.* (2000).

Execution of the methods: The principal decision affecting the execution is the choice of the selective advantage. The primary condition on the adequacy of

TABLE 7

Prediction errors (%) of rates of inbreeding from an extension of Burrow's method for a population with 20 sires

N_f	h^2	$n_o = 4$	$n_o = 8$
40	0.1	−24	−26
	0.2	−23	−23
	0.4	−21	−22
	0.6	−16	−20
100	0.1	−25	−20
	0.2	−24	−20
	0.4	−20	−18
	0.6	−17	−16

Values are 100% × ($\Delta F_{pred} - \Delta F_{sim}$)/$\Delta F_{sim}$; for corresponding ΔF_{sim}, see Table 3. N_f, number of dams; h^2, initial heritability; n_o, number of offspring per dam.

$s_{i(x)}$ is that, after conditioning on $s_{i(x)}$, the number of selected offspring of parent *i* and the contribution of those offspring are independent. In that case, (i) off-diagonal elements of $\Delta\mathbf{V}_{n(x)}$ are zero since there is no covariance between selection probabilities of sibs [and the term for deviations from Poisson simplifies to $-1/(8T)$ with constant family size; Bijma *et al.* 2000]; and (ii) generations are independent. This involves two issues that are addressed below: first, what components should be included in the set of selective advantages; and second, whether the linear effect of those components is sufficient or that terms of higher order are required. Finally, we discuss whether and how the present implementation accounts for the inheritance of nonlinear terms of the selective advantage and how this relates to the observed underprediction.

Components of the selective advantage: To make generations independent, a natural way forward is to define a selective advantage that fully removes any covariance between EBVs of sibs. With sib-index or BLUP selection, this involves more than the breeding value of the parent, because the average environmental effect of full- and half-sib families also contributes to this covariance. Therefore, an alternative parameterization was tested that had selective advantages consisting of EBVs and prediction errors (see Woolliams *et al.* 1999) and fully removed covariances between EBVs of sibs. However, this alternative was substantially more complicated and resulted in similar underprediction for schemes with many parents (results not shown). Residual correlations between EBVs of sibs, therefore, are not the principal source of the observed underprediction.

Linear vs. higher-order terms: The use of a linear selective advantage to remove covariances between EBVs of sibs may be insufficient to make generations independent, because the relation between the number of selected offspring and the selective advantage is nonlinear. The nonlinearity originates from the nonlinear relation between the EBV of the offspring and its selection score, shown in Figure 4. Therefore, when assuming that the conditional mean is linear in the selective advantage (*i.e.*, using a linear Λ-model), sibs will have prediction errors of their selection score ($S = 0$ or 1, not selected or selected) in common, making their selection probabilities dependent. Thus, although the linear terms of the selective advantage may fully remove covariances between EBVs of sibs, the nonlinear relation between selection probabilities and EBVs implies that a covariance between the selection probabilities of sibs will remain and that generations will not be fully independent. From the equivalence of the present method and the drift approach (Santiago and Caballero 1995) in special cases (Bijma *et al.* 2000), it follows that the need to model the nonlinear relation will also be encountered when extending the drift approach to BLUP selection.

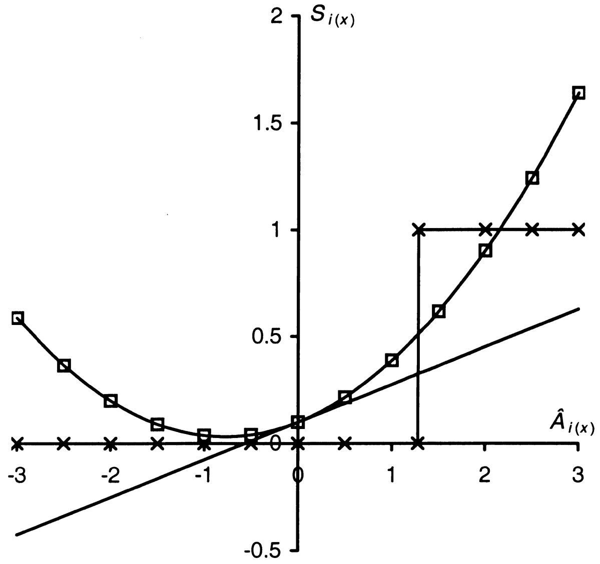

Figure 4.—Relation between selection score ($s_{i(x)}$) and estimated breeding value ($\hat{A}_{i(x)}$) for a selected proportion of 10%; (—) from linear model ($E[S_{i(x)}] = p_x + i_x p_x \sigma_{\hat{A}}^{-1}\hat{A}_{i(x)}$) (□) from quadratic model ($E[S_{i(x)}] = p_x + i_x p_x \sigma_{\hat{A}}^{-1}\hat{A}_{i(x)} + 1/2 i_x p_x t_x \sigma_{\hat{A}}^{-2}\hat{A}^2_{i(x)}$; t_x = standardized truncation point); (×) true selection score. Note that $\hat{A}_{i(x)}$ is in SD.

The observed nonlinearity prompted the consideration of a fully deterministic quadratic model to describe the relationship between selective advantages and contributions. This proved difficult, since it involves third and fourth moments of the two-sided truncated 4-variate normal distribution, to derive elements of Π. It is important to note also that with a quadratic model, there will be remaining covariances between selection probabilities of sibs (see Figure 4), so that the correction for deviations from Poisson will also be needed.

Nonlinearity and inheritance of selective advantage: In the present prediction, the first term of Equation 1 was implemented using a linear model for the relationship between contributions and selective advantages. Thus the first term of Equation 1 fully accounts for the inheritance of the linear effect of the selective advantage. The correction for deviations from Poisson fully accounts for the nonlinearity when calculating $\Delta\mathbf{V}_{n(x)}$ (Equations B9 to B29), but inheritance of the nonlinear part is partially ignored, in particular when using $\delta_x = \boldsymbol{\alpha}^{\mathrm{T}} \Delta\mathbf{V}_{n(x)}\boldsymbol{\alpha}$ instead of using Equation 9. The underprediction encountered for schemes with many parents, therefore, is due to the inheritance of the nonlinear part of the selective advantage, which is not accounted for by the first or by the second term of Equation 1 when using a linear model. This conclusion is supported by the observation of Woolliams and Bijma (2000), who found that the underprediction disappeared in schemes with high intraclass correlations between sibs and no inheritance of selective advantage (*e.g.*, with sib index selection, $h^2 = 0$, and large weight given to family information). Further improvement of the accuracy for such schemes with BLUP selection and many parents requires the development of a nonlinear model to predict expected contributions, which fully accounts for the inheritance of selective advantage, as, for example, the quadratic model that was implemented using simulation.

Implications: The results indicate that, with BLUP selection, relationships between ΔF and population parameters differ qualitatively from random or mass selection, the main difference being the dominant role of selection intensity compared to the number of parents. For example, with $N_{\mathrm{m}} = 20$, $d = 2$, $n_{\mathrm{o}} = 4$, and $h^2 = 0.1$, simultaneously *increasing* the number of parents and the number of offspring per dam by a factor of four (giving $N_{\mathrm{m}} = 80$, $d = 2$, $n_{\mathrm{o}} = 16$) *increases* the rate of inbreeding from 0.0184 to 0.0210. This shows that the number of candidates per parent may be as, or more important than, the number of parents, which will change perceptions about procedures and designs of breeding schemes to effectively reduce rates of inbreeding. Furthermore, doubling the number of parents fails to halve the rate of inbreeding, and although this was remarked upon by Santiago and Caballero (1995) in the context of mass selection, with BLUP the impact of doubling the number of parents is even less, and substantially less. Increasing the number of dams may even increase the rate of inbreeding in particular cases.

By understanding the forces governing the rate of inbreeding, perceptions of the desirability of naïve selection on EBVs may also be changed. The results showed that in some cases 83% of the selected sires failed to contribute in the long term, which seems to be a waste of resources. This is an indication of the inefficiency of BLUP selection compared to more advanced procedures (Meuwissen 1997; Grundy *et al.* 1998). Thus, unless the time horizon is limited to a single generation, it is better to incorporate the good genes from all the parents rather than spending substantial effort raising offspring from the parents that will not contribute. The cost of raising offspring from parents that are destined not to contribute in the long term is a hidden cost of the high rates of inbreeding associated with BLUP selection.

The systematic nature of the underprediction for schemes with $N_{\mathrm{m}} > 20$ allows for a rule of thumb to correct these predictions. When 11% is added to the predicted values, all predictions are within ±8% of the simulation results. This is simplistic, but may prove valuable for practical purposes and holds for the wide range of alternatives investigated in this article. When using this correction, the fully deterministic prediction with the linear model seems to have sufficient accuracy for most practical purposes. Therefore, for breeding schemes where BLUP selection is being conducted, the methodology developed here allows the design of such schemes to maximize genetic gain for a fixed rate of inbreeding on a fully deterministic, and thus computationally feasible, manner.

Extensions: The current prediction procedure can be extended directly to populations with multitrait BLUP selection, using a multitrait pseudo-BLUP index (Villanueva *et al.* 1993; Kerr 1998), or where the heritability in BLUP evaluations is artificially increased to avoid excessive inbreeding (Grundy *et al.* 1994). Neither of these extensions requires the development of new theory. With multitrait selection, the selective advantage may consist of the sum of the true breeding values for the respective traits weighted by their economic value and the EBV may be replaced by the estimate of the aggregate genotype.

Fetsje Bijma is acknowledged for giving helpful suggestions and Johan Van Arendonk for giving P.B. the opportunity to visit J.A.W. This research was financially supported by the Netherlands Technology Foundation (STW) and was coordinated by the Life Science Foundation (ALW). J.A.W. gratefully acknowledges the Ministry of Agriculture, Fisheries and Food (United Kingdom) for financial support.

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Communicating editor: R. G. SHAW

APPENDIX A

Approximate BLUP selection index: Index weights are calculated as $\mathbf{b} = \mathbf{V}^{-1}\mathbf{g}$, where $\mathbf{V}$ is the 6×6 (co)variance matrix of information sources in $\mathbf{x}_i$ and $\mathbf{g}$ is the 6×1 vector of covariances between information sources in $\mathbf{x}_i$ and the breeding value of the candidate. Nonzero elements of $\mathbf{V}$ are $V_{11} = \sigma^2_{\mathrm{m}}$, $V_{22} = \sigma^2_{\mathrm{f}}\ (1 - 1/d)$, $V_{33} = \sigma^2_{\mathrm{f}}/d$, $V_{44} = [\sigma^2_{\mathrm{A,m}} + \sigma^2_{\mathrm{A,f}}/d + (\tfrac{1}{2}\sigma^2_{\mathrm{A,0}} + \sigma^2_{\mathrm{E}})/(n_{\mathrm{o}}d)]$, $V_{55} = [\sigma^2_{\mathrm{A,f}} + (\tfrac{1}{2}\sigma^2_{\mathrm{A,0}} + \sigma^2_{\mathrm{E}})/n_{\mathrm{o}}](1 - 1/d)$, $V_{66} = (\tfrac{1}{2}\sigma^2_{\mathrm{A,0}} + \sigma^2_{\mathrm{E}})\ (1 - 1/n_{\mathrm{o}})$, $V_{14} = V_{41} = \tfrac{1}{2}\sigma^2_{\mathrm{m}}$, $V_{34} = V_{43} = \tfrac{1}{2}\sigma^2_{\mathrm{f}}/d$, and $V_{25} = V_{52} = \tfrac{1}{2}\sigma^2_{\mathrm{f}}(1 - 1/d)$; and $\mathbf{g}^{\mathrm{T}} = \{\tfrac{1}{2}\sigma^2_{\mathrm{m}}, \tfrac{1}{2}\sigma^2_{\mathrm{f}}\ (1 - 1/d), \tfrac{1}{2}\sigma^2_{\mathrm{f}}/d, [\sigma^2_{\mathrm{A,m}} + \sigma^2_{\mathrm{A,f}}/d + \tfrac{1}{2}\sigma^2_{\mathrm{A,0}}/(n_{\mathrm{o}}d)], [\sigma^2_{\mathrm{A,f}} + \tfrac{1}{2}\sigma^2_{\mathrm{A,0}}/n_{\mathrm{o}}]\ (1 - 1/d), \tfrac{1}{2}\sigma^2_{\mathrm{A,0}}(1 - 1/n_{\mathrm{o}})\}$, where T denotes the transpose, $\sigma^2_{\mathrm{A,0}}$ is the base generation additive genetic variance, σ^2_{E} is the environmental variance, σ^2_{m} and σ^2_{f} are the variance of the EBV among selected sires and dams, respectively, which are $\sigma^2_x = \sigma^2_{\mathrm{A}}\rho^2(\ 1 - k_x)$, where $\rho = \sqrt{\mathbf{b}^{\mathrm{T}}\mathbf{g}/\sigma^2_{\mathrm{A}}}$; $\sigma^2_{\mathrm{A,m}}$ and $\sigma^2_{\mathrm{A,f}}$ are the between-sire and between-dam family additive genetic variance, $\sigma^2_{\mathrm{A},x} = \tfrac{1}{4}\sigma^2_{\mathrm{A}}\ (1 - k_x\rho^2)$. The variance of EBV is $\sigma^2_{\hat{\mathrm{A}}} = \rho^2\sigma^2_{\mathrm{A}}$. Every generation, additive genetic variance is calculated from $\sigma^2_{\mathrm{A}} = \sigma^2_{\mathrm{A,m}} + \sigma^2_{\mathrm{A,f}} + \sigma^2_{\mathrm{A,0}}$. The above equations are iterated until equilibrium variances are reached (approximately five iterations). Intraclass correlations of sibs are corrected for the number of families being finite using an empirical analogy of the sample mean of the bivariate correlation coefficient, which is $\bar{\rho} \approx \rho - \rho(1 - \rho^2)/2n$ (KENDALL and STUART 1963, p. 390). For the current two-way classification, this is extended to $\bar{\rho}_{\mathrm{sibs}} = \rho_{\mathrm{sibs}} - \rho_{\mathrm{sibs}}\ (1 - \rho^2_{\mathrm{sibs}})(a/N_{\mathrm{m}} + b/N_{\mathrm{f}})$, where $\bar{\rho}_{\mathrm{sibs}}$ is the sample mean of the intraclass correlation and ρ_{sibs} is the true mean, calculated from $\rho_{\mathrm{FS}} = \mathbf{b}^{\mathrm{T}}\mathbf{C}_{\mathrm{FS}}\mathbf{b}/\sigma^2_{\hat{A}}$ and $\rho_{\mathrm{HS}} = \mathbf{b}^{\mathrm{T}}\mathbf{C}_{\mathrm{HS}}\mathbf{b}/\sigma^2_{\hat{A}}$, where $\mathbf{C}_{\mathrm{FS}}$ and $\mathbf{C}_{\mathrm{HS}}$ are the 6×6 covariance matrices of information sources of full sibs and of half sibs, respectively. Matrices $\mathbf{C}_{\mathrm{FS}}$ and $\mathbf{C}_{\mathrm{HS}}$ are identical to $\mathbf{V}$, except for $\mathbf{C}_{\mathrm{FS}}(6,\ 6) = -(\tfrac{1}{2}\sigma^2_{\mathrm{A,0}} + \sigma^2_{\mathrm{E}})/n_{\mathrm{o}}$, $\mathbf{C}_{\mathrm{HS}}(2,\ 2) = -\sigma^2_{\mathrm{f}}/d$, $\mathbf{C}_{\mathrm{HS}}\ (5,\ 5) = -[\sigma^2_{\mathrm{A,f}} + (\tfrac{1}{2}\sigma^2_{\mathrm{A,0}} + \sigma^2_{\mathrm{E}})/n_{\mathrm{o}}]/d$, $\mathbf{C}_{\mathrm{HS}}(2,\ 5) = \mathbf{C}_{\mathrm{HS}}(5,\ 2) = -\tfrac{1}{2}\sigma^2_{\mathrm{f}}/d$ and $\mathbf{C}_{\mathrm{HS}}(6,\ 6) = 0$. Coefficients a and b were determined empirically using simulated data, resulting in $a = 0.8634$, $b = 0.9540$ for full sibs and $a = 1.4075$, $b = 1.4581$ for half sibs. Note that calculation of a and b is once off; *i.e.*, the above values for a and b can be used for any breeding scheme and also for selection criteria other than BLUP.

APPENDIX B

Linear model

Elements of Λ: Elements of Λ, λ_{xy}, are the regression coefficient of the number of selected offspring of sex x on the selective advantage of the parent of sex y. A general procedure to derive Λ is in WOOLLIAMS *et al.* (1999). For the current purpose, single regressions instead of multiple regression can be used, because elements of the selective advantage are independent. Elements are $\lambda = b_{\hat{A}_{\mathrm{o}},s_{\mathrm{p}}}\ b_{S_{\mathrm{o}},A_{\mathrm{o}}}$, where $b_{\hat{A}_{\mathrm{o}},s_{\mathrm{p}}}$ is the regression coefficient of the EBV of the offspring on the selective advantage of the parent and $b_{S_{\mathrm{o}},\hat{A}_{\mathrm{o}}}$ is the regression of the selection score ($S_{\mathrm{o}} = 0$ or 1; *i.e.*, not selected or selected) of the offspring on its EBV. The first regression coefficient is $b_{\hat{A}_\mathrm{o},S_\mathrm{p}} = \mathbf{b}^\mathrm{T}\mathbf{c}_x/\mathrm{Var}(s_{i(x)})$, where $\mathbf{c}_x$ is the 6×1 vector of covariances between $\mathbf{x}_i$ of the offspring and $s_{i(x)}$ of the parent of sex x. The second regression coefficient is $b_{S_\mathrm{o},\hat{A}_\mathrm{o}} = i_o/\sigma_{\hat{A}}$ (Robertson, Appendix in DEMPSTER and LERNER 1950), where i_o is the selection intensity for the offspring. Resulting equations are

$$\lambda_{11} = [\mathbf{b}^\mathrm{T}\mathbf{c}_\mathrm{m}i_\mathrm{m}/\sigma_{\hat{A}}]/\sigma^2_{s(m)}, \tag{B1}$$

$$\lambda_{12} = [\mathbf{b}^\mathrm{T}\mathbf{c}_\mathrm{f}i_\mathrm{m}/\sigma_{\hat{A}}]/\sigma^2_{s(f)}, \tag{B2}$$

$$\lambda_{21} = [\mathbf{b}^\mathrm{T}\mathbf{c}_\mathrm{m}i_\mathrm{f}/\sigma_{\hat{A}}]/\sigma^2_{s(m)}, \tag{B3}$$

$$\lambda_{22} = [\mathbf{b}^\mathrm{T}\mathbf{c}_\mathrm{f}i_\mathrm{f}/\sigma_{\hat{A}}]/\sigma^2_{s(f)}, \tag{B4}$$

where $\mathbf{c}_\mathrm{m}^\mathrm{T} = [\sigma^2_\mathrm{m}(1 - 1/N_\mathrm{m}),\ 0,\ \sigma^2_\mathrm{f}\ (1 - 1/N_\mathrm{m})/d,\ \frac{1}{2}\sigma^2_{s(m)},\ 0,\ 0]$ and $\mathbf{c}_\mathrm{f}^\mathrm{T} = [\sigma^2_\mathrm{m}(1 - 1/N_\mathrm{m}),\ \sigma^2_\mathrm{f}\ (1 - 1/d),\ \sigma^2_\mathrm{f}\ (1 - 1/N_\mathrm{f})/d,\ \frac{1}{2}\sigma^2_{s(m)},\ \frac{1}{2}\sigma^2_\mathrm{A}(1 - k_\mathrm{f}\rho^2)(1 - 1/d),\ 0]$.

Elements of Π: Elements of Π, π_{xy}, are the regression coefficient of the selective advantage of sex x on the selective advantage of the parent of sex y. A general procedure to derive Π is in WOOLLIAMS *et al.* (1999). As with Λ, single regressions can be used, so that $\pi_\mathrm{op} = [\mathrm{Cov}(s_\mathrm{p},s_\mathrm{o}) - \mathrm{Cov}(s_\mathrm{p},\ \hat{A}_\mathrm{o})\ \mathrm{Cov}(s_\mathrm{o},\ \hat{A}_\mathrm{o})k_\mathrm{o}/\sigma^2_{\hat{A}}]/\mathrm{Var}(s_\mathrm{p})$, where subscripts p and o denote parent and offspring and (co)variances are taken before selection of the offspring. With $\mathrm{Cov}(s_\mathrm{p,}\ \hat{A}_\mathrm{o}) = \mathbf{b}^\mathrm{T}\mathbf{c}_x$ and $s_{i(x)}$ from Equations 2 and 3, resulting equations are

$$\pi_{11} = \tfrac{1}{2} - \mathbf{b}^\mathrm{T}\mathbf{c}_\mathrm{m}k_\mathrm{m}/\sigma^2_{s(m)} \tag{B5}$$

$$\pi_{21} = \tfrac{1}{2} - \mathbf{b}^\mathrm{T}\mathbf{c}_\mathrm{m}k_\mathrm{f}/\sigma^2_{s(m)} \tag{B6}$$

$$\pi_{12} = \tfrac{1}{2} - \mathbf{b}^\mathrm{T}\mathbf{c}_\mathrm{f}k_\mathrm{m}/\sigma^2_{s(f)} \tag{B7}$$

$$\pi_{22} = \tfrac{1}{2} - \mathbf{b}^\mathrm{T}\mathbf{c}_\mathrm{f}k_\mathrm{f}/\sigma^2_{s(f)}. \tag{B8}$$

Calculation of $\boldsymbol{\delta_x}$: Calculation of δ_m and δ_f requires the calculation of $\Delta\mathbf{V}_{n(x)}$ and further development of Equations 9 and 10.

Calculation of $\Delta V_{n(x)}$: Using Appendix D of WOOLLIAMS and BIJMA (2000),

$$\Delta\mathbf{V}_{n(m)}(1,\ 1) = E_s\{n_{i^*}(m)[n_{i^*}(m) - 1]\} - E_s[\mu^2_\mathrm{m}(m)] \tag{B9}$$

$$\begin{aligned}\Delta\mathbf{V}_{n(m)}(1,\ 2) = \Delta\mathbf{V}_{n(m)}(2,\ 1) &= E_s[n_{i^*}(m)n_{i^*}(f)]\\ &\quad - E_s[\mu_m(m)\mu_m(f)]\end{aligned} \tag{B10}$$

$$\Delta\mathbf{V}_{n(m)}(2,\ 2) = E_s\{n_{i^*}(f)[n_{i^*}(f) - 1]\} - E_s[\mu^2_\mathrm{m}(f)] \tag{B11}$$

$$\Delta\mathbf{V}_{n(f)}(1,\ 1) = E_s\{n_{ij}(m)[n_{ij}(m) - 1]\} - E_s[\mu^2_\mathrm{f}(m)] \tag{B12}$$

$$\begin{aligned}\Delta\mathbf{V}_{n(f)}(1,\ 2) = \Delta\mathbf{V}_{n(f)}(2,\ 1) &= E_s[n_{ij}(m)n_{ij}(f)]\\ &\quad - E_s[\mu_f(m)\mu_f(f)]\end{aligned} \tag{B13}$$

$$\Delta\mathbf{V}_{n(f)}(2,\ 2) = E_s\{n_{ij}(f)[n_{ij}(f) - 1]\} - E_s[\mu^2_\mathrm{f}(f)], \tag{B14}$$

where $n_{ij}(x)$ is the number of offspring of sex x selected from the ith sire family and the jth dam family, $n_{i^*}(x)$ is the total number of offspring of sex x selected from the ith sire family, and $\mu^2_x(y,\ y')$ denotes the product of the expected number of selected offspring of sex y and the expected number of selected offspring of sex y' of a parent of sex x conditional on its selective advantage. Elements are

$$E_s[\mu^2_\mathrm{m}(m)] = 1 + \lambda^2_{11}\sigma^2_{s1} \tag{B15}$$

$$E_s[\mu_\mathrm{m}(m)\mu_\mathrm{m}(f)] = d(1 + \lambda_{11}\lambda_{21}\sigma^2_{s1}) \tag{B16}$$

$$E_s[\mu^2_\mathrm{m}(f)] = d^2(1 + \lambda^2_{21}\sigma^2_{s1}) \tag{B17}$$

$$E_s[\mu^2_\mathrm{f}(m)] = (1 + \lambda^2_{12}\sigma^2_{s2})/d^2 \tag{B18}$$

$$E_s[\mu_f(m)\mu_f(f)] = (1 + \lambda_{12}\lambda_{22}\sigma^2_{s2})/d \tag{B19}$$

$$E_s[\mu^2_\mathrm{f}(f)] = 1 + \lambda^2_{22}\sigma^2_{s2} \tag{B20}$$

$$\begin{aligned}E_s\{n_{i^*}(m)[n_{i^*}(m) - 1]\} &= dE_s\{n_{ij}(m)[n_{ij}(m) - 1]\}\\ &\quad + d(d - 1)E_s[n_{ij}(m)n_{ik}(m)]\end{aligned} \tag{B21}$$

$$\begin{aligned}E_s[n_{i^*}(m)n_{i^*}(f)] &= dE_s[n_{ij}(m)n_{ij}(f)]\\ &\quad + d(d - 1)E_s[n_{ij}(m)n_{ik}(f)]\end{aligned} \tag{B22}$$

$$\begin{aligned}E_s\{n_{i^*}(f)[n_{i^*}(f) - 1]\} &= dE_s\{n_{ij}(f)[n_{ij}(f) - 1]\}\\ &\quad + d(d - 1)E_s[n_{ij}(f)n_{ik}(f)],\end{aligned} \tag{B23}$$

where

$$\begin{aligned}E_s\{n_{ij}(m)[n_{ij}(m) - 1]\} &= n_\mathrm{m}(n_\mathrm{m} - 1)\\ &\quad \times N_\mathrm{m}(N_\mathrm{m} - 1)/[T_\mathrm{m}(T_\mathrm{m} - 1)\\ &\qquad \times R(p_\mathrm{m},\ p_\mathrm{m},\ \bar{\rho}_\mathrm{FS})]\end{aligned} \tag{B24}$$

$$E_s[n_{ij}(m)n_{ij}(f)] = n_\mathrm{m}n_\mathrm{f}N_\mathrm{m}N_\mathrm{f}/[T_\mathrm{m}T_\mathrm{f}R(p_\mathrm{m},\ p_\mathrm{f},\ \bar{\rho}_\mathrm{FS})] \tag{B25}$$

$$\begin{aligned}E_s\{n_{ij}(f)[n_{ij}(f) - 1]\} &= n_\mathrm{f}(n_\mathrm{f} - 1)\\ &\quad \times N_\mathrm{f}(N_\mathrm{f} - 1)/[T_\mathrm{f}(T_\mathrm{f} - 1)\\ &\qquad \times R(p_\mathrm{f},\ p_\mathrm{f},\ \bar{\rho}_\mathrm{FS})]\end{aligned} \tag{B26}$$

and

$$E_s[n_{ij}(m)n_{ik}(m)] = n^2_\mathrm{m}N_\mathrm{m}(N_\mathrm{m} - 1)/[T_\mathrm{m}(T_\mathrm{m} - 1)R(p_\mathrm{m},\ p_\mathrm{m},\ \bar{\rho}_\mathrm{HS})] \tag{B27}$$

$$E_s[n_{ij}(m)n_{ik}(f)] = n_\mathrm{m}n_\mathrm{f}N_\mathrm{m}N_\mathrm{f}/[T_\mathrm{m}T_\mathrm{f}R(p_\mathrm{m},\ p_\mathrm{f},\ \bar{\rho}_\mathrm{HS})] \tag{B28}$$

$$E_s[n_{ij}(f)n_{ik}(f)] = n^2_\mathrm{f}N_\mathrm{f}(N_\mathrm{f} - 1)/[T_\mathrm{f}(T_\mathrm{f} - 1)R(p_\mathrm{f},\ p_\mathrm{f},\ \bar{\rho}_\mathrm{HS})], \tag{B29}$$

where $T_\mathrm{m} = T_\mathrm{f} = \frac{1}{2}T$ and $n_\mathrm{m} = n_\mathrm{f} = \frac{1}{2}n_\mathrm{o}$ for the current breeding schemes. Furthermore (MENDEL and ELSTON 1974), $R(p_x,\ p_y,\ \bar{\rho}_\mathrm{sibs}) = p_y/\Phi[(i_x\bar{\rho}_\mathrm{sibs} - t_y)(1 - k_x\bar{\rho}^2_\mathrm{sibs})^{-1/2}]$, where Φ is the normal distribution function and t_y is the standardized truncation point for sex y. When both males and females are involved, the most accurate value is obtained by using $x = m$ and $y = f$ (WRAY *et al.* 1994).

Calculation of Equations 9 and 10: In δ_x, terms due to $\boldsymbol{\alpha}$ are, for sires,

$$\delta_{\mathrm{m}}(\alpha) = \boldsymbol{\alpha}^{\mathrm{T}}\Delta\mathbf{V}_{n(m)}\boldsymbol{\alpha} = \alpha_{\mathrm{m}}^2\Delta\mathbf{V}_{n(m)}(1, 1) + 2\alpha_{\mathrm{m}}\alpha_{\mathrm{f}}\Delta\mathbf{V}_{n(m)}(1, 2) + \alpha_{\mathrm{f}}^2\Delta\mathbf{V}_{n(m)}(2, 2), \quad \text{(B30)}$$

and for dams,

$$\delta_{\mathrm{f}}(\alpha) = \boldsymbol{\alpha}^{\mathrm{T}}\Delta\mathbf{V}_{n(f)}\boldsymbol{\alpha} = \alpha_{\mathrm{m}}^2\Delta\mathbf{V}_{n(f)}(1, 1) + 2\alpha_{\mathrm{m}}\alpha_{\mathrm{f}}\Delta\mathbf{V}_{n(f)}(1, 2) + \alpha_{\mathrm{f}}^2\Delta\mathbf{V}_{n(f)}(2, 2). \quad \text{(B31)}$$

Terms due to $\boldsymbol{\beta}$ are, for sires,

$$\delta_{\mathrm{m}}(\beta) = [\beta_1^2\pi_{11}^2\Delta\mathbf{V}_{n(m)}(1, 1) + 2\beta_1\beta_2\pi_{11}\pi_{21}\Delta\mathbf{V}_{n(m)}(1, 2) + \beta_2^2\pi_{21}^2\Delta\mathbf{V}_{n(m)}\Delta\mathbf{V}_{n(m)}(2, 2)]\sigma_{s,1}^2, \quad \text{(B32)}$$

and for dams,

$$\delta_{\mathrm{f}}(\beta) = [\beta_1^2\pi_{12}^2\Delta\mathbf{V}_{n(f)}(1, 1) + 2\beta_1\beta_2\pi_{12}\pi_{22}\Delta\mathbf{V}_{n(f)}(1, 2) + \beta_2^2\pi_{22}^2\Delta\mathbf{V}_{n(f)}(2, 2)]\sigma_{s,2}^2 \quad \text{(B33)}$$

so that $\delta_{\mathrm{m}} = \delta_{\mathrm{m}}(\alpha) + \delta_{\mathrm{m}}(\beta)$ and $\delta_{\mathrm{f}} = \delta_{\mathrm{f}}(\alpha) + \delta_{\mathrm{f}}(\beta)$, which gives Equation 9.

APPENDIX C

Extension of Burrows method: The method of Burrows (1984a,b) is based on calculating the average coancestry after a single cycle of selection. Using Appendix D of Woolliams and Bijma (2000), the extension to two sexes is straightforward. From Equation 1 of Burrows (1984b), $\Delta F_{\mathrm{B}} = \frac{1}{8}Q_{\mathrm{HS}} + \frac{1}{4}Q_{\mathrm{FS}}$, where Q_{HS} is the probability that two selected offspring are half sibs and Q_{FS} is the probability that two selected offspring are full sibs. For two sexes, a distinction has to be made between male and female offspring, so that $Q_{\mathrm{HS}} = \frac{1}{4}Q_{\mathrm{HS}}(m, m) + \frac{1}{2}Q_{\mathrm{HS}}(m, f) + \frac{1}{4}Q_{\mathrm{HS}}(f, f)$ and $Q_{\mathrm{FS}} = \frac{1}{4}Q_{\mathrm{FS}}(m, m) + \frac{1}{2}Q_{\mathrm{FS}}(m, f) + \frac{1}{4}Q_{\mathrm{FS}}(f, f)$. Combining Burrows (1984b) and Appendix D of Woolliams and Bijma (2000), $Q_{\mathrm{HS}}(m, m) = n_{\mathrm{m}}(d - 1)/[(T_{\mathrm{m}} - 1)R(\alpha_{\mathrm{m}}, \alpha_{\mathrm{m}}, \bar{\rho}_{\mathrm{HS}})]$, $Q_{\mathrm{HS}}(m, f) = n_{\mathrm{m}}(d - 1)/[T_{\mathrm{m}}R(\alpha_{\mathrm{m}}, \alpha_{\mathrm{f}}, \bar{\rho}_{\mathrm{HS}})]$, $Q_{\mathrm{HS}}(f, f) = n_{\mathrm{f}}(d - 1)/[(T_{\mathrm{f}} - 1)R(\alpha_{\mathrm{f}}, \alpha_{\mathrm{f}}, \bar{\rho}_{\mathrm{HS}})]$, $Q_{\mathrm{FS}}(m, m) = (n_{\mathrm{m}} - 1)/[(T_{\mathrm{m}} - 1)R(\alpha_{\mathrm{m}}, \alpha_{\mathrm{m}}, \bar{\rho}_{\mathrm{FS}})]$, $Q_{\mathrm{FS}}(m, f) = n_{\mathrm{m}}/[T_{\mathrm{m}}R(\alpha_{\mathrm{m}}, \alpha_{\mathrm{f}}, \bar{\rho}_{\mathrm{FS}})]$, $Q_{\mathrm{FS}}(f, f) = (n_{\mathrm{f}} - 1)/[(T_{\mathrm{f}} - 1)R(\alpha_{\mathrm{f}}, \alpha_{\mathrm{f}}, \bar{\rho}_{\mathrm{FS}})]$, where $T_{\mathrm{m}} = T_{\mathrm{f}} = \frac{1}{2}T$ and $n_{\mathrm{m}} = n_{\mathrm{f}} = \frac{1}{2}n_{\mathrm{o}}$ for the current breeding schemes and $R(\alpha_x, \alpha_x, \bar{\rho}_{\mathrm{sibs}})$ is given in appendix b.

For random selection, the result reduces to $\Delta F_{\mathrm{B}} = \Delta F_{\mathrm{W}} + \frac{1}{2}[\Delta F_{\mathrm{W}} - 1/(8T)]/(T - 1) \approx \Delta F_{\mathrm{W}}$, where $\Delta F_{\mathrm{W}} = 1/(8N_{\mathrm{m}}) + 1/(8N_{\mathrm{f}}) - 1/(8T)$, which is Wright's equation for fixed n_{o}; ΔF_{B} accounts for sampling parents without replacement by using a hypergeometric distribution of family size, whereas ΔF_{W} uses a binomial approximation.