

Expected contribution theory for multiple selective advantages and overlapping generations

This document gives a detailed description of the method of expected long-term genetic contributions for multiple selective advantages and overlapping generations. In Section B the co-variance matrix \mathbf{V} is derived for additive maternal effects, which was applied in Rönnegård & Woolliams (2003). The parameters used are summarized in Table 1 below.

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Section A

Expected long-term genetic contributions with overlapping generations and multiple selective advantages

This section summarizes the theory of expected contributions with multiple selective advantages and overlapping generations as developed by Woolliams *et al.* (1999), Bijma & Woolliams (1999), Woolliams & Bijma (2000), and Bijma *et al.* (2000).

The linear predictor of the expected long-term genetic contribution $u_{i(q)}$ of individual i in category q is given by:

$$\mu_{i(q)} = \alpha_{i(q)} + \boldsymbol{\beta}_q^T (\mathbf{s}_{i(q)} - \bar{\mathbf{s}}_q) \quad [\text{A1}]$$

Let n_s be the number of defined selective advantages in $\mathbf{s}_{i(q)}$ and n_c be the number of categories. For simplicity of notation, the equations to calculate $\alpha_{i(q)}$ and $\boldsymbol{\beta}_q^T$ were

slightly changed by giving the age structure by a vector \mathbf{N} of length n_c (instead of a diagonal matrix \mathbf{N} in equations 7b and 9 in Woolliams *et al.*, 1999):

$$(\mathbf{N} \otimes \boldsymbol{\alpha}) = \left[\mathbf{G}^T + (\mathbf{G}^T \otimes \mathbf{D}^T) (\mathbf{I} - \mathbf{G}^T \otimes \boldsymbol{\Pi}^T)^{-1} (\mathbf{G}^T \otimes \boldsymbol{\Lambda}^T) \right] (\mathbf{N} \otimes \boldsymbol{\alpha}) \quad [\text{A2}]$$

$$(\mathbf{N} \otimes \boldsymbol{\beta}) = (\mathbf{I} - \mathbf{G}^T \otimes \boldsymbol{\Pi}^T)^{-1} (\mathbf{G}^T \otimes \boldsymbol{\Lambda}^T) (\mathbf{N} \otimes \boldsymbol{\alpha}) \quad [\text{A3}]$$

where \otimes denotes element-by-sub-matrix multiplication of matrices, \mathbf{I} is the $n_c n_s \times n_c n_s$ identity matrix, \mathbf{N} is a vector with elements N_k equal to the numbers of parents selected from each category, $\boldsymbol{\Pi}$ is a $n_c n_s \times n_c n_s$ matrix containing sub-matrices $\boldsymbol{\pi}_{pq}$ ($n_s \times n_s$) of regression coefficients of selective advantages of selected progeny in category p on selective advantages of parents in category q , $\boldsymbol{\Lambda}$ is a $n_c \times n_c n_s$ matrix containing sub-matrices $\boldsymbol{\lambda}_{pq}$ ($1 \times n_{sa}$) of regression coefficients of proportion selected in category p on selective advantages of parents in category q , \mathbf{G} is a $n_c \times n_c$ modified gene flow matrix connecting selected offspring to parental categories, \mathbf{D} is a $n_c n_s \times n_c$ matrix of deviations of selective advantages from the mean of the selected category, $\boldsymbol{\alpha}$ is a vector (length n_c) of elements α_q , and $\boldsymbol{\beta}$ is a vector of length $n_c n_s$ containing the sub-vectors $\boldsymbol{\beta}_q$.

Let $(\mathbf{s}_{i(q)} \ \mathbf{s}_{j(p)} \ I_{j(p)})^T$ have the partitioned covariance matrix:

$$\mathbf{V} = \begin{pmatrix} \mathbf{V}_{qq} & \mathbf{V}_{pq} & \mathbf{v}_p \\ \mathbf{V}_{pq}^T & \mathbf{V}_{pp} & \mathbf{v}_q \\ \mathbf{v}_p^T & \mathbf{v}_q^T & \sigma_I^2 \end{pmatrix} \quad [\text{A4}]$$

where p and q are progeny and parent categories, respectively, and $I_{j(p)}$ is the index upon which the selection of individual $j(p)$ will be determined. (\mathbf{V} is given in Section

B for $\mathbf{s}_{i(q)} = (A_{i(q)} \ M_{i(q)} \ C_{i(q)})^T$. $\mathbf{\Pi}$ and $\mathbf{\Lambda}$ are then obtained from (see Appendix B in Woolliams *et al.*, 1999):

$$\boldsymbol{\pi}_{pq} = \mathbf{V}_{pq}^* \mathbf{V}_{qq}^{-1} \quad [\text{A5}]$$

$$\boldsymbol{\lambda}_{pq} = i_p \boldsymbol{\sigma}_I^{-1} \mathbf{v}_q \mathbf{V}_{qq}^{-1} \quad [\text{A6}]$$

where \mathbf{V}_{pq}^* is the genetic (co)variance matrix *after* selection

$$\mathbf{V}_{pq}^* = (\mathbf{V}_{pq} - k_p \boldsymbol{\sigma}_I^{-2} \mathbf{v}_p \mathbf{v}_q^T) \quad [\text{A7}]$$

and k_p is the variance reduction term in category p .

Define $\mathbf{g}_{j(p)}$ as a vector of Mendelian sampling terms corresponding to the selective advantages in $\mathbf{s}_{i(p)}$ (in our paper $\mathbf{g}_{j(p)} = (a_{j(p)}, m_{j(p)}, 0)^T$). The annual genetic gain is then:

$$\Delta \mathbf{G} = \sum_{q=1}^{n_c} N_q \mathbb{E}[r_{i(q)} \mathbf{g}_{i(q)}] \quad [\text{A8}]$$

and

$$\mathbb{E}[r_{i(q)} \mathbf{g}_{i(q)}] = \alpha_q i_q \boldsymbol{\sigma}_I^{-1} \mathbf{v}_g + \boldsymbol{\beta}_q^T (\mathbf{V}_{pg} - k_q \boldsymbol{\sigma}_I^{-1} \mathbf{v}_p \mathbf{v}_g^T) \quad [\text{A9}]$$

follows by extension of Appendix B in Bijma & Woolliams (1999) to multiple selective advantages, where the matrices \mathbf{V}_{pg} , \mathbf{v}_g and \mathbf{v}_p are covariance matrices of $(\mathbf{s}_{j(p)} \ \mathbf{g}_{j(p)})^T$, $(\mathbf{g}_{j(p)} \ I_{j(p)})^T$ and $(\mathbf{s}_{j(p)} \ I_{j(p)})^T$, respectively.

Rates of inbreeding per year, ΔF , are predicted as (equation 29 in Woolliams & Bijma, 2000):

$$\mathbb{E}[\Delta F] = \frac{1}{2} \sum_{s \text{ males}} n_s \mathbb{E}(u_{i,s}^2) + \frac{1}{2} \sum_{s \text{ females}} n_s \mathbb{E}(u_{i,s}^2) + \frac{1}{8} \sum_s n_s \delta_s \quad [\text{A10}]$$

where n_s is the number of individuals with a certain life history of reproduction defined by the categories that an individual was selected in. The third term is the correction for non-Poisson distribution of family size (Bijma *et al.*, 2000). We assume parent selection such that (equation 11 in Bijma *et al.*, 2000):

$$\sum_{s_{sex}} n_s E(u_{i,s}^2) = \sum_{k=1}^{n_c} n_k E(u_{i,k}^2) + \sum_{k=1}^{n_c-1} \sum_{l=k+1}^{n_c} \min(n_l, n_k) E(u_{i,k}, u_{i,l}) \quad [\text{A11}]$$

where n_k is the number of individuals in category k .

By extending equations 14 and 15 in Bijma *et al.* (2000) to multiple selective advantages we get the first term in [A11] as:

$$E(u_{i,k}^2) = \alpha_k^2 + (1 - 1/n_k) \boldsymbol{\beta}_k \mathbf{V}_{kk}^* \boldsymbol{\beta}_k^T + d \left\{ \overline{\alpha_f^2} - \overline{\alpha_f}^2 + \left[\overline{(1 - 1/n_l) \boldsymbol{\beta}_l \mathbf{V}_{ll}^* \boldsymbol{\beta}_l^T} \right]_f \right\}$$

for males, and for females

$$E(u_{i,k}^2) = \alpha_k^2 + (1 - 1/n_k) \boldsymbol{\beta}_k \mathbf{V}_{kk}^* \boldsymbol{\beta}_k^T + \frac{1}{d^2} \left\{ \overline{\alpha_m^2} - \overline{\alpha_m}^2 + \left[\overline{(1 - 1/n_l) \boldsymbol{\beta}_l \mathbf{V}_{ll}^* \boldsymbol{\beta}_l^T} \right]_m \right\}$$

where bars with subscripts m or f denote weighted averages over mate categories.

Furthermore, the cross product in [A11] is (equation 16 in Bijma *et al.*, 2000):

$$E(u_{i,k}, u_{i,l}) = \alpha_k \alpha_l + (1 - 1/n_\mu) \boldsymbol{\beta}_k \mathbf{V}_{\mu\mu}^* \boldsymbol{\beta}_l^T + \alpha_\mu \boldsymbol{\beta}_\nu / \sigma_l (i_\mu \mathbf{v}_\mu - i_\nu \mathbf{v}_\nu)$$

where subscript μ denotes the category of k and l with the smallest number of individuals, and subscript ν denotes the category with the largest number of individuals.

The generation interval, L is defined as the time in which the long-term contributions

sum to unity (Woolliams *et al.*, 1999): $L = 1 / \sum_{k=1}^{n_c} n_k \alpha_k$. The predicted rate of

inbreeding per generation, ΔF_L , may then be calculated as $\Delta F_L = E(\Delta F) \times L$.

The iterative scheme to predict Λ , Π , α , β and $\Delta\mathbf{G}$ with multiple selective advantages follows the same principle as the scheme for a single selective advantage given in Woolliams *et al.* (1999). Bulmer's (1971) equilibrium (co)variances are calculated by iterating between estimated effects of linkage disequilibrium due to selection

$$\mathbf{V}_{qq}^* = \left(\mathbf{V}_{pp} - k_p \sigma_I^{-2} \mathbf{v}_p \mathbf{v}_p^T \right) \text{ and estimated effects of recombination}$$

$$\mathbf{V}_{pp} = \mathbf{V}_{gg} + \frac{1}{4} \sum_q \left[2g_{0,pq} \mathbf{V}_{qq}^* + 2g_{0,pq} \boldsymbol{\delta}_q^T \boldsymbol{\delta}_q \right], \text{ where } g_{0,pq} \text{ are elements in Hill's (1974)}$$

conventional gene flow matrix with $2g_{0,pq}$ being the proportion of progeny in sex p having parents in category q , $\boldsymbol{\delta}_q$ is the deviation in direct and maternal breeding values of the selected individuals in category q , and the matrix \mathbf{V}_{gg} is the covariance matrix of the Mendelian sampling terms $\mathbf{g}_{j(p)}$. Note that $\boldsymbol{\delta}_q$ depends on $\Delta\mathbf{G}$ and that the variance of common maternal environment, c^2 , is unaffected by selection. Λ , Π , α , β and $\Delta\mathbf{G}$ are recalculated each iteration until equilibrium is reached.

Section B

Co-variance matrices of selective advantages for Willham's (1963) model

For selective advantages defined as $\mathbf{s}_{i(q)} = \left(A_{i(q)} \ M_{i(q)} \ C_{i(q)} \right)^T$ the elements of the sub-matrices of \mathbf{V} in eq. [A4], assuming mass selection, are:

$$\sigma_I^2 = V(A_i) + V(M_d) + \text{Cov}(A_d, M_d) + V(C_d) + V(E_i)$$

$$\mathbf{v}_p = \begin{pmatrix} V(A_i) + \frac{1}{2} \text{Cov}(A_d, M_d) \\ \text{Cov}(A_i, M_i) + \frac{1}{2} V(M_d) \\ 0 \end{pmatrix} \quad \mathbf{V}_{pp} = \begin{pmatrix} V(A_i) & \text{Cov}(A_i, M_i) & 0 \\ \text{Cov}(A_i, M_i) & V(M_i) & 0 \\ 0 & 0 & V(C_i) \end{pmatrix}$$

For sire categories

$$\mathbf{V}_{qq} = \begin{pmatrix} V(A_s) & \text{Cov}(A_s, M_s) & 0 \\ \text{Cov}(A_s, M_s) & V(M_s) & 0 \\ 0 & 0 & 0 \end{pmatrix} \quad \mathbf{V}_{pq} = \frac{1}{2} \mathbf{V}_{qq} \quad \mathbf{v}_q = \begin{pmatrix} \frac{1}{2} V(A_s) \\ \frac{1}{2} \text{Cov}(A_s, M_s) \\ 0 \end{pmatrix}$$

and for dam categories

$$\mathbf{V}_{qq} = \begin{pmatrix} V(A_d) & \text{Cov}(A_d, M_d) & 0 \\ \text{Cov}(A_d, M_d) & V(M_d) & 0 \\ 0 & 0 & V(C_d) \end{pmatrix}$$

$$\mathbf{V}_{pq} = \begin{pmatrix} \frac{1}{2} V(A_d) & \frac{1}{2} \text{Cov}(A_d, M_d) & 0 \\ \frac{1}{2} \text{Cov}(A_d, M_d) & \frac{1}{2} V(M_d) & 0 \\ 0 & 0 & 0 \end{pmatrix} \quad \mathbf{v}_q = \begin{pmatrix} \frac{1}{2} V(A_d) + \text{Cov}(A_d, M_d) \\ \frac{1}{2} \text{Cov}(A_d, M_d) + V(M_d) \\ V(C_d) \end{pmatrix}$$

The covariance matrices of $(\mathbf{s}_{j(p)} \ \mathbf{g}_{j(p)})^T$ and $(\mathbf{g}_{j(p)} \ I_{j(p)})^T$ in equation [A8] are:

$$\mathbf{V}_{pg} = \begin{pmatrix} V(a_i) & \text{Cov}(a_i, m_i) & 0 \\ \text{Cov}(a_i, m_i) & V(m_i) & 0 \\ 0 & 0 & 0 \end{pmatrix} \quad \mathbf{v}_g = \begin{pmatrix} V(a_i) \\ \text{Cov}(a_i, m_i) \\ 0 \end{pmatrix}$$

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Table 1 Notation of parameters

$\Delta F, \Delta F_L$	annual rates of inbreeding and rates of inbreeding per generation
$\Delta G_{dir}, \Delta G_{mat}$	direct and maternal genetic gain per year
$\Delta \mathbf{G}, \Delta G$	vector of annual genetic gain and total genetic gain ($\Delta G_{dir} + \Delta G_{mat}$)
P_i, A_i, E_i	phenotype, additive direct genetic effect and environmental effect
M_d, C_d	additive maternal genetic effect and environmental maternal effect of the dam
$\mathbf{s}_{i(q)}$	vector of selective advantages for individual i in category q equal to $(A_i \ M_i \ C_i)^T$; mean over all selected in category q is $\bar{\mathbf{s}}_q$
$r_{i(q)}, u_{i(q)}, \mu_{i(q)}$	long-term genetic contribution, expected long-term genetic contribution and linear predictor of long-term genetic contributions
$\boldsymbol{\alpha}_q, \boldsymbol{\beta}_q$	vectors of the coefficients for $\mu_{i(q)}$
λ_{pq}	regression coefficients of proportion selected in category p on $\mathbf{s}_{i(q)}$ for parents in category q
$\boldsymbol{\pi}_{pq}$	regression coefficients of $\mathbf{s}_{j(p)}$ on $\mathbf{s}_{i(q)}$ for parents in category q
$a_i, m_i, \mathbf{g}_{i(p)}$	direct and maternal Mendelian sampling terms of individual i , and vector of Mendelian sampling terms equal to $(a_i \ m_i \ 0)^T$
h_A^2, h_M^2, h_W^2	direct, maternal and Willham heritabilities
c^2, ρ, σ_I^2	common environmental variance, direct-maternal genetic correlation, and phenotypic variance
N_m, N_f, d	no. male parents, no. female parents, and dams per sire (N_f/N_m)
\mathbf{N}	vector of no. of individuals in each category
i_p, k_p, i	intensity of selection and variance reduction term in sex p , and mean selection intensity
<u>Subscripts</u>	
$p, q, i(p)$	indicators of categories, $i(p)$ denotes individual in category p
m, f	indicators of male and female
i, d, s	indicators of individual, dam and sire
