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Derivation of the Standard Error of Multibreed Restricted Maximum Likelihood Estimates of Covariance Components Computed Using an Expectation-Maximization Algorithm

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General Background

The log-likelihood of the complete data (Elzo, 1994) is:

$$
\begin{aligned}
\ln[f(u_a, u_{n\bullet}, v|\phi)] = \text{constant} &+ \ln[f(u_a|\phi)] \\
&+ \ln[f(u_{n1}|\phi)] \\
&+ \ln[f(u_{n2}|\phi)] \\
&\ \ \vdots \\
&+ \ln[f(u_{nK}|\phi)] \\
&+ \ln[f(v|\phi)
\end{aligned}
$$

where

$$\ln[f(u_a|\phi)] = -\tfrac{1}{2} \sum_{ag=1}^{nbgcom} \sum_{i=1}^{n_{ag}} [\ln|G_{0ag}| + u'_{agi} G_{0ag}^{-1} u_{agi}]$$

$$\ln[f(u_{nk}|\phi)] = -\tfrac{1}{2} \sum_{i=1}^{n_{bu}} [\ln|\mathrm{G_{0nk}}| + u'_{nki} G_{0nk}^{-1} u_{nki}],\ \mathrm{k} = 1, \ldots, \mathrm{K}$$

$$\ln[f(v|\phi)] = -\tfrac{1}{2} \sum_{m=1}^{M} \sum_{i=1}^{n_m} [\ln|R_{0m}^{*}| + \mathrm{v}'_{mi} (R_{0m}^{*})^{-1} v_{mi}]$$

The information matrix of the multibreed REML estimates of covariance components computed using a generalized expectation-maximization algorithm (heretofore MREMLEM covariance estimates) is equal to (Louis, 1982):

$$I_{K'y, \phi=\phi^{*}} = I_{u_a, u_{n\bullet}, v} - I_{u_a, u_{n\bullet}, v|K'y, \phi=\phi^{*}}$$

where

$$I_{u_a, u_{n\bullet}, v} = -E_{\phi}\left[\left\{\frac{\partial^2 \ln[f(u_a, u_{n\bullet}, v|\phi)]}{\partial\phi_j \partial\phi_k}\right\}\middle| K'y, \phi = \phi^{*}\right], \text{ and}$$

$$I_{u_a, u_{n\bullet}, v|K'y, \phi=\phi^{*}} = E_{\phi}\left[\left\{\frac{\partial \ln[f(u_a, u_{n\bullet}, v|\phi)]}{\partial\phi_j}\right\}\left\{\frac{\partial \ln[f(u_a, u_{n\bullet}, v|\phi)]}{\partial\phi_k}\right\}'\middle| K'y, \phi = \phi^{*}\right].$$

Explicit equations of the two terms of the information matrix for MREMLEM covariance estimates will now be derived using additive genetic effects (u_a). Because of the form of the MREMLEM covariance component equations (e.g., equation [12], Appendix, Elzo, 1994), residual effects (v) may contribute to additive and(or) nonadditive genetic covariance terms depending on the genetic model used (e.g., sirematernal grandsire model).

Derivation of the Variance of MREMLEM Estimates of Additive Genetic Covariances

Derivation of I_{u_a}

$$I_{u_a} = -E_\phi\left[\left\{\frac{\partial^2 \ln[f(u_a|\phi)]}{\partial\phi_j\partial\phi_k}\right\}\middle| K'y, \phi = \phi^*\right]$$

The first derivative of $\ln[f(u_a|\phi)]$ with respect to ϕ is equal to:

$$\left\{\frac{\partial \ln[f(u_a|\phi)]}{\partial\phi_j}\right\} = \left\{-\tfrac{1}{2}\sum_{ag=1}^{nbgcom}\left[n_{ag}tr\left(G_{0ag}^{-1}\frac{\partial G_{0ag}}{\partial\phi_j}\right) - tr\left(G_{0ag}^{-1}\frac{\partial G_{0ag}}{\partial\phi_j}G_{0ag}^{-1}\sum_{i=1}^{n_{ag}}u_{agi}u'_{agi}\right)\right]\right\}$$

The second derivative of $\ln[f(u_a|\phi)]$ with respect to ϕ is equal to:

$$\left\{\frac{\partial^2 \ln[f(u_a|\phi)]}{\partial\phi_j\partial\phi_k}\right\} = \left\{\begin{array}{c} \tfrac{1}{2}\sum_{ag=1}^{nbgcom}\left[n_{ag}tr\left(G_{0ag}^{-1}\frac{\partial G_{0ag}}{\partial\phi_k}G_{0ag}^{-1}\frac{\partial G_{0ag}}{\partial\phi_j}\right)\right] \\ -\tfrac{1}{2}\sum_{ag=1}^{nbgcom}\left[tr\left(G_{0ag}^{-1}\frac{\partial G_{0ag}}{\partial\phi_j}G_{0ag}^{-1}\frac{\partial G_{0ag}}{\partial\phi_k}G_{0ag}^{-1}\sum_{i=1}^{n_{ag}}u_{agi}u'_{agi}\right)\right] \\ -\tfrac{1}{2}\sum_{ag=1}^{nbgcom}\left[tr\left(G_{0ag}^{-1}\frac{\partial G_{0ag}}{\partial\phi_k}G_{0ag}^{-1}\frac{\partial G_{0ag}}{\partial\phi_j}G_{0ag}^{-1}\sum_{i=1}^{n_{ag}}u_{agi}u'_{agi}\right)\right] \end{array}\right\}$$

$$\left\{\frac{\partial^2 \ln[f(u_a|\phi)]}{\partial\phi_j\partial\phi_k}\right\} = \left\{\begin{array}{c} \tfrac{1}{2}\sum_{ag=1}^{nbgcom}\left[n_{ag}tr\left(G_{0ag}^{-1}\frac{\partial G_{0ag}}{\partial\phi_k}G_{0ag}^{-1}\frac{\partial G_{0ag}}{\partial\phi_j}\right)\right] \\ -\sum_{ag=1}^{nbgcom}\left[tr\left(G_{0ag}^{-1}\frac{\partial G_{0ag}}{\partial\phi_j}G_{0ag}^{-1}\frac{\partial G_{0ag}}{\partial\phi_k}G_{0ag}^{-1}\sum_{i=1}^{n_{ag}}u_{agi}u'_{agi}\right)\right] \end{array}\right\}$$

The expectation of the second derivative of $\ln[f(u_a|\phi)]$ with respect to ϕ is equal to:

$$E_\phi\left[\left\{\frac{\partial^2 \ln[f(u_a|\phi)]}{\partial\phi_j\partial\phi_k}\right\}\middle| K'y, \phi = \phi^*\right] = \left\{\begin{array}{c} \tfrac{1}{2}\sum_{ag=1}^{nbgcom}\left[n_{ag}tr\left(G_{0ag}^{-1}\frac{\partial G_{0ag}}{\partial\phi_k}G_{0ag}^{-1}\frac{\partial G_{0ag}}{\partial\phi_j}\right)\right] \\ -\sum_{ag=1}^{nbgcom}\left[tr\left(G_{0ag}^{-1}\frac{\partial G_{0ag}}{\partial\phi_j}G_{0ag}^{-1}\frac{\partial G_{0ag}}{\partial\phi_k}G_{0ag}^{-1}\sum_{i=1}^{n_{ag}}E\left[u_{agi}u'_{agi}|K'y, \phi = \phi^*\right]\right)\right] \end{array}\right\}$$

$$E_{\phi}\left[\left\{\frac{\partial^2 \ln[f(u_a|\phi)]}{\partial\phi_j\partial\phi_k}\right\}\middle| K'y, \phi=\phi^*\right] = \left\{\begin{array}{l} \frac{1}{2}\sum_{ag=1}^{ndgcom}\left[n_{ag}tr\left(G_{0ag}^{-1}\frac{\partial G_{0ag}}{\partial\phi_k}G_{0ag}^{-1}\frac{\partial G_{0ag}}{\partial\phi_j}\right)\right] \\ -\sum_{ag=1}^{ndgcom}\left[tr\left(G_{0ag}^{-1}\frac{\partial G_{0ag}}{\partial\phi_j}G_{0ag}^{-1}\frac{\partial G_{0ag}}{\partial\phi_k}G_{0ag}^{-1}S_{0ag\bullet}^{*}\right)\right]\end{array}\right\}$$

where

$$S_{0ag\bullet}^{*} = \sum_{i=1}^{n_{ag}} E\left[u_{agi}u'_{agi} | K'y, \phi=\phi^*\right]$$

$$S_{0ag\bullet}^{*} = \sum_{i=1}^{n_{ag}}\left[\hat{u}_{agi}\hat{u}'_{agi} + \mathbf{var}(\hat{u}_{agi} - u_{agi})\right].$$

Thus,

$$I_{u_a} = -E_{\phi}\left[\left\{\frac{\partial^2 \ln[f(u_a|\phi)]}{\partial\phi_j\partial\phi_k}\right\}\middle| K'y, \phi=\phi^*\right] = \left\{\begin{array}{l} -\frac{1}{2}\sum_{ag=1}^{ndgcom}\left[n_{ag}tr\left(G_{0ag}^{-1}\frac{\partial G_{0ag}}{\partial\phi_k}G_{0ag}^{-1}\frac{\partial G_{0ag}}{\partial\phi_j}\right)\right] \\ +\sum_{ag=1}^{ndgcom}\left[tr\left(G_{0ag}^{-1}\frac{\partial G_{0ag}}{\partial\phi_j}G_{0ag}^{-1}\frac{\partial G_{0ag}}{\partial\phi_k}G_{0ag}^{-1}S_{ag\bullet}^{*}\right)\right]\end{array}\right\}$$

Derivation of $I_{u_a|K'y,\phi=\phi^*}$

$$I_{u_a|K'y,\phi=\phi^*} = E_{\phi}\left[\left\{\frac{\partial \ln[f(u_a|\phi)]}{\partial\phi_j}\right\}\left\{\frac{\partial \ln[f(u_a|\phi)]}{\partial\phi_k}\right\}'\middle| K'y, \phi=\phi^*\right]$$

where

$$\left\{\frac{\partial \ln[f(u_a|\phi)]}{\partial\phi_j}\right\} = \left\{-\frac{1}{2}\sum_{ag=1}^{ndgcom}\left[n_{ag}tr\left(G_{0ag}^{-1}\frac{\partial G_{0ag}}{\partial\phi_j}\right) - tr\left(G_{0ag}^{-1}\frac{\partial G_{0ag}}{\partial\phi_j}G_{0ag}^{-1}\sum_{i=1}^{n_{ag}}u_{agi}u'_{agi}\right)\right]\right\},$$

and

$$\left\{\frac{\partial \ln[f(u_a|\phi)]}{\partial\phi_k}\right\} = \left\{-\frac{1}{2}\sum_{ag'=1}^{ndgcom}\left[n_{ag'}tr\left(G_{0ag'}^{-1}\frac{\partial G_{0ag'}}{\partial\phi_k}\right) - tr\left(G_{0ag'}^{-1}\frac{\partial G_{0ag'}}{\partial\phi_k}G_{0ag'}^{-1}\sum_{i'=1}^{n_{ag'}}u_{ag'i'}u'_{ag'i'}\right)\right]\right\}.$$

Let

$$A = \left\{ -\tfrac{1}{2} \sum_{ag=1}^{nbgcom} \left[n_{ag} tr\left(G_{0ag}^{-1} \frac{\partial G_{0ag}}{\partial \phi_j} \right) \right] \right\},$$

$$B = \left\{ -\tfrac{1}{2} \sum_{ag=1}^{nbgcom} \left[-tr\left(G_{0ag}^{-1} \frac{\partial G_{0ag}}{\partial \phi_j} G_{0ag}^{-1} \sum_{i=1}^{n_{ag}} u_{agi} u'_{agi} \right) \right] \right\},$$

$$A' = \left\{ -\tfrac{1}{2} \sum_{ag'=1}^{nbgcom} \left[n_{ag'} tr\left(G_{0ag'}^{-1} \frac{\partial G_{0ag'}}{\partial \phi_k} \right) \right] \right\}' \text{, and}$$

$$B' = \left\{ -\tfrac{1}{2} \sum_{ag'=1}^{nbgcom} \left[-tr\left(G_{0ag'}^{-1} \frac{\partial G_{0ag'}}{\partial \phi_k} G_{0ag'}^{-1} \sum_{i'=1}^{n_{ag'}} u_{ag'i'} u'_{ag'i'} \right) \right] \right\}'.$$

Thus,

$$I_{u_a|K'y,\phi=\phi^*} = E_\phi\left[(A+B)(A'+B') \middle| K'y, \phi = \phi^* \right]$$

$$I_{u_a|K'y,\phi=\phi^*} = E_\phi\left[(AA' + AB' + BA' + BB') \middle| K'y, \phi = \phi^* \right]$$

$$I_{u_a|K'y,\phi=\phi^*} = \left\{ \begin{array}{l} E_\phi\left[AA' | K'y, \phi = \phi^* \right] \\ + E_\phi\left[AB' | K'y, \phi = \phi^* \right] \\ + E_\phi\left[BA' | K'y, \phi = \phi^* \right] \\ + E_\phi\left[BB' | K'y, \phi = \phi^* \right] \end{array} \right\}$$

The first term of $I_{u_a|K'y,\phi=\phi^*}$ is equal to:

$$E_\phi[AA'|K'y, \phi = \phi^*] = E_\phi\left[\left\{ -\tfrac{1}{2} \sum_{ag=1}^{nbgcom} \left[n_{ag} tr\left(G_{0ag}^{-1} \frac{\partial G_{0ag}}{\partial \phi_j} \right) \right] \right\} \left\{ -\tfrac{1}{2} \sum_{ag'=1}^{nbgcom} \left[n_{ag'} tr\left(G_{0ag'}^{-1} \frac{\partial G_{0ag'}}{\partial \phi_k} \right) \right] \right\}' \middle| K'y, \phi = \phi^* \right]$$

$$E_\phi[AA'|K'y, \phi = \phi^*] = \left\{ \tfrac{1}{4} \sum_{ag=1}^{nbgcom} \sum_{ag'=1}^{nbgcom} E_\phi\left[n_{ag} tr\left(G_{0ag}^{-1} \frac{\partial G_{0ag}}{\partial \phi_j} \right) n_{ag'} tr\left(G_{0ag'}^{-1} \frac{\partial G_{0ag'}}{\partial \phi_k} \right) \middle| K'y, \phi = \phi^* \right] \right\}$$

$$E_\phi[AA'|K'y, \phi = \phi^*] = \left\{ \tfrac{1}{4} \sum_{ag=1}^{nbgcom} \sum_{ag'=1}^{nbgcom} \left[n_{ag} tr\left(G_{0ag}^{-1} \frac{\partial G_{0ag}}{\partial \phi_j} \right) n_{ag'} tr\left(G_{0ag'}^{-1} \frac{\partial G_{0ag'}}{\partial \phi_k} \right) \right] \right\}$$

The second term of $I_{u_a|K'y,\phi=\phi^*}$ is equal to:

$$E_\phi[AB'|K'y,\phi=\phi^*] = E_\phi\left[\left\{-\tfrac{1}{2}\sum_{ag=1}^{nbgcom}\left[n_{ag}tr\left(G_{0ag}^{-1}\frac{\partial G_{0ag}}{\partial\phi_j}\right)\right]\right\}\left\{-\tfrac{1}{2}\sum_{ag'=1}^{nbgcom}\left[-tr\left(G_{0ag'}^{-1}\frac{\partial G_{0ag'}}{\partial\phi_k}G_{0ag'}^{-1}\sum_{i'=1}^{n_{ag'}}u_{ag'i'}u'_{ag'i'}\right)\right]\right\}'\middle|K'y,\phi=\phi^*\right]$$

$$E_\phi[AB'|K'y,\phi=\phi^*] = \left\{-\tfrac{1}{4}\sum_{ag=1}^{nbgcom}\sum_{ag'=1}^{nbgcom}E_\phi\left[n_{ag}tr\left(G_{0ag}^{-1}\frac{\partial G_{0ag}}{\partial\phi_j}\right)tr\left(G_{0ag'}^{-1}\frac{\partial G_{0ag'}}{\partial\phi_k}G_{0ag'}^{-1}\sum_{i'=1}^{n_{ag'}}u_{ag'i'}u'_{ag'i'}\right)\middle|K'y,\phi=\phi^*\right]\right\}$$

$$E_\phi[AB'|K'y,\phi=\phi^*] = \left\{-\tfrac{1}{4}\sum_{ag=1}^{nbgcom}\sum_{ag'=1}^{nbgcom}n_{ag}tr\left(G_{0ag}^{-1}\frac{\partial G_{0ag}}{\partial\phi_j}\right)tr\left(G_{0ag'}^{-1}\frac{\partial G_{0ag'}}{\partial\phi_k}G_{0ag'}^{-1}\sum_{i'=1}^{n_{ag'}}E_\phi[u_{ag'i'}u'_{ag'i'}|K'y,\phi=\phi^*]\right)\right\}$$

$$E_\phi[AB'|K'y,\phi=\phi^*] = \left\{-\tfrac{1}{4}\sum_{ag=1}^{nbgcom}\sum_{ag'=1}^{nbgcom}n_{ag}tr\left(G_{0ag}^{-1}\frac{\partial G_{0ag}}{\partial\phi_j}\right)tr\left(G_{0ag'}^{-1}\frac{\partial G_{0ag'}}{\partial\phi_k}G_{0ag'}^{-1}S^*_{0ag'\bullet}\right)\right\}$$

Similarly, the third term of $I_{u_a|K'y,\phi=\phi^*}$ is equal to:

$$E_\phi[BA'|K'y,\phi=\phi^*] = E_\phi\left[\left\{-\tfrac{1}{2}\sum_{ag=1}^{nbgcom}\left[-tr\left(G_{0ag}^{-1}\frac{\partial G_{0ag}}{\partial\phi_j}G_{0ag}^{-1}\sum_{i=1}^{n_{ag}}u_{agi}u'_{agi}\right)\right]\right\}\left\{-\tfrac{1}{2}\sum_{ag'=1}^{nbgcom}\left[n_{ag}tr\left(G_{0ag'}^{-1}\frac{\partial G_{0ag'}}{\partial\phi_k}\right)\right]\right\}'\middle|K'y,\phi=\phi^*\right]$$

$$E_\phi[BA'|K'y,\phi=\phi^*] = \left\{-\tfrac{1}{4}\sum_{ag=1}^{nbgcom}\sum_{ag'=1}^{nbgcom}tr\left(G_{0ag}^{-1}\frac{\partial G_{0ag}}{\partial\phi_j}G_{0ag}^{-1}S^*_{0ag\bullet}\right)n_{ag'}tr\left(G_{0ag'}^{-1}\frac{\partial G_{0ag'}}{\partial\phi_k}\right)\right\}$$

The fourth term of $I_{u_a|K'y,\phi=\phi^*}$ is equal to:

$$E_\phi[BB'|K'y,\phi=\phi^*] = E_\phi\left[\left\{-\tfrac{1}{2}\sum_{ag=1}^{nbgcom}\left[-tr\left(G_{0ag}^{-1}\frac{\partial G_{0ag}}{\partial\phi_j}G_{0ag}^{-1}\sum_{i=1}^{n_{ag}}u_{agi}u'_{agi}\right)\right]\right\}\left\{-\tfrac{1}{2}\sum_{ag'=1}^{nbgcom}\left[-tr\left(G_{0ag'}^{-1}\frac{\partial G_{0ag'}}{\partial\phi_k}G_{0ag'}^{-1}\sum_{i'=1}^{n_{ag'}}u_{ag'i'}u'_{ag'i'}\right)\right]\right\}'\middle|K'y,\phi=\phi^*\right]$$

$$E_\phi[BB'|K'y,\phi=\phi^*] = \left\{\tfrac{1}{4}\sum_{ag=1}^{nbgcom}\sum_{ag'=1}^{nbgcom}E_\phi\left[tr\left(G_{0ag}^{-1}\frac{\partial G_{0ag}}{\partial\phi_j}G_{0ag}^{-1}\sum_{i=1}^{n_{ag}}u_{agi}u'_{agi}\right)tr\left(G_{0ag'}^{-1}\frac{\partial G_{0ag'}}{\partial\phi_k}G_{0ag'}^{-1}\sum_{i'=1}^{n_{ag'}}u_{ag'i'}u'_{ag'i'}\right)\right]\middle|K'y,\phi=\phi^*\right\}$$

$$E_\phi[BB'|K'y,\phi=\phi^*] = \left\{\tfrac{1}{4}\sum_{ag=1}^{nbgcom}\sum_{ag'=1}^{nbgcom}E_\phi\left[\left(\sum_{i=1}^{n_{ag}}u'_{agi}G_{0ag}^{-1}\frac{\partial G_{0ag}}{\partial\phi_j}G_{0ag}^{-1}u_{agi}\right)\left(\sum_{i'=1}^{n_{ag'}}u'_{ag'i'}G_{0ag'}^{-1}\frac{\partial G_{0ag'}}{\partial\phi_k}G_{0ag'}^{-1}u_{ag'i'}\right)\right]\middle|K'y,\phi=\phi^*\right\}$$

$$E_{\phi}[BB'|K'y,\phi=\phi^{*}]=\left\{\frac{1}{4}\sum_{ebg=1}^{nbgcom}\sum_{ebg'=1}^{nbgcom}\sum_{i=1}^{n_{ebg}}\sum_{i'=1}^{n_{ebg'}}E_{\phi}\left[\left(u'_{ebg\,i}G_{0ebg}^{-1}\frac{\partial G_{0ebg}}{\partial\phi_{j}}G_{0ebg}^{-1}u_{ebg\,i}\right)\left(u'_{ebg'i'}G_{0ebg'}^{-1}\frac{\partial G_{0ebg'}}{\partial\phi_{k}}G_{0ebg'}^{-1}u_{ebg'i'}\right)\right]\Big|K'y,\phi=\phi^{*}\right\}$$

Note:

1. The distribution of u given the data and the REML covariance estimates at convergence is:

$$(u|K'y,\phi=\phi^{*})\sim MVN[\hat{u},\mathrm{var}(\hat{u}-u)]$$

or

$$(u|K'y,\phi=\phi^{*})\sim MVN[\hat{u},C^{*}]$$

where

$C^{*}=$ (LHS)$^{-1}$ of the MME.

2. The expectation of the product of the two bilinear forms in the equation above, using a *simplified notation*, is:

$$E_{\phi}[(u_{i}'A_{j}u_{i})(u_{i'}'A_{k}u_{i'})|K'y,\phi=\phi^{*}]$$
$$=$$
$$\mathbf{cov}_{\phi}[(u_{i}'A_{j}u_{i},u_{i'}'A_{k}u_{i'})|K'y,\phi=\phi^{*}]$$
$$+$$
$$E_{\phi}[(u_{i}'A_{j}u_{i})|K'y,\phi=\phi^{*}]\,E_{\phi}[(u_{i'}'A_{k}u_{i'})|K'y,\phi=\phi^{*}]$$

where

i] by equation 58, page 66, Searle (1971),

$$\mathrm{cov}_{\phi}[(u_{i}'A_{j}u_{i},u_{i'}'A_{k}u_{i'})|K'y,\phi=\phi^{*}]=2tr(A_{j}C_{ii'}^{*}A_{k}C_{i'i}^{*})+4\hat{u}_{i}'A_{j}C_{ii'}^{*}A_{k}\hat{u}_{i'}$$

where

$C_{ii'}^{*}=$ block of (LHS)$^{-1}$ between animals i and i′, and

$C_{i'i}^{*}=C_{ii'}^{*}{}'$

ii] by equation 40, page 55, Searle (1971),

$$E_{\phi}[(u_{i}'A_{j}u_{i})|K'y,\phi=\phi^{*}]=tr(A_{j}C_{ii}^{*})+\hat{u}_{i}'A_{j}\hat{u}_{i}=tr[A_{j}(\hat{u}_{i}\hat{u}_{i}'+C_{ii}^{*})]=tr[A_{j}S_{i}^{*}]$$

where $C_{ii}^{*}=$ **block of (LHS)$^{-1}$ for animal i, and** $S_{i}^{*}=\hat{u}_{i}\hat{u}_{i}'+C_{ii}^{*}$ **.**

and,

$$E_{\phi}[(u_{i'}'A_{k}u_{i'})|K'y,\phi=\phi^{*}]=tr(A_{k}C_{i'i'}^{*})+\hat{u}_{i'}'A_{k}\hat{u}_{i'}=tr[A_{k}(\hat{u}_{i'}\hat{u}_{i'}'+C_{i'i'}^{*})]=tr[A_{k}S_{i'}^{*}]$$

where $C_{i'i'}^{*}=$ block of (LHS)$^{-1}$ for animal i'

Thus,

$$E_{\phi}[BB'|K'y,\phi=\phi'] = \left\{ \frac{1}{4} \sum_{ag=1}^{ndgcom} \sum_{ag'=1}^{ndgcom} \sum_{i=1}^{n_{ag}} \sum_{i'=1}^{n_{ag'}} \left(\begin{array}{c} \operatorname{cov}_{\phi}\left[\left(u'_{agi} G_{0ag}^{-1} \frac{\partial G_{0ag}}{\partial \phi_j} G_{0ag}^{-1} u_{agi}\right), \left(u'_{ag'i'} G_{0ag'}^{-1} \frac{\partial G_{0ag'}}{\partial \phi_k} G_{0ag'}^{-1} u_{ag'i'}\right)\right] \Big| K'y, \phi=\phi' \\ + E_{\phi}\left[\left(u'_{agi} G_{0ag}^{-1} \frac{\partial G_{0ag}}{\partial \phi_j} G_{0ag}^{-1} u_{agi}\right) \Big| K'y,\phi=\phi'\right] E_{\phi}\left[\left(u'_{ag'i'} G_{0ag'}^{-1} \frac{\partial G_{0ag'}}{\partial \phi_k} G_{0ag}^{-1} u_{ag'i'}\right) \Big| K'y,\phi=\phi'\right] \end{array} \right) \right\}$$

$$E_{\phi}[BB'|K'y,\phi=\phi^{*}] = \left\{ \frac{1}{4} \sum_{ag=1}^{ndgcom} \sum_{ag'=1}^{ndgcom} \sum_{i=1}^{n_{ag}} \sum_{i'=1}^{n_{ag'}} \left(\begin{array}{c} \left[2tr\left(G_{0ag}^{-1} \frac{\partial G_{0ag}}{\partial \phi_j} G_{0ag}^{-1} C^{*}_{ii'} G_{0ag'}^{-1} \frac{\partial G_{0ag'}}{\partial \phi_k} G_{0ag'}^{-1} C^{*}_{i'i}\right)\right] \\ + \left[4\left(\hat{u}'_{agi} G_{0ag}^{-1} \frac{\partial G_{0ag}}{\partial \phi_j} G_{0ag}^{-1} C^{*}_{ii'} G_{0ag'}^{-1} \frac{\partial G_{0ag'}}{\partial \phi_k} G_{0ag}^{-1} \hat{u}_{ag'i'}\right)\right] \\ + \left[tr\left(G_{0ag}^{-1} \frac{\partial G_{0ag}}{\partial \phi_j} G_{0ag}^{-1} (\hat{u}_{agi}\hat{u}'_{agi} + C^{*}_{ii})\right)\right]\left[tr\left(G_{0ag'}^{-1} \frac{\partial G_{0ag'}}{\partial \phi_k} G_{0ag'}^{-1} (\hat{u}_{ag'i'}\hat{u}'_{ag'i'} + C^{*}_{i'i'})\right)\right] \end{array} \right) \right\}$$

$$E_{\phi}[BB'|K'y,\phi=\phi^{*}] = \left\{ \frac{1}{4} \sum_{ag=1}^{ndgcom} \sum_{ag'=1}^{ndgcom} \sum_{i=1}^{n_{ag}} \sum_{i'=1}^{n_{ag'}} \left(\begin{array}{c} \left[2tr\left(G_{0ag}^{-1} \frac{\partial G_{0ag}}{\partial \phi_j} G_{0ag}^{-1} C^{*}_{ii'} G_{0ag'}^{-1} \frac{\partial G_{0ag'}}{\partial \phi_k} G_{0ag'}^{-1} C^{*}_{i'i}\right)\right] \\ + \left[4\left(\hat{u}'_{agi} G_{0ag}^{-1} \frac{\partial G_{0ag}}{\partial \phi_j} G_{0ag}^{-1} C^{*}_{ii'} G_{0ag'}^{-1} \frac{\partial G_{0ag'}}{\partial \phi_k} G_{0ag'}^{-1} \hat{u}_{ag'i'}\right)\right] \\ + \left[tr\left(G_{0ag}^{-1} \frac{\partial G_{0ag}}{\partial \phi_j} G_{0ag}^{-1} S^{*}_{0agi}\right)\right]\left[tr\left(G_{0ag'}^{-1} \frac{\partial G_{0ag'}}{\partial \phi_k} G_{0ag'}^{-1} S^{*}_{0ag'i'}\right)\right] \end{array} \right) \right\}$$

$$E_{\phi}[BB'|K'y,\phi=\phi^{*}] = \left\{ \frac{1}{4} \sum_{ag=1}^{ndgcom} \sum_{ag'=1}^{ndgcom} \sum_{i=1}^{n_{ag}} \sum_{i'=1}^{n_{ag'}} \left(\begin{array}{c} \left[2tr\left(G_{0ag}^{-1} \frac{\partial G_{0ag}}{\partial \phi_j} G_{0ag}^{-1} C^{*}_{ii'} G_{0ag'}^{-1} \frac{\partial G_{0ag'}}{\partial \phi_k} G_{0ag'}^{-1} C^{*}_{i'i}\right)\right] \\ + \left[4tr\left(G_{0ag}^{-1} \frac{\partial G_{0ag}}{\partial \phi_j} G_{0ag}^{-1} C^{*}_{ii'} G_{0ag'}^{-1} \frac{\partial G_{0ag'}}{\partial \phi_k} G_{0ag'}^{-1} \hat{u}_{ag'i'} \hat{u}'_{agi}\right)\right] \\ + \left[tr\left(G_{0ag}^{-1} \frac{\partial G_{0ag}}{\partial \phi_j} G_{0ag}^{-1} S^{*}_{0agi}\right)\right]\left[tr\left(G_{0ag'}^{-1} \frac{\partial G_{0ag'}}{\partial \phi_k} G_{0ag'}^{-1} S^{*}_{0ag'i'}\right)\right] \end{array} \right) \right\}$$

Equations for the Variance of MREMLEM Estimates of Additive Genetic Covariances

$$I_{u_a} = \left\{ \begin{array}{l} -\frac{1}{2} \sum_{ag=1}^{nbgcom} \left[n_{ag} tr\left(G_{0ag}^{-1} \frac{\partial G_{0ag}}{\partial \phi_k} G_{0ag}^{-1} \frac{\partial G_{0ag}}{\partial \phi_j} \right) \right] \\ + \sum_{ag=1}^{nbgcom} \left[tr\left(G_{0ag}^{-1} \frac{\partial G_{0ag}}{\partial \phi_j} G_{0ag}^{-1} \frac{\partial G_{0ag}}{\partial \phi_k} G_{0ag}^{-1} S_{0ag\bullet}^{*} \right) \right] \end{array} \right\}$$

where $S_{0ag\bullet}^{*} = \sum_{i=1}^{n_{ag}} \left[\hat{u}_{agi} \hat{u}_{agi}' + \mathrm{var}(\hat{u}_{agi} - u_{agi}) \right]$,

and

$$I_{u_a | K'y, \phi = \phi^*} = \left\{ \begin{array}{l} E_{\phi}\left[AA' | K'y, \phi = \phi^* \right] \\ + E_{\phi}\left[AB' | K'y, \phi = \phi^* \right] \\ + E_{\phi}\left[BA' | K'y, \phi = \phi^* \right] \\ + E_{\phi}\left[BB' | K'y, \phi = \phi^* \right] \end{array} \right\}$$

where

$$E_{\phi}[AA' | K'y, \phi = \phi^*] = \left\{ \frac{1}{4} \sum_{ag=1}^{nbgcom} \sum_{ag'=1}^{nbgcom} \left[n_{ag} tr\left(G_{0ag}^{-1} \frac{\partial G_{0ag}}{\partial \phi_j} \right) n_{ag'} tr\left(G_{0ag'}^{-1} \frac{\partial G_{0ag'}}{\partial \phi_k} \right) \right] \right\},$$

$$E_{\phi}[AB' | K'y, \phi = \phi^*] = \left\{ -\frac{1}{4} \sum_{ag=1}^{nbgcom} \sum_{ag'=1}^{nbgcom} n_{ag} tr\left(G_{0ag}^{-1} \frac{\partial G_{0ag}}{\partial \phi_j} \right) tr\left(G_{0ag'}^{-1} \frac{\partial G_{0ag'}}{\partial \phi_k} G_{0ag'}^{-1} S_{0ag'\bullet}^{*} \right) \right\},$$

$$E_{\phi}[BA' | K'y, \phi = \phi^*] = \left\{ -\frac{1}{4} \sum_{ag=1}^{nbgcom} \sum_{ag'=1}^{nbgcom} tr\left(G_{0ag}^{-1} \frac{\partial G_{0ag}}{\partial \phi_j} G_{0ag}^{-1} S_{0ag\bullet}^{*} \right) n_{ag'} tr\left(G_{0ag'}^{-1} \frac{\partial G_{0ag'}}{\partial \phi_k} \right) \right\}, \text{ and}$$

$$E_{\phi}[BB' | K'y, \phi = \phi^*] = \left\{ \frac{1}{4} \sum_{ag=1}^{nbgcom} \sum_{ag'=1}^{nbgcom} \sum_{i=1}^{n_{ag}} \sum_{i'=1}^{n_{ag'}} \left(\begin{array}{l} \left[2tr\left(G_{0ag}^{-1} \frac{\partial G_{0ag}}{\partial \phi_j} G_{0ag}^{-1} C_{ii'}^{*} G_{0ag'}^{-1} \frac{\partial G_{0ag'}}{\partial \phi_k} G_{0ag'}^{-1} C_{i'i}^{*} \right) \right] \\ + \left[4tr\left(G_{0ag}^{-1} \frac{\partial G_{0ag}}{\partial \phi_j} G_{0ag}^{-1} C_{ii'}^{*} G_{0ag'}^{-1} \frac{\partial G_{0ag'}}{\partial \phi_k} G_{0ag'}^{-1} \hat{u}_{ag'i'} \hat{u}_{agi}' \right) \right] \\ + \left[tr\left(G_{0ag}^{-1} \frac{\partial G_{0ag}}{\partial \phi_j} G_{0ag}^{-1} S_{0agi}^{*} \right) \right] \left[tr\left(G_{0ag'}^{-1} \frac{\partial G_{0ag'}}{\partial \phi_k} G_{0ag'}^{-1} S_{0ag'i'}^{*} \right) \right] \end{array} \right) \right\}.$$

Similar sets of formulas can be derived for nonadditive genetic and for residual effects.

Equations for the Variance of MREMLEM Estimates of Nonadditive Genetic Covariances

$$I_{u_{nk}} = \left\{ \begin{array}{l} -\frac{1}{2}\left[n_{bu} tr\left(G_{0nk}^{-1} \frac{\partial G_{0nk}}{\partial \phi_k} G_{0nk}^{-1} \frac{\partial G_{0nk}}{\partial \phi_j} \right) \right] \\ + \left[tr\left(G_{0nk}^{-1} \frac{\partial G_{0nk}}{\partial \phi_j} G_{0nk}^{-1} \frac{\partial G_{0nk}}{\partial \phi_k} G_{0nk}^{-1} S_{0nk\bullet}^{*} \right) \right] \end{array} \right\}$$

where $S_{0nk\bullet}^{*} = \sum_{i=1}^{n_{bu}} \left[\hat{u}_{nki} \hat{u}'_{nki} + \mathrm{var}(\hat{u}_{nki} - u_{nki}) \right]$,

and

$$I_{u_{nk}|K'y,\phi=\phi^*} = \left\{ \begin{array}{l} E_\phi\left[AA' | K'y, \phi = \phi^* \right] \\ + E_\phi\left[AB' | K'y, \phi = \phi^* \right] \\ + E_\phi\left[BA' | K'y, \phi = \phi^* \right] \\ + E_\phi\left[BB' | K'y, \phi = \phi^* \right] \end{array} \right\}$$

where

$$\boldsymbol{E_\phi[AA' | K'y, \phi = \phi^*]} = \left\{ \frac{1}{4}\left[n_{bu} tr\left(G_{0nk}^{-1} \frac{\partial G_{0nk}}{\partial \phi_j} \right) n_{bu} tr\left(G_{0nk}^{-1} \frac{\partial G_{0nk}}{\partial \phi_k} \right) \right] \right\},$$

$$E_\phi[AB' | K'y, \phi = \phi^*] = \left\{ -\frac{1}{4} n_{bu} tr\left(G_{0nk}^{-1} \frac{\partial G_{0nk}}{\partial \phi_j} \right) tr\left(G_{0nk}^{-1} \frac{\partial G_{0nk}}{\partial \phi_k} G_{0nk}^{-1} S_{0nk\bullet}^{*} \right) \right\},$$

$$E_\phi[BA' | K'y, \phi = \phi^*] = \left\{ -\frac{1}{4} tr\left(G_{0nk}^{-1} \frac{\partial G_{0nk}}{\partial \phi_j} G_{0nk}^{-1} S_{0nk\bullet}^{*} \right) n_{nk'} tr\left(G_{0nk}^{-1} \frac{\partial G_{0nk}}{\partial \phi_k} \right) \right\}, \text{ and}$$

$$E_\phi[BB' | K'y, \phi = \phi^*] = \left\{ \frac{1}{4} \sum_{i=1}^{n_{bu}} \sum_{i'=1}^{n_{bu}} \left(\begin{array}{l} \left[2tr\left(G_{0nk}^{-1} \frac{\partial G_{0nk}}{\partial \phi_j} G_{0nk}^{-1} C_{nii'}^{*} G_{0nk}^{-1} \frac{\partial G_{0nk}}{\partial \phi_k} G_{0nk}^{-1} C_{ni'i}^{*} \right) \right] \\ + \left[4tr\left(G_{0nk}^{-1} \frac{\partial G_{0nk}}{\partial \phi_j} G_{0nk}^{-1} C_{nii'}^{*} G_{0nk}^{-1} \frac{\partial G_{0nk}}{\partial \phi_k} G_{0nk}^{-1} \hat{u}_{nki} \hat{u}'_{nki} \right) \right] \\ + \left[tr\left(G_{0nk}^{-1} \frac{\partial G_{0nk}}{\partial \phi_j} G_{0nk}^{-1} S_{0nki}^{*} \right) \right] \left[tr\left(G_{0nk}^{-1} \frac{\partial G_{0nk}}{\partial \phi_k} G_{0nk}^{-1} S_{0nki}^{*} \right) \right] \end{array} \right) \right\}.$$

Equations for the Variance of MREMLEM Estimates of Residual Covariances

$$I_v = \left\{ \begin{array}{l} -\frac{1}{2}\sum_{m=1}^{M}\left[n_m tr\left(R_{0m}^{-1}\frac{\partial R_{0m}}{\partial \phi_k} R_{0ag}^{-1}\frac{\partial R_{0m}}{\partial \phi_j} \right) \right] \\ -\sum_{m=1}^{M}\left[tr\left(R_{0m}^{-1}\frac{\partial R_{0m}}{\partial \phi_j} R_{0m}^{-1}\frac{\partial R_{0m}}{\partial \phi_k} R_{0m}^{-1} S_{0m\bullet}^{*} \right) \right] \end{array} \right\}$$

where $S_{0m\bullet}^{*} = \sum_{i=1}^{n_m}\left[\hat{v}_{mi}\hat{v}_{mi}' + \mathrm{var}(\hat{v}_{mi} - v_{mi}) \right]$,

and

$$I_{v|K'y,\phi=\phi^{*}} = \left\{ \begin{array}{l} E_{\phi}\left[AA' | K'y, \phi = \phi^{*} \right] \\ + E_{\phi}\left[AB' | K'y, \phi = \phi^{*} \right] \\ + E_{\phi}\left[BA' | K'y, \phi = \phi^{*} \right] \\ + E_{\phi}\left[BB' | K'y, \phi = \phi^{*} \right] \end{array} \right\}$$

where

$$E_{\phi}[AA' | K'y, \phi = \phi^{*}] = \left\{ \frac{1}{4}\sum_{m=1}^{M}\sum_{m'=1}^{M}\left[n_m tr\left(R_{0m}^{-1}\frac{\partial R_{0m}}{\partial \phi_j} \right) n_{m'} tr\left(R_{0m'}^{-1}\frac{\partial R_{0m'}}{\partial \phi_k} \right) \right] \right\},$$

$$E_{\phi}[AB' | K'y, \phi = \phi^{*}] = \left\{ -\frac{1}{4}\sum_{m=1}^{M}\sum_{m'=1}^{M} n_m tr\left(R_{0m}^{-1}\frac{\partial R_{0m}}{\partial \phi_j} \right) tr\left(R_{0m'}^{-1}\frac{\partial R_{0m'}}{\partial \phi_k} R_{0m'}^{-1} S_{0m'\bullet}^{*} \right) \right\},$$

$$E_{\phi}[BA' | K'y, \phi = \phi^{*}] = \left\{ -\frac{1}{4}\sum_{m=1}^{M}\sum_{m'=1}^{M} tr\left(R_{0m}^{-1}\frac{\partial R_{0m}}{\partial \phi_j} R_{0m}^{-1} S_{0m\bullet}^{*} \right) n_{m'} tr\left(R_{0m'}^{-1}\frac{\partial R_{0m'}}{\partial \phi_k} \right) \right\}, \text{ and}$$

$$E_{\phi}[BB' | K'y, \phi = \phi^{*}] = \left\{ \frac{1}{4}\sum_{m=1}^{M}\sum_{m'=1}^{M}\sum_{i=1}^{n_m}\sum_{i'=1}^{n_{m'}} \left(\begin{array}{l} \left[2tr\left(R_{0m}^{-1}\frac{\partial R_{0m}}{\partial \phi_j} R_{0m}^{-1} C_{Rii'}^{*} R_{0m'}^{-1}\frac{\partial R_{0m'}}{\partial \phi_k} R_{0m}^{-1} C_{Ri'i}^{*} \right) \right] \\ + \left[4tr\left(R_{0m}^{-1}\frac{\partial R_{0m}}{\partial \phi_j} R_{0m}^{-1} C_{Rii'}^{*} R_{0m'}^{-1}\frac{\partial R_{0m'}}{\partial \phi_k} R_{0m'}^{-1} \hat{v}_{mi}\hat{v}_{mi}' \right) \right] \\ + \left[tr\left(R_{0m}^{-1}\frac{\partial R_{0m}}{\partial \phi_j} R_{0m}^{-1} S_{0mi}^{*} \right) \right]\left[tr\left(R_{0m'}^{-1}\frac{\partial R_{0m'}}{\partial \phi_k} R_{0m'}^{-1} S_{0mi'}^{*} \right) \right] \end{array} \right) \right\},$$

and

$C_{Rii'}^{*} = ii'th$ block of $\mathrm{var}(\hat{v} - v)$.

Thus, the information matrix of the MREMLEM covariance estimates is equal to:

$$I_{K'y,\phi=\phi^{*}} = \left\{ I_{u_a,u_{na},\nu} - I_{u_a,u_{na},\nu|K'y,\phi=\phi^{*}} \right\}$$

$$I_{K'y,\phi=\phi^{*}} = \left\{ \begin{array}{c} \left\{ I_{u_a} - I_{u_a|K'y,\phi=\phi^{*}} \right\} \\ \oplus \left\{ I_{u_{na}} - I_{u_{na}|K'y,\phi=\phi^{*}} \right\} \\ + \left\{ I_{\nu} - I_{\nu|K'y,\phi=\phi^{*}} \right\} \end{array} \right\}$$

where all terms are as defined above.

Covariance Matrix of MREMLEM Covariance Estimates

$$\left\{ I_{K'y,\phi=\phi^{*}} \right\}^{-1} = \left\{ \begin{array}{c} \left\{ I_{u_a} - I_{u_a|K'y,\phi=\phi^{*}} \right\} \\ \oplus \left\{ I_{u_{na}} - I_{u_{na}|K'y,\phi=\phi^{*}} \right\} \\ + \left\{ I_{\nu} - I_{\nu|K'y,\phi=\phi^{*}} \right\} \end{array} \right\}^{-1}$$

Standard Error of MREMLEM Covariance Estimates

Square roots of the diagonal elements of the covariance matrix of MREMLEM covariance estimates yield standard errors.

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