# Approximate Variance for Heritability Estimates

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Notation:

$a$ : estimate of the additive genetic variance.

$e$ : estimate of the environmental or residual variance.

$p$ : estimate of the phenotypic variance.

Assuming

$$p = a + e$$

and the heritability

$$h^2 = \frac{a}{p} = \frac{a}{a+e}.$$

The negative inverse of the average information matrix gives us estimates $\left(I_A^{-1}\right)$ for the variance of the estimators var($a$) and var($e$) but also the covariance between the estimates $a$ and $e$ (cov($a$, $e$)).

In general terms, the variance of a function $f(\sigma)$ can be obtained as

$$\mathrm{var}(f(\sigma)) = \frac{\partial f(\sigma)}{\partial \sigma'} \mathrm{var}(\sigma) \frac{\partial f(\sigma)}{\partial \sigma'}$$

In this case

$$f(\sigma) = h^2 = \frac{a}{a+e}$$

and

$$\sigma = \begin{pmatrix} a \\ e \end{pmatrix}.$$

The two partial derivatives are

$$\frac{\partial h^2}{\partial a} = \frac{1}{a+e} - \frac{a}{(a+e)^2} = \frac{h^2(1-h^2)}{a},$$

$$\frac{\partial h^2}{\partial e} = -\frac{a}{(a+e)^2} = -\frac{h^2(h^2)}{a},$$

and

$$\mathrm{var}(\sigma) = \begin{pmatrix} \mathrm{var}(a) & \mathrm{cov}(a,e) \\ \mathrm{cov}(e,a) & \mathrm{var}(p) \end{pmatrix}$$

with appropriate entries taken from $I_A^{-1}$. Combining all of this information, you get

$$\mathrm{var}(f(\sigma)) = \frac{\partial f(\sigma)}{\partial \sigma'} \mathrm{var}(\sigma) \frac{\partial f(\sigma)}{\partial \sigma'}$$

$$= \left( \frac{h^2(1-h^2)}{a} \quad -\frac{h^2(h^2)}{a} \right) \begin{pmatrix} \mathrm{var}(a) & \mathrm{cov}(a,e) \\ \mathrm{cov}(e,a) & \mathrm{var}(p) \end{pmatrix} \begin{pmatrix} \frac{h^2(1-h^2)}{a} \\ -\frac{h^2(h^2)}{a} \end{pmatrix}$$

$$= \left( \frac{h^2}{a} \right)^2 \left( (1-h^2)^2 \, \mathrm{var}(a) - 2(1-h^2)h^2 \, \mathrm{cov}(a,e) + (h^2)^2 \, \mathrm{var}(e) \right)$$

This last quantity can easily be computed with the information obtained from the output of AIREMLF90. The question is how this is the same to what is written down in the ASREML manual. Here you have to realize that they present this in terms of $a$ and $p$ and not $a$ and $e$. By using the fact that $p = a + e$ and as a result:

var($p$) = var($a$) + var($e$) + 2cov($a$, $e$), we can get the formula in the
ASREML manual.


The formula above has two pieces that involve $e$ (var($e$) and cov($a$, $e$)). It is easy to replace $e$ with $p - a$. You get

var($e$) = var($p - a$) = var($p$) + var($a$) − 2cov($a$, $p$).

Here, you can replace cov($a, e$) with cov($a, p - a$) = cov($a, p$) − var($a$), and you get

var($e$) = var($p$) + var($a$) − 2cov($a, p$).

You also need

cov($a, e$) = cov($a, p$) − var($a$)

directly from the formula above.

Now replace the appropriate pieces in

$$\text{var}(h)^2 = \left(\frac{h^2}{a}\right)^2 \left((1-h^2)^2 \, \text{var}(a) - 2(1-h^2)h^2 \, \text{cov}(a,e) + (h^2)^2 \, \text{var}(e)\right)$$

$$= \left(\frac{h^2}{a}\right)^2 \left((1-h^2)^2 \, \text{var}(a) - 2(1-h^2)h^2 (\text{cov}(a,p) - \text{var}(a)) + (h^2)^2 (\text{var}(p) + \text{var}(a) - 2\,\text{cov}(a,p))\right)$$

$$= \left(\frac{h^2}{a}\right)^2 \left((1 - 2h^2 + (h^2)^2 + 2h^2 - 2(h^2)^2 + (h^2)^2)\text{var}(a) - 2(h^2 - (h^2)^2 + (h^2)^2)\text{cov}(a,p) + (h^2)^2 \, \text{var}(p)\right)$$

$$= \left(\frac{h^2}{a}\right)^2 \left(\text{var}(a) + (h^2)^2 \, \text{var}(p) - 2h^2 \, \text{cov}(a,p)\right)$$

$$= (h^2)^2 \left(\frac{\text{var}(a)}{a^2} + \frac{(h^2)^2 \, \text{var}(p)}{a^2} - 2\frac{h^2 \, \text{cov}(a,p)}{a^2}\right)$$

$$= \left(\frac{a}{p}\right)^2 \left(\frac{\text{var}(a)}{a^2} + \frac{\text{var}(p)}{p^2} - 2\frac{\text{cov}(a,p)}{ap}\right)$$

The last quantity is the one out of the ASREML manual, they replaced a with n for numerator and p with d for denominator. Their formula is correct for any ratio of the estimates, not only the heritability.

# Approximate Variance for Correlation Estimates

Notation:

$x_i$      : estimate of the variance for trait i.

$x_j$      : estimate of the variance for trait j.

$x_{ij}$      : estimate of the covariance between trait i and j.

The variance and covariance can be additive, environmental, or phenotypic. The correlation will be denoted by $r$ and is determined as

$$r = \frac{x_{12}}{\sqrt{x_1 x_2}}.$$

The negative inverse of the average information matrix gives us estimates $\left(I_A^{-1}\right)$ for the variance of the estimators var($x_1$), var($x_1$), and cov($x_{12}$) but also the covariance between the various estimates (cov($x_1, x_2$), cov($x_1, x_{12}$), cov($x_2, x_{12}$)).

We can use the same general formula

$$\mathrm{var}(f(\sigma)) = \frac{\partial f(\sigma)}{\partial \sigma'} \mathrm{var}(\sigma) \frac{\partial f(\sigma)}{\partial \sigma'}$$

to obtain the variance of the correlation estimate. Now we have

$$f(\sigma) = r = \frac{x_{12}}{\sqrt{x_1 x_2}} \text{ and } \sigma = \begin{pmatrix} x_1 \\ x_2 \\ x_{12} \end{pmatrix}.$$

The three partial derivatives are

$$\frac{\partial r}{\partial x_1} = -\frac{r}{2x_1},$$

$$\frac{\partial r}{\partial x_2} = -\frac{r}{2x_2},$$

and

$$\frac{\partial r}{\partial x_{12}} = \frac{r}{x_{12}}.$$

Then

$$\text{var}(r) = \begin{pmatrix} -\dfrac{r}{2x_1} & -\dfrac{r}{2x_2} & \dfrac{r}{x_{12}} \end{pmatrix} \begin{pmatrix} \text{var}(x_1) & \text{cov}(x_1, x_2) & \text{cov}(x_1, x_{12}) \\ \text{cov}(x_2, x_1) & \text{var}(x_2) & \text{cov}(x_2, x_{12}) \\ \text{cov}(x_{12}, x_1) & \text{cov}(x_{12}, x_2) & \text{var}(x_{12}) \end{pmatrix} \begin{pmatrix} -\dfrac{r}{2x_1} \\ -\dfrac{r}{2x_2} \\ \dfrac{r}{x_{12}} \end{pmatrix}.$$

Multiplying this out gives

$$\text{var}(r) = r^2 \left( \frac{\text{var}(x_1)}{4x_1^2} + \frac{\text{var}(x_2)}{4x_2^2} + \frac{\text{var}(x_{12})}{x_{12}^2} + \frac{\text{cov}(x_1, x_2)}{2x_1 x_2} - \frac{\text{cov}(x_1, x_{12})}{x_1 x_{12}} - \frac{\text{cov}(x_2, x_{12})}{x_2 x_{12}} \right).$$

# An Example

For a simple animal model, the derivative of the heritability estimate is

$$\frac{\partial \frac{\sigma_e^2}{\sigma_a^2 + \sigma_e^2}}{\partial \sigma_e^2} = -\frac{\sigma_a^2}{\left(\sigma_a^2 + \sigma_e^2\right)^2} = -\frac{h^4}{\sigma_a^2} \, .$$

Using

$$\frac{\partial h^2}{\partial \boldsymbol{\sigma}'} = \left[ \frac{h^2 - h^4}{\sigma_a^2} \quad -\frac{h^4}{\sigma_a^2} \right], \; \text{Var}(\hat{\sigma}) = -\mathbf{I}_A^{-1}, \text{ and } \boldsymbol{\sigma} = \left[\sigma_a^2 \; \sigma_e^2 \right],$$

the standard error of the heritability estimate is derived from

$$\text{SE}\left(h^2\right) = \sqrt{\frac{\partial h^2}{\partial \boldsymbol{\sigma}'} \text{Var}(\hat{\boldsymbol{\sigma}}) \frac{\partial h^2}{\partial \boldsymbol{\sigma}'}} \, .$$

Likewise, using the derivative of the correlation ($r_A$) between $a_i$ and $a_j$, the standard error is calculated with

$$\text{SE}\left(r_A\right) = \sqrt{\frac{\partial r_A}{\partial \boldsymbol{\sigma}'} \text{Var}(\hat{\boldsymbol{\sigma}}) \frac{\partial r_A}{\partial \boldsymbol{\sigma}'}}$$

where

$$\frac{\partial r_A}{\partial \boldsymbol{\sigma}'} = \left[ -\frac{r_A}{2\sigma_{a_i}^2} \quad -\frac{r_A}{2\sigma_{a_j}^2} \quad -\frac{r_A}{\text{Cov}(a_i, a_j)} \right]$$

and

$$\boldsymbol{\sigma} = \left[\sigma_{a_i}^2 \; \sigma_{a_j}^2 \; \text{Cov}(a_i, a_j)\right].$$