

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 (I_A^{-1}) for the variance of the estimators $\text{var}(a)$ and $\text{var}(e)$ but also the covariance between the estimates a and e ($\text{cov}(a, e)$).

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

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

In this case

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

and

$$\sigma = \begin{pmatrix} a \\ e \end{pmatrix}. \quad \text{sigma is a vector so var(sigma) is a matrix}$$

The two partial derivatives are

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

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

and

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

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

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

This is the equation you need!

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

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

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:

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

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

$$\text{var}(e) = \text{var}(p - a) = \text{var}(p) + \text{var}(a) - 2\text{cov}(a, p).$$

Here, you can replace $\text{cov}(a, e)$ with $\text{cov}(a, p - a) = \text{cov}(a, p) - \text{var}(a)$, and you get

$$\text{var}(e) = \text{var}(p) + \text{var}(a) - 2\text{cov}(a, p).$$

You also need

$$\text{cov}(a, e) = \text{cov}(a, p) - \text{var}(a)$$

directly from the formula above.

Now replace the appropriate pieces in

$$\begin{aligned} \text{var}(h)^2 &= \left(\frac{h^2}{a}\right)^2 \left((1-h^2)^2 \text{var}(a) - 2(1-h^2)h^2 \text{cov}(a, e) + (h^2)^2 \text{var}(e) \right) \\ &= \left(\frac{h^2}{a}\right)^2 \left((1-h^2)^2 \text{var}(a) - 2(1-h^2)h^2 (\text{cov}(a, p) - \text{var}(a)) + (h^2)^2 (\text{var}(p) + \text{var}(a) - 2\text{cov}(a, p)) \right) \\ &= \left(\frac{h^2}{a}\right)^2 \left((1-2h^2 + (h^2)^2 + 2h^2 - 2(h^2)^2 + (h^2)^2) \text{var}(a) - 2(h^2 - (h^2)^2 + (h^2)^2) \text{cov}(a, p) + (h^2)^2 \text{var}(p) \right) \\ &= \left(\frac{h^2}{a}\right)^2 \left(\text{var}(a) + (h^2)^2 \text{var}(p) - 2h^2 \text{cov}(a, p) \right) \\ &= (h^2)^2 \left(\frac{\text{var}(a)}{a^2} + \frac{(h^2)^2 \text{var}(p)}{a^2} - 2 \frac{h^2 \text{cov}(a, p)}{a^2} \right) \\ &= \left(\frac{a}{p}\right)^2 \left(\frac{\text{var}(a)}{a^2} + \frac{\text{var}(p)}{p^2} - 2 \frac{\text{cov}(a, p)}{ap} \right) \end{aligned}$$

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 (I_A^{-1}) for the variance of the estimators $\text{var}(x_1)$, $\text{var}(x_2)$, and $\text{cov}(x_1, x_2)$ but also the covariance between the various estimates $(\text{cov}(x_1, x_2), \text{cov}(x_1, x_{12}), \text{cov}(x_2, x_{12}))$.

We can use the same general formula

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

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

This is the equation you need!

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

Multiplying this out gives

$$\text{var}(r) = r^2 \left(\frac{\text{var}(x_1)}{4x_1^2} + \frac{\text{var}(x_2)}{4x_2^2} + \frac{\text{var}(x_{12})}{x_{12}^2} + \frac{\text{cov}(x_1, x_2)}{2x_1x_2} - \frac{\text{cov}(x_1, x_{12})}{x_1x_{12}} - \frac{\text{cov}(x_2, x_{12})}{x_2x_{12}} \right).$$

An Example

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

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

Using

$$\frac{\partial h^2}{\partial \boldsymbol{\sigma}'} = \begin{bmatrix} \frac{h^2 - h^4}{\sigma_a^2} & -\frac{h^4}{\sigma_a^2} \end{bmatrix}, \text{ Var}(\hat{\boldsymbol{\sigma}}) = -\mathbf{I}_A^{-1}, \text{ and } \boldsymbol{\sigma} = \begin{bmatrix} \sigma_a^2 & \sigma_e^2 \end{bmatrix},$$

the standard error of the heritability estimate is derived from

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

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

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

where

$$\frac{\partial r_A}{\partial \boldsymbol{\sigma}'} = \begin{bmatrix} -\frac{r_A}{2\sigma_{a_i}^2} & -\frac{r_A}{2\sigma_{a_j}^2} & -\frac{r_A}{\text{Cov}(a_i, a_j)} \end{bmatrix}$$

and

$$\boldsymbol{\sigma} = \begin{bmatrix} \sigma_{a_i}^2 & \sigma_{a_j}^2 & \text{Cov}(a_i, a_j) \end{bmatrix}.$$