

Calculating Standard Errors with AIREMLF90 Output

Heritability and Genetic Correlations

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May 9, 2017

Introduction

This vignette is designed to help people calculate standard errors of heritability and genetic correlations with output from airemlf90, in the BLUPF90 family of programs (Miszta et al., 2002). The following equations are given by Dr. Bert Klei and revised by S. Tsuruta in a PDF titled *Approximate Variance for Heritability Estimates*. Only important equations are given in this document. Please refer to the full document for further clarification.

Calculating the SE of a heritability estimate

Definitions:

a: estimate of additive genetic variance

e: estimate of residual variance

p: estimate of phenotypic variance

The equation for heritability is therefore:

$$h^2 = \frac{a}{a + e} = \frac{a}{p} \quad (1)$$

We need two things to get the SE. The partial derivative formulas and values from the inverse of the AI matrix that is output below the Final Estimates portion of the output.

The two partial derivatives are:

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

$$\frac{\partial h^2}{\partial e} = -\frac{a}{(a + e)^2} = -\frac{h^2(h^2)}{a} \quad (3)$$

Sigma is equal to:

$$\sigma = \begin{pmatrix} a \\ e \end{pmatrix} \quad (4)$$

Therefore the variance is:

$$var(\sigma) = \begin{pmatrix} var(a) & cov(a,e) \\ cov(e,a) & var(e) \end{pmatrix} \quad (5)$$

These numbers can be taken from the inverse of AI matrix (Sampling Variance) part of the output.

The equation needed to solve for the SE of heritability is a row vector of partial derivatives by the $var(\sigma)$ matrix and then a column vector of partial derivatives resulting in a single number, the variance. Simply take the square root to obtain the SE of σ .

$$var(h^2) = \left(\frac{h^2(1-h^2)}{a} - \frac{h^2(h^2)}{a} \right) \begin{pmatrix} var(a) & cov(a,e) \\ cov(e,a) & var(e) \end{pmatrix} \begin{pmatrix} \frac{h^2(1-h^2)}{a} \\ -\frac{h^2(h^2)}{a} \end{pmatrix} \quad (6)$$

Don't forget to take the square root of the variance to get the SE:

$$SE(h^2) = \sqrt{var(h^2)} \quad (7)$$

Example with output

The following is example output from a single trait analysis of a simple animal model.

Final Estimates

Genetic variance(s) for effect 4

1.6779

Residual variance(s)

11.435

inverse of AI matrix (Sampling Variance)

0.40950E-01 -0.20986E-01

-0.20986E-01 0.46718E-01

Correlations from inverse of AI matrix

1.0000 -0.47980

-0.47980 1.0000

SE for R

0.21614

SE for G

0.20236

This is typical output from airemlf90. Showing the final estimates of a and e , the inverse of the AI matrix, correlations from inverse of the AI matrix, and SE for R and G.

Heritability:

$$h^2 = \frac{1.6779}{1.6779 + 11.435} = 0.127957965 \quad (8)$$

We then need to partial derivatives to create the vectors.

$$\frac{\partial h^2}{\partial a} = \frac{0.127958(1 - 0.127958)}{1.6779} = 0.0665 \quad (9)$$

$$\frac{\partial h^2}{\partial e} = -\frac{0.127958(0.127958)}{1.6779} = -0.009758 \quad (10)$$

Now we can extract the $var(\sigma)$ from the output. These will come from the inverse of AI matrix (Sampling Variance) portion of the output (right below your final estimates).

WARNING: BE CAREFUL!

This is a simple example, when things get more complicated the best thing you can do is square the numbers from the SE for R or SE for G in the output (the very bottom of the output). Then find these numbers (variances) in the inverse AI matrix. This allows you to track which variances are which in the inverse AI matrix.

$$var(\sigma) = \begin{pmatrix} 0.40950E-01 & -0.20986E-01 \\ -0.20986E-01 & 0.46718E-01 \end{pmatrix} \quad (11)$$

Now all we need to do is create the vector of partial derivatives and pre and post multiply it by the $var(\sigma)$ (row and then column vector).

$$var(h^2) = (0.0665-0.009758) \begin{pmatrix} 0.40950E-01 & -0.20986E-01 \\ -0.20986E-01 & 0.46718E-01 \end{pmatrix} \begin{pmatrix} 0.0665 \\ -0.009758 \end{pmatrix} = 0.00021278 \quad (12)$$

To get the SE of heritability. Simply take the square root.

$$SE(h^2) = \sqrt{var(h^2)} = \sqrt{0.00021278} = 0.01459 \quad (13)$$

R users can use the following code to calculate standard errors.

```
> # variance estimates
> a <- 1.6779
> e <- 11.435
> p <- a + e
> h2 <- a / p
> # partial derivatives
> pda <- (h2 * (1-h2)) / a
> pde <- -((h2 * h2) / a)
> # create row and column vector of partial derivatives
> vector.pd <- matrix(data=c(pda,pde), nrow=1, ncol=2)
> vector.pd.t <- t(vector.pd)
> vector.pd

      [,1]      [,2]
[1,] 0.06650261 -0.009758174

> vector.pd.t

      [,1]
[1,] 0.066502607
[2,] -0.009758174

> # create var(sigma) matrix from inverse AI matrix from output
> values <- c(0.40950E-01,-0.20986E-01,-0.20986E-01,0.46718E-01)
> matrix.sigma <- matrix(values, nrow=2, ncol=2)
> matrix.sigma

      [,1]      [,2]
[1,] 0.040950 -0.020986
[2,] -0.020986 0.046718

> # complete matrix multiplication to get var(h2) and then se(h2)
> var.h2 <- vector.pd %*% matrix.sigma %*% vector.pd.t
> se.h2 <- sqrt(var.h2)
> se.h2

      [,1]
[1,] 0.01458737
```

Calculating the SE of a genetic correlation

Definitions:

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

This vignette is for genetic correlations, but it can be generalized to additive, environmental, or phenotypic variances and covariances.

The correlation can be calculated as:

$$r = \frac{x_{12}}{\sqrt{x_1 x_2}} \quad (14)$$

The sigma in this situation is:

$$\sigma = \begin{pmatrix} x_1 \\ x_2 \\ x_{12} \end{pmatrix} \quad (15)$$

The partial derivatives are:

$$\frac{\partial r}{\partial x_1} = \frac{r}{2x_1} \quad (16)$$

$$\frac{\partial r}{\partial x_2} = \frac{r}{2x_2} \quad (17)$$

$$\frac{\partial r}{\partial x_{12}} = \frac{r}{x_{12}} \quad (18)$$

The $var(\sigma)$ becomes:

$$var(\sigma) = \begin{pmatrix} var(x_1) & cov(x_1, x_2) & cov(x_1, x_{12}) \\ cov(x_2, x_1) & var(x_2) & cov(x_2, x_{12}) \\ cov(x_{12}, x_1) & cov(x_{12}, x_2) & var(x_{12}) \end{pmatrix} \quad (19)$$

The final equation becomes

$$var(r) = \begin{pmatrix} -\frac{r}{2x_1} & -\frac{r}{2x_2} & \frac{r}{x_{12}} \end{pmatrix} \begin{pmatrix} var(x_1) & cov(x_1, x_2) & cov(x_1, x_{12}) \\ cov(x_2, x_1) & var(x_2) & cov(x_2, x_{12}) \\ cov(x_{12}, x_1) & cov(x_{12}, x_2) & var(x_{12}) \end{pmatrix} \begin{pmatrix} -\frac{r}{2x_1} \\ -\frac{r}{2x_2} \\ \frac{r}{x_{12}} \end{pmatrix} \quad (20)$$

$$SE(r) = \sqrt{var(r)} \quad (21)$$

Example: Calculating SE of the genetic correlation

The following is a typical airemlf90 output for a two trait analysis. As you can see it's a little more complex.

Final Estimates

Genetic variance(s) for effect 4

1.6988 0.90703

0.90703 1.3339

correlations

1.0000 0.60253

0.60253 1.0000

eigenvectors

0.63356 -0.77369

-0.77369 -0.63356

eigenvalues

0.59119 2.4416

Residual variance(s)

11.466 5.9395

5.9395 7.5748

correlations

1.0000 0.63731

0.63731 1.0000

eigenvectors

0.58681 -0.80973

-0.80973 -0.58681

eigenvalues

3.2705 15.771

inverse of AI matrix (Sampling Variance)

0.41540E-01 0.22280E-01 0.11951E-01 -0.21210E-01 -0.11370E-01 -0.61022E-02

0.22280E-01 0.21435E-01 0.16582E-01 -0.11382E-01 -0.10820E-01 -0.83368E-02

0.11951E-01 0.16582E-01 0.22931E-01 -0.61141E-02 -0.83474E-02 -0.11349E-01

-0.21210E-01 -0.11382E-01 -0.61141E-02 0.47097E-01 0.24636E-01 0.12860E-01

-0.11370E-01 -0.10820E-01 -0.83474E-02 0.24636E-01 0.22648E-01 0.16940E-01

-0.61022E-02 -0.83368E-02 -0.11349E-01 0.12860E-01 0.16940E-01 0.22114E-01

Correlations from inverse of AI matrix

1.0000 0.74666 0.38720 -0.47954 -0.37068 -0.20134

0.74666 1.0000 0.74791 -0.35824 -0.49106 -0.38292

0.38720 0.74791 1.0000 -0.18605 -0.36629 -0.50400

-0.47954 -0.35824 -0.18605 1.0000 0.75434 0.39850

-0.37068 -0.49106 -0.36629 0.75434 1.0000 0.75693

-0.20134 -0.38292 -0.50400 0.39850 0.75693 1.0000

SE for R

0.21702 0.15049

0.15049 0.14871

SE for G

0.20381 0.14641

0.14641 0.15143

The variance and covariance estimates are from the genetic variance(s) for effect 4 (animal effect).

$$x_1 = 1.6988$$

$$x_2 = 1.3339$$

$$x_{12} = 0.90703$$

$$r = \frac{0.90703}{\sqrt{(1.6988)(1.3339)}} = 0.6025 \quad (22)$$

The partial derivatives are:

$$\frac{\partial r}{\partial x_1} = \frac{0.6025442}{2(1.6988)} = 0.1773441 \quad (23)$$

$$\frac{\partial r}{\partial x_2} = \frac{0.6025442}{2(1.3339)} = 0.225881 \quad (24)$$

$$\frac{\partial r}{\partial x_{12}} = \frac{0.6025442}{0.90703} = 0.6643046 \quad (25)$$

$$var(r) = \begin{pmatrix} -0.1773441 & -0.225881 & 0.6643046 \end{pmatrix} \begin{pmatrix} 0.41540E-1 & 0.11951E-1 & 0.22280E-1 \\ 0.11951E-1 & 0.22931E-1 & 0.16582E-1 \\ 0.22280E-1 & 0.16582E-1 & 0.21435E-1 \end{pmatrix} \begin{pmatrix} -0.1773441 \\ -0.225881 \\ 0.6643046 \end{pmatrix} \quad (26)$$

$$var(r) = 0.002667373 \quad (27)$$

$$SE(r) = \sqrt{var(r)} = 0.05164662 \quad (28)$$

Again, BE CAREFUL!

Compare the inverse AI matrix to the $var(\sigma)$. These are not in the same order. The order along the diagonal for $var(\sigma)$ is $var(x_1)$, $var(x_2)$, $var(x_{12})$. However, the inverse AI matrix is in the order $var(x_1)$, $var(x_{12})$, $var(x_2)$. Again, it's easiest to square the values in the SE for R or SE for G matrix at the very end of the output to find the correct values in the inverse AI matrix.

The following R code can be used to do all calculations.

```
> # estimates
> x1 <- 1.6988
> x2 <- 1.3339
> x12 <- 0.90703
> # calculate r
> r <- x12 / sqrt(x1*x2)
> # calculate partial derivatives
> pdx1 <- - r / (2*x1)
> pdx2 <- - r / (2*x2)
> pdx12 <- r / (x12)
> # create vector of partial derivatives
> vector.pd <- matrix(c(pdx1,pdx2,pdx12),nrow=1, ncol=3)
> vector.pd.t <- t(vector.pd)
> # create var(sigma) matrix from inverse AI matrix
> sigma.matrix <- matrix(c(0.41540E-1, 0.11951E-1, 0.22280E-1,
+                          0.11951E-1, 0.22931E-1, 0.16582E-1,
+                          0.22280E-1, 0.16582E-1, 0.21435E-1),
+                          nrow=3, ncol=3)
> # final matrix multiplication
> var.r <- vector.pd %*% sigma.matrix %*% vector.pd.t
> var.r

      [,1]
[1,] 0.002667373

> # take sqrt of the variance to get SE
> se.r <- sqrt(var.r)
> se.r

      [,1]
[1,] 0.05164662

>
```