How to fit an animal model

An ecologist guide

Julien Martin[1] Matthieu Videlier[2]

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[1]Univeristy of Ottawa, julien.martin@uottawa.ca
[2]UQAM, videlier.mathieu@courrier.uqam.ca

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Preface

This book is a collection of tutorial from the excellent paper by (**?**). Instead of just copy pasting the tutorial in a bookdown format, the tutorials have been updated to work with the newest version of the softwares and extended to present other softwares. **However, this is still a work in progress.**

> Do not take anything in this manual as gospel.

Contributors

List of people who contributed to update and extend tutorials:

- Eric Postma updated the previous tutorial from asreml-r 3 to asreml-r 4
- Julien Martin developed and maintains the site
- Mathieu Videlier added (and continues to add) more details in the document

Chapitre 1

Introduction

The book is provides a series of tutorials (and accompanying data files) to fit animal model in `R` using different packages (`ASReml-R`, `gremlin`, `MCMCglmm` and `brms/stan`) . You will need to carefully follow the instructions below to first download the data files and second install the R packages. Before beginning the tutorial, we assume the reader has successfully installed the chosen R package on their computer and has saved the required data files to an appropriate directory from which they will be read. Full instructions for how to do this are provided with software distributions.

To work though the different tutorial I would recommend to create a folder where you will save your different `R` scripts for the tutorials.

In addition, the tutorial is here to help researchers in their coding and understanding of models and outputs, but it is required that you read and understand the literature in quantitative genetics and animal model.

1.1 Data

1.1.1 Data files

You will need to download 3 data files for the tutorial in `R`:

- gryphon.csv: data on gryphon birth weight and morphology
- gryphonRM.csv: data on gryphon repeated measurement of lay date.
- gryphonped.csv: data on the associated pedigree of the data gryphon

In addition, some models presented in the tutorials can take a while to run (sometimes > 1 hour), thus we are also providing the model outputs to allow you continue the tutorial without waiting for the model to run. (But you are free to run models)

The files are available here I recommend to save the data and Rdata files in a subfolder `data` in the folder you will use as your working directory for R and where you will save your R scripts. It should be noted that the tutorial are using this structure to read or save data.

1.1.2 Notes on data and pedigree

It is always important to take time to think carefully about the strengths and potential limitations of your pedigree information before embarking on quantitative genetic analyses. Pedigree Viewer, written by Brian Kinghorn, is an extremely useful application for visualizing pedigrees, and can be downloaded from: http://www-personal.une.edu.au/~bkinghor/pedigree.htm. `Pedantics` an R package written by Michael Morrissey and distributed through CRAN (http://cran.r-project.org/) can also be used for this and offers some nice additional features for visualizing pedigree structures and generating associated statistics. Before you begin running through the tutorials, we advise taking a moment to look at the pedigree files provided with them using Pedigree Viewer or Pedantics.

1.2 R

You should check that you have the most current version of R and R packages. You can check the number of the current version on CRAN. If you need to update (or install) R packages, use `install.packages()` and follow the prompted instructions.

1.2.1 R packages

1.2.1.1 asreml-r

ASReml-R is commercial software published by VSN international (http://www.vsni.co.uk/software/asreml/). This package is not free and requires a key access. Additional information and guide can be find in the Asreml-R manual: (https://asreml.kb.vsni.co.uk/wp-content/uploads/sites/3/2018/02/ASReml-R-Reference-Manual-4.pdf)

1.2.1.2 gremlin

`gremlin` is a little monster appearing if you feed a mugwai after midnight. It is also a great and promising software written by Pr. Matthew E. Wolak to fit mixed models using a frequentist approach .

1.2.1.3 MCMCglmm

`MCMCglmm` is an R package for Bayesian mixed model analysis written by Pr. Jarrod Hadfield. It is a freeware distributed through CRAN (http://cran.r-project.org/). Information and guide about the package can be find in the user manual and vignettes (http://cran.r-project.org/web/packages/MCMCglmm/index.html). Reference: (**?**, **?**).

This module provides some information that applies to MCMCglmm-based analyses in general, but that will not be included in other tutorials. Most importantly, this applies to some of the simplest ways of determining the performance of a run using MCMCglmm, i.e., verification of the validity of of the posterior distribution. This tutorial is not a substitute for working through the MCMCglmm course notes, which is available from CRAN (the Comprehensive R ArchiveNetwork, http://cran.r-project.org/, or can be accessed in R using the command vignette("CourseNotes","MCMCglmm")). These tutorials do not introduce one of the main advantages of using MCMCglmm for analyses of data from natural populations -the ability to properly model non-normal responses. These capabilities are introduced in the documentation that is distributed with MCMCglmm, and available from CRAN. Another specific animal guide for MCMCglmm can be find (https://devillemereuil.legtux.org/wp-content/uploads/2021/09/tuto_en.pdf). Pr. Pierre de Villemereuil provide more information in Bayesian concept and focus more on non-gaussian variable.

1.2.1.4 brms

`brms` provides an interface to fit Bayesian generalized multivariate (non-)linear multilevel models using `Stan`, which is a C++ package for obtaining full Bayesian inference (see https://mc-stan.org/). The formula syntax is an extended version of the syntax applied in the 'lme4' package to provide a familiar and simple interface for performing regression analyses.

It should be noted that if `brms` is able to fit animal model the parametrization used is not the most efficient and can take quite longer than using a different parametrization directly in `stan`.

Chapitre 2

Univariate animal model

This tutorial will demonstrate how to run a univariate animal model to estimate genetic variance in birth weight in the mighty gryphons.

2.1 Scenario and data

2.1.1 Scenario

In a population of gryphons there is strong positive selection on birth weight with heavier born individuals having, on average higher fitness. To find out whether increased birth weight will evolve in response to the selection, and if so how quickly, we want to estimate the heritability of birth weight.

2.1.2 Data files

Open `gryphonped.csv` and `gryphon.csv` in your text editor. The structure and contents of these files is fairly self-explanatory. The pedigree file `gryphonped.csv` contains three columns containing unique IDs that correspond to each animal, its father, and its mother. Note that this is a multigenerational pedigree, with the earliest generation (for which parentage information is necessarily missing) at the beginning of the file. For later-born individuals maternal identities are all known but paternity information is incomplete (a common situation in real world applications).

The phenotype data, as well as additional factors and covariates that we may wish to include in our model are contained in `gryphon.csv`. Columns correspond to individual identity (`animal`), maternal identity (`mother`), year of birth (`byear`), sex (`sex`, where `1` is female and `2` is male), birth weight (`bwt`), and tarsus length (`tarsus`). Each row of the data file contains a record for a different offspring individual. Note that all individuals included in the data file must be included as offspring in the pedigree file.

We can read the data file, using `read.csv()` which consider by default that `NA` is the symbol for missing values and that the first line of the file contains the column headers.

It is a good idea to make sure that all variables are correctly assigned as numeric or factors:

```
gryphon$animal <- as.factor(gryphon$animal)
gryphon$mother <- as.factor(gryphon$mother)
gryphon$byear <- as.factor(gryphon$byear)
gryphon$sex <- as.factor(gryphon$sex)
gryphon$bwt <- as.numeric(gryphon$bwt)
gryphon$tarsus <- as.numeric(gryphon$tarsus)
str(gryphon)
```

```
## 'data.frame':    1084 obs. of  6 variables:
##  $ animal: Factor w/ 1084 levels "1","2","3","5",..: 864 1076 549 989 1030 751 987 490 9
##  $ mother: Factor w/ 429 levels "1","2","3","8",..: 362 268 216 375 396 289 328 255 347
##  $ byear : Factor w/ 34 levels "968","970","971",..: 1 1 2 2 2 2 3 3 3 3 ...
##  $ sex   : Factor w/ 2 levels "1","2": 1 1 2 1 2 1 2 1 1 1 ...
##  $ bwt   : num  10.77 9.3 3.98 5.39 12.12 ...
##  $ tarsus: num  24.8 22.5 12.9 20.5 NA ...
```

Similarly we can read in the pedigree file, using `read.csv()` which consider by default that `NA` is the symbol for missing values and that the first line of the file contains the column headers.

```
## 'data.frame':    1309 obs. of  3 variables:
##  $ id    : int  1306 1304 1298 1293 1290 1288 1284 1283 1282 1278 ...
##  $ father: int  NA NA NA NA NA NA NA NA NA NA ...
##  $ mother: int  NA NA NA NA NA NA NA NA NA NA ...
```

```
gryphonped$id <- as.factor(gryphonped$id)
gryphonped$father <- as.factor(gryphonped$father)
gryphonped$mother <- as.factor(gryphonped$mother)
str(gryphonped)
```

```
## 'data.frame':    1309 obs. of  3 variables:
##  $ id    : Factor w/ 1309 levels "1","2","3","4",..: 1306 1304 1298 1293 1290 1288 1284
##  $ father: Factor w/ 158 levels "4","13","18",..: NA NA NA NA NA NA NA NA NA NA ...
##  $ mother: Factor w/ 429 levels "1","2","3","8",..: NA NA NA NA NA NA NA NA NA NA ...
```

Now that we have imported the data and the pedigree file, we are ready to fit an animal model.

2.2 Asreml-R

2.2.1 Running the model

First we need to load the `asreml` library:

```
library(asreml)
```

To be able to fit an animal model, Asreml-r needs (the inverse of) the relationship matrix using the ainverse function:

```
ainv <- ainverse(gryphonped)
```

We are now ready to specify our first model:

```
model1 <- asreml(
  fixed = bwt ~ 1, random = ~ vm(animal, ainv),
  residual = ~ idv(units),
  data = gryphon,
  na.action = na.method(x = "omit", y = "omit")
)
```

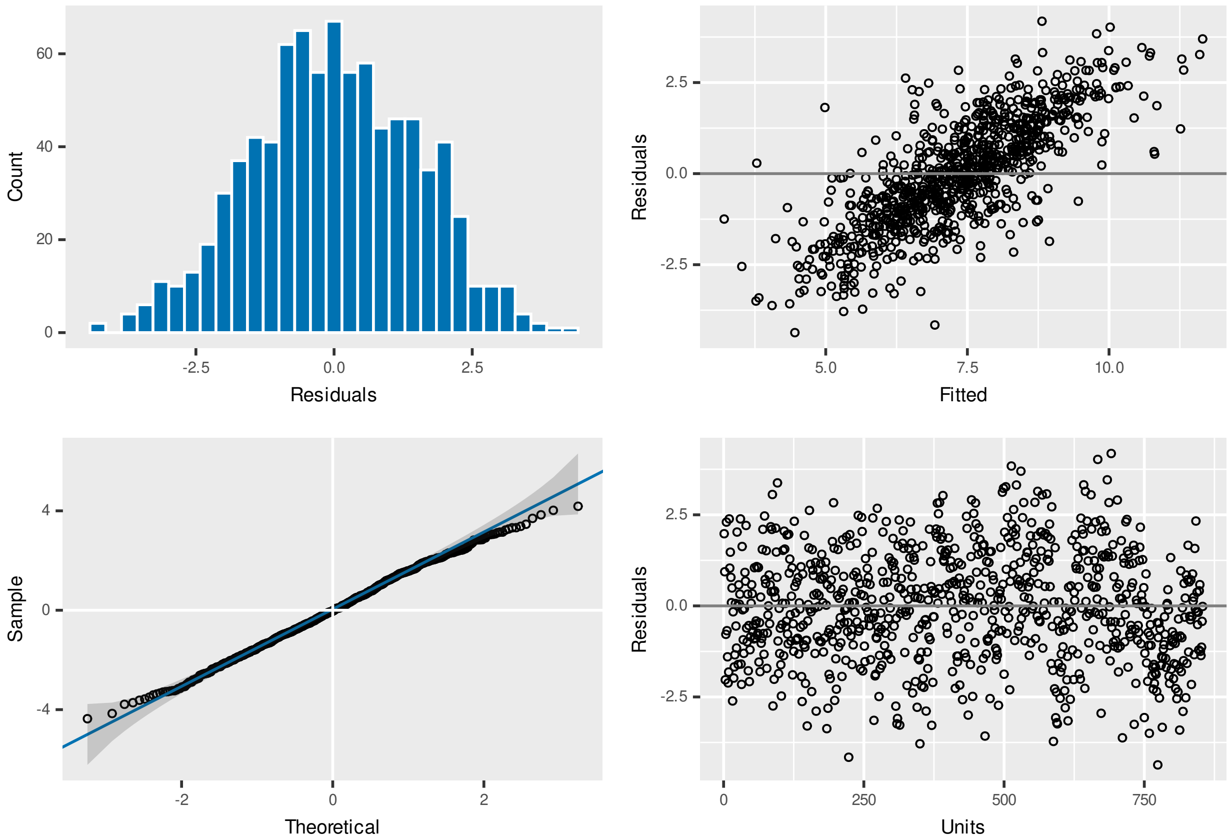
```
## Model fitted using the sigma parameterization.
## ASReml 4.1.0 Tue Nov 29 16:53:29 2022
##           LogLik        Sigma2     DF     wall    cpu
##  1     -4128.454           1.0    853 16:53:29    0.0
##  2     -3284.272           1.0    853 16:53:29    0.0
##  3     -2354.992           1.0    853 16:53:29    0.0
##  4     -1710.357           1.0    853 16:53:29    0.0
##  5     -1363.555           1.0    853 16:53:29    0.0
##  6     -1263.516           1.0    853 16:53:29    0.0
##  7     -1247.854           1.0    853 16:53:29    0.0
##  8     -1247.185           1.0    853 16:53:29    0.0
##  9     -1247.183           1.0    853 16:53:29    0.0
```

In this model, `bwt` is the response variable and the only fixed effect is the intercept, denoted as `1`. The only random effect we have fitted is `animal`, which will provide an estimate of V_A. Our random `animal` effect is connected to the inverse related matrix `ainv` which integrate the relativeness or pedigree information.
`data=` specifies the name of the dataframe that contains our variables. Finally, we inform `asreml()` what to when it encounters `NA`s in either the dependent or predictor variables (in this case we choose to remove the records). If you use the argument "include" instead of "omit", model will keep the NA. With x="include", the model will exchange `NA` with 0. Be careful you need to standardize your trait so the mean will be equal to 0, if not estimates (including covariance in multivariate models) could be strongly biased due to the the missing values considered as 0. y="include" will exchange `NA` with a factor labeled `mv` which will be included in the sparse equation. For more details see Asreml-R manual.

A note of the specification of the structure of the residuals: This simple univariate model will run fine without `residual=~idv(units)`. However, if you are going to use `vpredict()` to calculate the heritability (see below), without specifying the residuals in this way will result in a standard error for the heritability that is incorrect.

Any model has assumption which need to be checked. The model can be plot which help visualizing the distribution of the model residual and check the different assumptions.

```r
plot(model1)
```



To see the estimates for the variance components, we run:

```r
summary(model1)$varcomp
```

```
##                    component std.error  z.ratio bound %ch
## vm(animal, ainv)   3.395398 0.6349915 5.347154     P   0
## units!units        3.828602 0.5185919 7.382687     P   0
## units!R            1.000000        NA       NA     F   0
```

We fitted a single random effect so we partitioned the phenotypic variance into two components. The `vm(animal, ainv)` variance component is V_A and is estimated as 3.4. Given that the ratio of V_A to its standard error (`z.ratio`) is considerably larger than 2 (*i.e.* the parameter estimate is more than 2 SEs from zero), this looks likely to be significant. The `units!units` component refers to the residual variance V_R, and `units$R` should be ignored. If you don't include `residual=~idv(units)`in your model specification, `units$R` will provide you with the residual variance.

2.2.2 Estimating heritability

We can calculate the h^2 of birth weight from the components above since $h^2 = V_A/V_P = V_A/(V_A+V_R)$. Thus according to this model, h^2 = 3.4 / (3.4 + 3.83) = 0.47.

Alternatively we can use the `vpredict()` function to calculate h^2 and its standard error. `vpredict()`function has two structures, first the model used (here `model1`) and then the estimate name with its associated equation. The equation used different `V` and their associated numbers depend of the order of the different random and residual effects included in the model.

```
vpredict(model1, h2.bwt ~ V1 / (V1 + V2))
```

```
##         Estimate         SE
## h2.bwt 0.4700163 0.07650881
```

2.2.3 Adding fixed effects

To add fixed effects to a univariate model, we simply modify the model statement. For example, we might know (or suspect) that birth weight is a sexually dimorphic trait and therefore fit in the model.

```
model2 <- asreml(
  fixed = bwt ~ 1 + sex,
  random = ~ vm(animal, ainv),
  residual = ~ idv(units),
  data = gryphon,
  na.action = na.method(x = "omit", y = "omit")
)
```

```
## Model fitted using the sigma parameterization.
## ASReml 4.1.0 Tue Nov 29 16:53:30 2022
##          LogLik        Sigma2     DF     wall    cpu
##  1     -3364.126          1.0    852 16:53:30    0.0
##  2     -2702.117          1.0    852 16:53:30    0.0
##  3     -1978.916          1.0    852 16:53:30    0.0
##  4     -1487.834          1.0    852 16:53:30    0.0
##  5     -1236.350          1.0    852 16:53:30    0.0
##  6     -1172.771          1.0    852 16:53:30    0.0
##  7     -1165.270          1.0    852 16:53:30    0.0
##  8     -1165.093          1.0    852 16:53:30    0.0
##  9     -1165.093          1.0    852 16:53:30    0.0
```

Now we can look at the fixed effects parameters and assess their significance with a conditional Wald F-test:

```
summary(model2, coef = TRUE)$coef.fixed
wald.asreml(model2, ssType = "conditional", denDF = "numeric")
```

```
##              solution std error  z.ratio
## sex_1        0.000000        NA       NA
## sex_2        2.206996 0.1619974 13.62365
```

```
## (Intercept) 6.058669 0.1718244 35.26082

## Model fitted using the sigma parameterization.

## Warning in asreml(fixed = bwt ~ 1 + sex, random = ~vm(animal, ainv), residual =
## ~idv(units), : Algebraic derivatives for denominator df not available.

## ASReml 4.1.0 Tue Nov 29 16:53:30 2022
##           LogLik        Sigma2     DF     wall    cpu
##  1     -1165.093           1.0    852 16:53:30    0.0
##  2     -1165.093           1.0    852 16:53:31    0.0
## Calculating denominator DF

## $Wald
##
##             Df denDF  F.inc  F.con Margin          Pr
## (Intercept)  1   251 3491.0 3491.0        0.00000e+00
## sex          1   831  185.6  185.6      A 2.70204e-38
##
## $stratumVariances
##                         df Variance vm(animal, ainv) units!units
## vm(animal, ainv) 752.28476 5.957254        0.9864077           1
## units!units       99.71524 2.938413        0.0000000           1
```

The very small probability (`Pr`) in the Wald test above shows that `sex` is a highly significant fixed effect, and from the parameter estimates (`summary(model2,coef=T)$coef.fixed`) we can see that the average male (sex 2) is 2.2 kg ($\pm$ 0.16 SE) heavier than the average female (sex 1). However, when we look at the variance components in the model including `sex` as a fixed effect, we see that they have changed slightly from the previous model:

```
summary(model2)$varcomp
```

```
##                  component std.error  z.ratio bound %ch
## vm(animal, ainv)  3.060441 0.5243571 5.836558     P   0
## units!units       2.938412 0.4161473 7.060991     P   0
## units!R           1.000000        NA       NA     F   0
```

In fact since `sex` effects were previously contributing to the residual variance of the model, our estimate of V_R (denoted `units!R` in the output) is now slightly lower than before. This has an important consequence for estimating heritability since if we calculate V_P as V_A+V_R then as we include fixed effects we will soak up more residual variance driving V_P. Assuming that V_A is more or less unaffected by the fixed effects fitted then as V_P goes down we expect our estimate of h^2 will go up:

```
(h2.1 <- vpredict(model1, h2.bwt ~ V1 / (V1 + V2)))
```

```
##         Estimate         SE
## h2.bwt 0.4700163 0.07650881
```

```r
(h2.2 <- vpredict(model2, h2.bwt ~ V1 / (V1 + V2)))
```

```
##         Estimate         SE
## h2.bwt 0.510171 0.07432388
```

Here h^2 has increased slightly from 0.47 to 0.51. Which is the better estimate? It depends on what your question is. The first is an estimate of the proportion of variance in birth weight explained by additive effects, the latter is an estimate of the proportion of variance in birth weight *after conditioning on sex* that is explained by additive effects.

An important piece of advice, each researcher should be consistent in how they name their estimates and always correctly describe which estimates they are using conditional or not (to avoid any confusion).

2.2.4 Adding random effects

This is done by simply modifying the model statement in the same way. For instance fitting:

```r
model3 <- asreml(
  fixed = bwt ~ 1 + sex,
  random = ~ vm(animal, ainv) + byear,
  residual = ~ idv(units),
  data = gryphon,
  na.action = na.method(x = "omit", y = "omit")
)
```

```
## Model fitted using the sigma parameterization.
## ASReml 4.1.0 Tue Nov 29 16:53:31 2022
##           LogLik        Sigma2     DF     wall    cpu
##  1     -2742.658           1.0    852 16:53:31    0.0
##  2     -2237.268           1.0    852 16:53:31    0.0
##  3     -1690.453           1.0    852 16:53:31    0.0
##  4     -1328.910           1.0    852 16:53:31    0.0
##  5     -1154.597           1.0    852 16:53:31    0.0
##  6     -1116.992           1.0    852 16:53:31    0.0
##  7     -1113.809           1.0    852 16:53:31    0.0
##  8     -1113.772           1.0    852 16:53:31    0.0
##  9     -1113.772           1.0    852 16:53:31    0.0
```

```r
summary(model3)$varcomp
```

```
##                    component std.error  z.ratio bound %ch
## byear              0.8862604 0.2695918 3.287416     P   0
## vm(animal, ainv) 2.7068665 0.4422140 6.121169     P   0
## units!units        2.3092415 0.3451025 6.691466     P   0
## units!R            1.0000000        NA       NA     F   0
```

```r
(h2.3 <- vpredict(model3, h2.bwt ~ V2 / (V1 + V2 + V3)))
```

```
##         Estimate         SE
## h2.bwt 0.4586068 0.06740364
```

Here the variance in `bwt` explained by `byear` is 0.89 and, based on the `z.ratio`, appears to be significant (>2). Thus we would conclude that year-to-year variation (*e.g.*, in weather, resource abundance) contributes to V_P. Note that although V_A has changed somewhat, as most of what is now partitioned as a birth year effect was previously partitioned as V_R. Thus what we have really done here is to partition environmental effects into those arising from year-to-year differences versus everything else, and we do not really expect much change in h^2 (since now $h^2 = V_A/(V_A + V_{BY} + V_R)$).

However, we get a somewhat different result if we also add a random effect of `mother` to test for maternal effects:

```r
model4 <- asreml(
  fixed = bwt ~ 1 + sex,
  random = ~ vm(animal, ainv) + byear + mother,
  residual = ~ idv(units),
  data = gryphon,
  na.action = na.method(x = "omit", y = "omit")
)
```

```
## Model fitted using the sigma parameterization.
## ASReml 4.1.0 Tue Nov 29 16:53:31 2022
##          LogLik        Sigma2     DF     wall    cpu
##  1     -2033.178          1.0    852 16:53:31    0.0
##  2     -1723.734          1.0    852 16:53:31    0.0
##  3     -1396.354          1.0    852 16:53:31    0.0
##  4     -1193.012          1.0    852 16:53:31    0.0
##  5     -1107.946          1.0    852 16:53:31    0.0
##  6     -1095.327          1.0    852 16:53:31    0.0
##  7     -1094.816          1.0    852 16:53:31    0.0
##  8     -1094.815          1.0    852 16:53:31    0.0
```

```r
summary(model4)$varcomp
```

```
##                   component std.error  z.ratio bound %ch
## byear             0.8820313 0.2632455 3.350604     P   0
## mother            1.1184698 0.2386239 4.687167     P   0
## vm(animal, ainv) 2.2985320 0.4962496 4.631806     P   0
## units!units       1.6290034 0.3714154 4.385934     P   0
## units!R           1.0000000        NA       NA     F   0
```

```
(h2.4 <- vpredict(model4, h2.bwt ~ V1 / (V1 + V2 + V3 + V4)))
```

```
##         Estimate         SE
## h2.bwt 0.1487898 0.03861552
```

Here partitioning of significant maternal variance has resulted in a further decrease in V_R but also a decrease in V_A. The latter is because maternal effects of the sort we simulated (fixed differences between mothers) will have the consequence of increasing similarity among maternal siblings. Consequently they can look very much like additive genetic effects and if present, but unmodelled, represent a type of "common environment effect" that can - and will - cause upward bias in V_A and so h^2. The "common environment" can be conceived as the inextricable sum of the maternal additive genetic effect (such as maternal loci) and the maternal environment or permanent environment (such as litter or nest environment created or modified by the mother).

2.2.5 Testing significance of random effects

An important point to note in this tutorial is that while the `z.ratio` (`component/std.error`) reported is a good indicator of likely statistical significance (>1.96?), the standard errors are approximate and are not recommended for formal hypothesis testing. A better approach is to use likelihood-ratio tests (LRT).

For example, to test the significance of maternal effects we could compare models with and without the inclusion of maternal identity as a random effect and compare the final log-likelihoods of these models.

```
model4$loglik
```

```
## [1] -1094.815
```

shows that the model including maternal identity has a log-likelihood of -1094.815, and

```
model3$loglik
```

```
## [1] -1113.772
```

shows that the model excluding maternal identity has a log-likelihood of -1113.772.

A test statistic equal to twice the absolute difference in these log-likelihoods is assumed to be distributed as Chi square with `one` degree of freedom (one term of difference between the two models). In this case we would conclude that the maternal effects are highly significant since: 2 $\times$ (-1094.8145793 - -1113.7719147) equals 37.9146708, and the p-value that comes with this is:

```
1 - pchisq(2 * (model4$loglik - model3$loglik), 1)
```

```
## [1] 7.390738e-10
```

As P < 0.0001 we would therefore conclude that the additional of maternal identity as a random effect significantly improves the fit of the model, given an increase in log-likelihood of approximately 19.

2.2.6 Further partitioning the variance

A population can be further fragmented into different groups or categories (such as females and males, juveniles and adults or treated and untreated). Some scientific questions require further and deeper analysis of the variance. To avoid multiple model (one for each group), we can directly partition the variance between groups in a unique model. In addition, by doing so, we can also test if the variance are different between groups.

As example, we decide to take the model4 and partition its additive genetic variance and residual variance by sex. It is possible to further partition the other random effects but it will complexity the animal model and requires sufficient sample size.

First, it required to order the dataset by group (here sex).

```
gryphon <- gryphon[order(gryphon$sex), ]
```

To partition variances between sex, two distinct functions are require `at()` for the random level, and `dsum()` for the residual level:

```
model_SEX <- asreml(
  fixed = bwt ~ 1 + sex,
  random = ~ at(sex):vm(animal, ainv) + byear + mother,
  residual = ~ dsum(~ units | sex),
  data = gryphon,
  na.action = na.method(x = "omit", y = "omit")
)
```

```
## Multi-section model using the sigma parameterization.
## ASReml 4.1.0 Tue Nov 29 16:53:31 2022
##           LogLik        Sigma2     DF     wall    cpu
##  1     -1142.164           1.0    852 16:53:31    0.0
##  2     -1126.308           1.0    852 16:53:31    0.0
##  3     -1111.536           1.0    852 16:53:31    0.0
##  4     -1105.383           1.0    852 16:53:31    0.0
##  5     -1104.375           1.0    852 16:53:31    0.0
##  6     -1104.364           1.0    852 16:53:31    0.0
```

```
summary(model_SEX)$varcomp
```

```
##                               component std.error  z.ratio bound %ch
## byear                         0.9001595 0.2690012 3.346303     P 0.0
## mother                        1.3396184 0.2663118 5.030263     P 0.0
```

```
## at(sex, 1):vm(animal, ainv) 1.4372390 0.6514306 2.206281     P 0.1
## at(sex, 2):vm(animal, ainv) 1.9861434 0.9974302 1.991261     P 0.3
## sex_1!R                     2.1706213 0.5542492 3.916327     P 0.0
## sex_2!R                     1.7112948 0.8246188 2.075256     P 0.3
```

By partitioning the additive genetic variance and the residual variance, the model estimates the V_A and V_R for each group (sex). Doing so, we can calculate the h^2 for each group of sex. Here, it's important to know in which order the variances are estimated to extract the correct variance in the heritability equation.

```
(h2.F <- vpredict(model_SEX, h2.bwt ~ V3 / (V1 + V2 + V3 + V5)))
```

```
##          Estimate        SE
## h2.bwt 0.2457811 0.1070794
```

```
(h2.M <- vpredict(model_SEX, h2.bwt ~ V4 / (V1 + V2 + V4 + V6)))
```

```
##          Estimate        SE
## h2.bwt 0.3345244 0.1619218
```

To test if the variances are different between sexes, we can compare the model partitioned `model_SEX` and the previous model without the partitioning `model4` in a likelihood ratio test (LRT) with 2 degrees of freedom since models have two components of variance of difference.

```
model_SEX$loglik
```

```
## [1] -1104.364
```

```
model4$loglik
```

```
## [1] -1094.815
```

```
1 - pchisq(2 * (model_SEX$loglik - model4$loglik), 2)
```

```
## [1] 1
```

Here, we can see the point estimates of h^2 seems to differ between sexes (0.25 and 0.33), but their SE overlaps. LRT give more information and showed that partitioning the variance and the residual between sexes did not improved the fit of the model and so their variance are not significantly different.

```
h2.sex <- rbind(h2.F, h2.M)

plot(c(0.95, 1.05) ~ h2.sex[, 1], xlim = c(0, 0.8), ylim = c(0.5, 1.5), , xlab = "", ylab
arrows(y0 = 0.95, x0 = h2.sex[1, 1] - h2.sex[1, 2], y1 = 0.95, x1 = h2.sex[1, 1] + h2.sex[
```

```
arrows(y0 = 1.05, x0 = h2.sex[2, 1] - h2.sex[2, 2], y1 = 1.05, x1 = h2.sex[2, 1] + h2.sex[
mtext("Narrow-sense heritability (±se)", side = 1, las = 1, adj = 0.4, line = 3, cex = 1.6
axis(2, at = 1, labels = c("birth weight"), las = 3, cex.axis = 1.6)
```

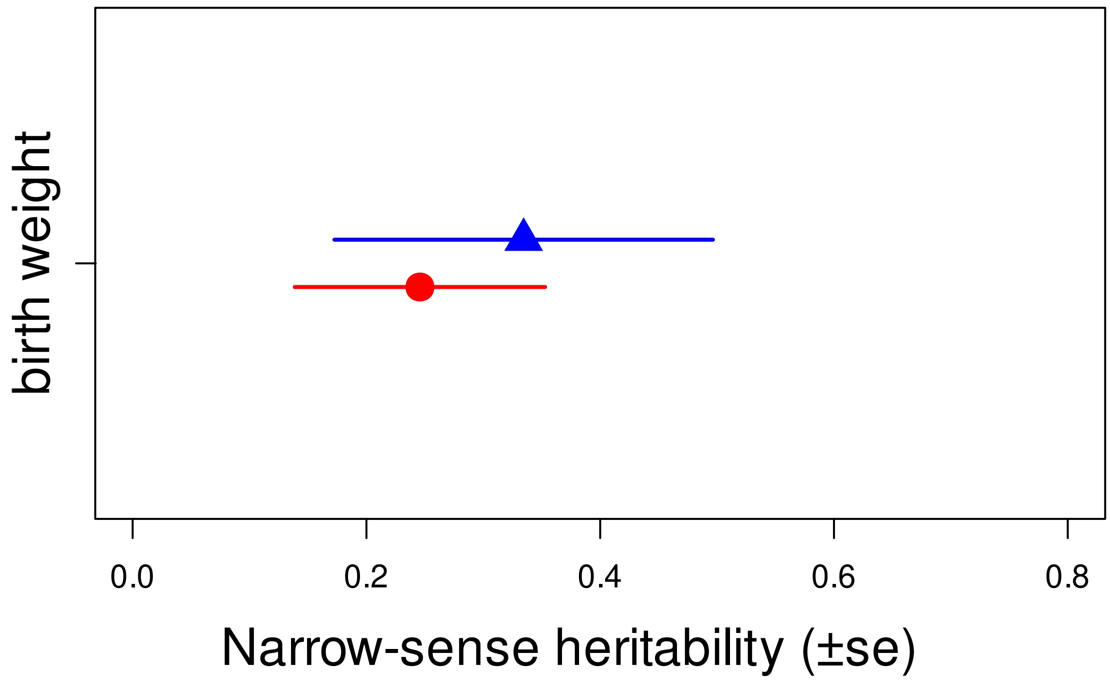


Figure 2.1: Female and male heritability of birth weight

2.2.7 Modification of the varaince matrix parameters

Variance represents the deviation of the distribution and it expected to be a positive values. Due to a lack of power, a structural problem in the dataset or a very low variance, Asreml-r often fixes the variance to a boundary `B` instead of a positive value `P`. When it is happen, it is generally a good idea to examine it.

To examine the boundary effect, we can explore an alternative model where the model allowed a unstructured parameter for the variance of interest or the entire variance matrix. For this example: we allowed the model to estimate any values (so allowing possible negative values of estimates) for the random and residual matrix.

First, we create a temporary model `model.temp` with the exact structure to modify.

```
model.temp <- asreml(
  fixed = bwt ~ 1,
```

```
  random = ~ vm(animal, ainv) + byear + mother,
  residual = ~ idv(units),
  data = gryphon,
  na.action = na.method(x = "omit", y = "omit"),
  start.values = T
)
G.temp <- model.temp$vparameters[(1:3), ]
G.temp$Constraint <- "U"
R.temp <- model.temp$vparameters[-(1:3), ]
R.temp$Constraint[2] <- "U"
```

The argument `start.values=T` allowed the `model.temp` to change its random parameters. We can create the two different matrices and specify which parameters will be modified. For this example we modified the G and the R matrix to fit all variance to be `U` unstructured. it is important to note for the R matrix the line `units!R` has to be fix to 1, so it will never change.

The object G.temp and R.temp can be implemented in the following model as new parameters using the argument `R.param` and `G.param`.

```
model5 <- asreml(
  fixed = bwt ~ 1 + sex,
  random = ~ vm(animal, ainv) + byear + mother,
  residual = ~ idv(units),
  data = gryphon,
  na.action = na.method(x = "omit", y = "omit"),
  R.param = R.temp, G.param = G.temp
)
```

```
## Model fitted using the sigma parameterization.
## ASReml 4.1.0 Tue Nov 29 16:53:32 2022
##           LogLik        Sigma2     DF     wall     cpu
##  1     -2033.178           1.0    852 16:53:32     0.0
##  2     -1723.734           1.0    852 16:53:32     0.0
##  3     -1396.354           1.0    852 16:53:32     0.0
##  4     -1193.012           1.0    852 16:53:32     0.0
##  5     -1107.946           1.0    852 16:53:32     0.0
##  6     -1095.327           1.0    852 16:53:32     0.0
##  7     -1094.816           1.0    852 16:53:32     0.0
##  8     -1094.815           1.0    852 16:53:32     0.0
```

```
summary(model5)$varcomp
```

```
##                    component std.error  z.ratio bound %ch
## byear              0.8820313 0.2632455 3.350604     U   0
## mother             1.1184698 0.2386239 4.687167     U   0
```

```
## vm(animal, ainv) 2.2985320 0.4962496 4.631806     U   0
## units!units      1.6290034 0.3714154 4.385934     U   0
## units!R          1.0000000        NA       NA     F   0
```

Since `model4` did not showed boundary, `the model5` is very similar.

2.2.8 Covariance between two random effects

Some research questions require to estimate the covariance between two random effects within a univariate model.To do so, we can use the argument `str`. As an example, we fit a model which estimate the covariance between the additive genetic variance and the mother variance. Both variances require to operate on the same level, thus `animal` and `mother` require to be associated to the pedigree information.

The argument `str`has two components: first the equation term with the two random effects `~vm(animal,Ainv)+vm(mother, ainv)` and second the structural term `~us(2):id(number)`. Here within the structural term, we fit a 2x2 unstructured matrix `us(2)` which estimated the variance and the covariance between the random effects in the equation term. To successfully work, the structural term also requires the number of level identified within `id()`. Here a small tip, if you don't know the number of level identified within id(), run the model with a random number. The model will not converge and a error message will appear like this one: `Size of direct product (4) does not conform with total size of included terms (2618)`. The error message can help you determine the required level within the `str` function, as here 2618 divide by 2. In addition, it is necessary the random effects

```r
model.temp2 <- asreml(
  fixed = bwt ~ 1,
  random = ~ str(~ vm(animal, ainv) + vm(mother, ainv), ~ us(2):id(1309)) + byear,
  residual = ~ idv(units),
  data = gryphon,
  na.action = na.method(x = "omit", y = "omit"),
  start.values = T
)

G.temp2 <- model.temp2$vparameters[(1:4), ]
G.temp2$Constraint <- "U"
model6 <- asreml(
  fixed = bwt ~ 1 + sex,
  random = ~ str(~ vm(animal, ainv) + vm(mother, ainv), ~ us(2):id(1309)) + byear,
  residual = ~ idv(units),
  data = gryphon,
  na.action = na.method(x = "omit", y = "omit"),
  # equate.levels = c("animal", "mother"),
  , G.param = G.temp2
)
summary(model6)$varcomp
```

We have successfully produced a code to estimate the covariance between two random effects. However for this example, the dataset is not sufficient to properly estimate it and the model did not converge but you have the idea of how to use the function `str`.

Additional and final tip: It is happen that Asreml will estimate negative variance if you allow the variance matrix to be unstructured. A negative variance is counter-intuitive meaning statistically the mean within the random effect is less similar than expected by chance. However a possible biological reason can be hypothesized such as a sibling competition within the nest creating a negative among-individual covariance within the nest.Thus to test this hypotheses,it is required to estimate the covariance between two random effects.

2.3 gremlin

TODO (maybe just bother Matthew to do it)

Meanwhile

Figure 2.2: Keep it dry and do no feed after midnight.

2.4 MCMCglmm

2.4.1 Running the model

First load MCMCglmm:

```
library(MCMCglmm)
```

The first model we will fit is a simple animal model with no fixed effects, and only an 'animal' random effect relating individuals to their additive genetic values through the pedigree.

First we are going to define the priors. In a way we might want to avoid using priors, because we would like all of the information in our analysis to come from our data. By default MCMCglmm uses improper priors, but this can cause inferential and numerical problems. We will specify priors for the animal effect and the residual variance using the following code:

```
prior1.1 <- list(
  G = list(G1 = list(V = 1, nu = 0.002)),
  R = list(V = 1, nu = 0.002)
)
```

A prior allowed the model to fit different variance structures. With the unique random effect "animal", we partitioned the phenotypic variance into two distinct variances matrices `G` (additive genetic) and `R` (residual). This prior specification is the simplistic one and often used because it was believed to be relatively uninformative, and is equivalent to an inverse-gamma prior with shape and scale equal to 0.001. In many cases it is relatively uninformative but when the posterior distribution for the variances has support close to zero it can behave poorly. Parameter expanded priors (See Chapter 8 of the MCMCglmm CourseNotes, available from CRAN) are gaining in popularity due to their better behaviour but for the purposes of this tutorial we will stick with the inverse-gamma prior.

We have told MCMCglmm to pay little heed to our prior expectation (V) by specifying a small degree of belief parameter (nu) of 0.002. Since this is a univariate analysis, the priors are matrix of order 1 and thus nu>0 is the smallest degree of belief that provides what is known as a 'proper' prior, avoiding numerical problems. In fact, there is a lot of information in the data regarding the marginal distributions of the parameters, and MCMCglmm will run most of the models that we suggest in these tutorials without priors. However, this is poor practice, but we will therefore use this simple priors throughout these tutorials. We can now fit an animal model. The model to decompose variation in birth weight into genetic and residual effects is as follows:

The lower case "animal" is a can be a **special** word for MCMCglmm. If a `pedigree` argument is provided then `MCMCglmm` will recognize the term `animal` as the term to use to estimate additive genetic variance. When the argument `pedigree` is not provided then the word `animal` is not different than any other variable. However, instead of providing a pedigree argument to the call to MCMCglmm function, it is much more flexible to use the `ginv` argument to specify the random effect that must be linked to the pedigree (with the inverse relatedness matrix). We thus first estimate the inverse relatedness matrix using `inverseA()` then fit the animal model.

```
Ainv <- inverseA(gryphonped)$Ainv
model1.1 <- MCMCglmm(bwt ~ 1,
  random = ~animal, ginv = list(animal = Ainv),
  data = gryphon, prior = prior1.1
```

```
)
```

```
##
##                          MCMC iteration = 0
##
##                          MCMC iteration = 1000
##
##                          MCMC iteration = 2000
##
##                          MCMC iteration = 3000
##
##                          MCMC iteration = 4000
##
##                          MCMC iteration = 5000
##
##                          MCMC iteration = 6000
##
##                          MCMC iteration = 7000
##
##                          MCMC iteration = 8000
##
##                          MCMC iteration = 9000
##
##                          MCMC iteration = 10000
##
##                          MCMC iteration = 11000
##
##                          MCMC iteration = 12000
##
##                          MCMC iteration = 13000
```

After typing this code, MCMCglmm will run, taking about 20 seconds on a modern desktop computer. The progress of the run will be printed to the screen. Also, note the warning message will be printed at the end of the run. This is natural too. In order for the MCMC algorithm to work, MCMCglmm must keep track of effects associated with unmeasured individuals appearing in the pedigree. This will not affect the answers, but when many unmeasured individuals exist, it can hinder the ability of the algorithm to explore the parameter space (more on this, and a solution, later). Lets have a look at the MCMCglmm outputs. First we will evaluate how confident we can be that MCMCglmm found good answers. By entering

```
plot(model1.1$Sol)
```

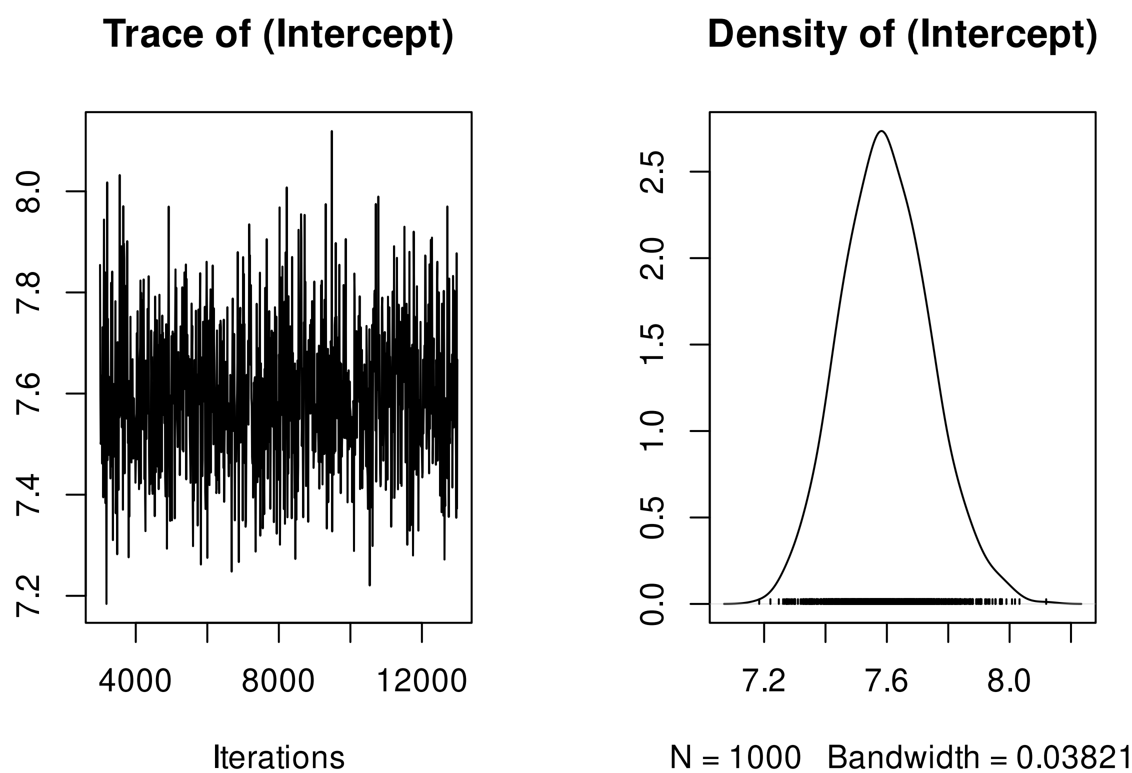


Figure 2.3: The posterior distribution of the fixed effect (the intercept, or mean) in model 1.1

in the console, we get Figure 2.2. The plot on the left shows a time series of the values of 1000 samples of the posterior distribution of the the model intercept (mean birth weight). The plot on the right shows the same data as a distribution. Complicated statistical methods for estimating population means are of course of little interest; rather, we are examining these outputs to check that MCMCglmm's algorithms worked well for our data and for this model. The important point here is that a consistent amount of variation around a largely unchanging mean value of the intercept was obtained (which give this fluctuating trace concentrated around the mean), and the posterior distribution of the intercept appears to be valid. More rigorous means of evaluation the independence of the samples in the posterior distribution (evaluating autocorrelation) are discussed in the MCMCglmm CourseNotes, available from CRAN. Note that your output for `model 1.1` may not be identical to this due to Monte Carlo (random number) error. So every times, you run the model, you will get similar but slightly different results.

The posterior distributions of the the variance components are generally of more interest to animal model users. We can view plots of the posterior distribution for the variance components for model 1.1 by

```
plot(model1.1$VCV)
```

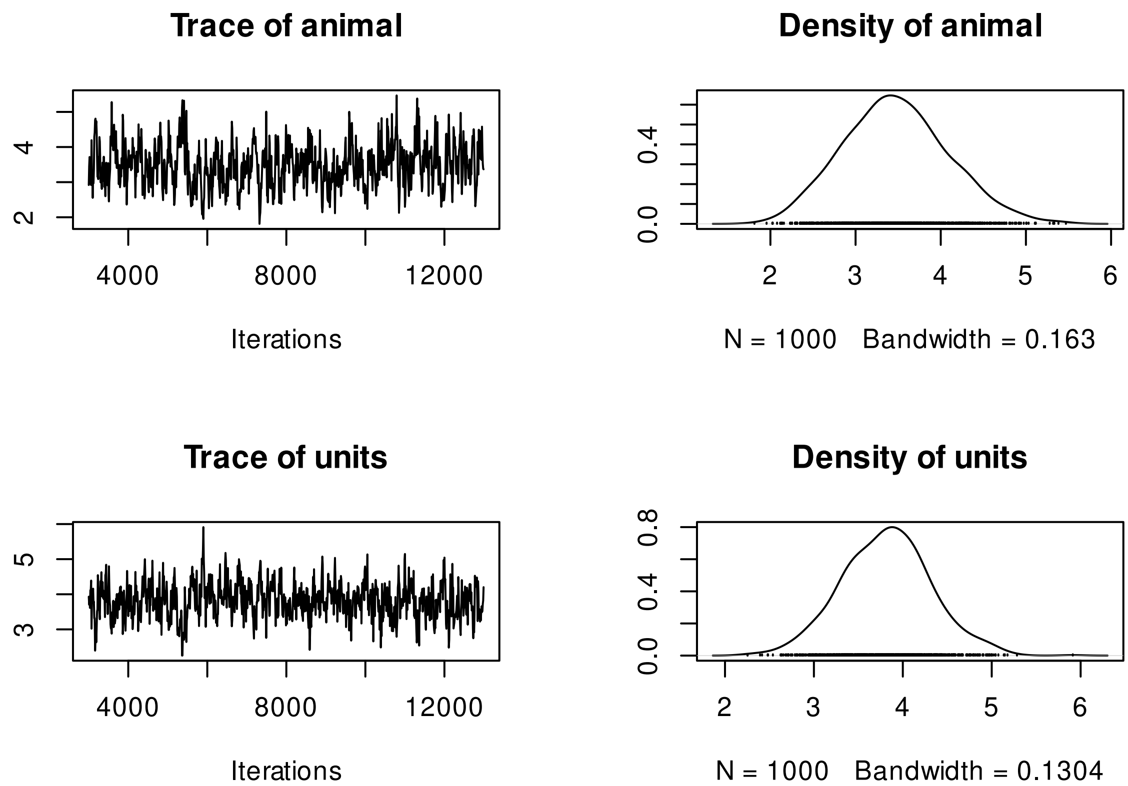


Figure 2.4: The posterior distributions of the variance components of model 1.1, based on an analysis with the default values for nitt, burnin, and thin in MCMCglmm

which generates Figure 2.3. Here we see distributions of the estimates of the additive genetic (animal) and residual (units) effects. These samples contain some autocorrelation, i.e., trends are apparent in the left-hand plot. We can deal with this easily.

2.4.2 Change in iteration and sampling

We will simply re-run the model for a longer number of iterations, and sample the chain less frequently. So far we have been running MCMCglmm with its default values. These defaults are a total run length of 13000 iterations, the first 3000 of which are discarded as a 'burn-in' period to make sure that the converges to the part of the parameter space where the maximum likelihood exists. The remaining 10000 iterations are sampled (estimates retained) every 10 iterations (the thinning interval). Because the values in the left-hand plots in figure 2.2 to appear to have different values at the beginning of the run, we might suspect that a longer burn-in period might be required. We can reduce the autocorrelation by lengthening the rest of the run and sampling the chain less frequently. The following code runs the same model 1.1, but is likely to produce better samples of the posterior distributions. This model should take about two minutes to analyze.

```
model1.1 <- MCMCglmm(bwt ~ 1,
  random = ~animal, ginv = list(animal = Ainv),
```

```
  data = gryphon, nitt = 65000, thin = 50, burnin = 15000,
  prior = prior1.1, verbose = FALSE
)
```

Notes that we have now included the argument verbose=FALSE in the MCMCglmm call. We will continue this throughout the tutorial so that more complete screen outputs can be included in this document without using too much space.Note that the autocorrelation is much reduced. A more compact way to evaluate the validity of the posterior distributions is to calculate autocorrelation among samples, as follows:

```
autocorr.diag(model1.1$VCV)
```

```
##                 animal        units
## Lag 0      1.000000000  1.000000000
## Lag 50     0.209039004  0.173955831
## Lag 250   -0.017811690 -0.028870690
## Lag 500   -0.007328492  0.008719608
## Lag 2500   0.050325531  0.056367451
```

We will consider these levels of autocorrelation acceptable, at least for the purposes of this tutorial. Ideally, all samples of the posterior distribution should be independent, and the autocorrelation for all lag values greater than zero should be near zero. However, in practice this will not strictly be achievable for all analytic scenarios. Certainly the levels of autocorrelation observed here should not be tolerated in any formal analysis. Note that the validity of posterior distributions of any analysis should always be checked; however, for brevity we will not continue to be so consistently diligent throughout the rest of these tutorials. We can now proceed with confidence to recover some more information from these samples. We can obtain estimates of the additive genetic and residual variance by calculating the modes of the posterior distributions:

```
posterior.mode(model1.1$VCV)
```

```
##   animal    units
## 3.310074 3.728226
```

We can obtain the Bayesian equivalent of confidence intervals by calculating the the values of the estimates that bound 95% (or any other proportion) of the posterior distributions:

```
HPDinterval(model1.1$VCV)
```

```
##           lower    upper
## animal 2.185154 4.567025
## units  2.899000 4.922814
## attr(,"Probability")
## [1] 0.95
```

2.4.3 Change priors parameters

We specified weak priors in this analyses. Now we will check whether or not proper priors would have influenced the results that we obtained. The simplest way to do this is to re-run the model with different priors. In the previous model we specified a prior where the size of genetic and residual variance were similar. Here we construct priors with a larger degree of belief parameter (`nu`), and we will specify that a large proportion (95%) of the variation is under genetic control (`V`).Thus, the residual variance contains 05% of the phenotypic variance.

```
p.var <- var(gryphon$bwt, na.rm = TRUE)
prior1.1.2 <- list(
  G = list(G1 = list(V = matrix(p.var * 0.95), nu = 1)),
  R = list(V = matrix(p.var * 0.05), nu = 1)
)

model1.1.2 <- MCMCglmm(bwt ~ 1,
  random = ~animal, ginv = list(animal = Ainv),
  data = gryphon, prior = prior1.1.2, nitt = 65000, thin = 50,
  burnin = 15000, verbose = FALSE
)
posterior.mode(model1.1$VCV)
```

```
##   animal    units
## 3.310074 3.728226
```

```
posterior.mode(model1.1.2$VCV)
```

```
##   animal    units
## 3.299524 4.026746
```

and we can therefore conclude that the difference in the priors has little effect on the outcome of the analysis. This is typical for an analysis where lots of data are available relative to the complexity of the model, but is often not the case. In all cases, it is important to check the effect of priors on conclusions drawn from a model. In addition, you can also specify the prior with previous knowledge or expectation for the variance.

2.4.4 Estimating heritability

A useful property of Bayesian posterior distributions is that we can apply almost any transformation to these distributions and they will remain valid. This applies to the calculation of heritability. We can obtain an estimate of the heritability by applying the basic formula $h^2 = V_A/V_P$ to each sample of the posterior distribution:

```
posterior.heritability1.1 <- model1.1$VCV[, "animal"] /
  (model1.1$VCV[, "animal"] + model1.1$VCV[, "units"])
```

```
posterior.mode(posterior.heritability1.1)
```

```
##      var1
## 0.4603614
```

```
HPDinterval(posterior.heritability1.1, 0.95)
```

```
##          lower     upper
## var1 0.3236453 0.6079976
## attr(,"Probability")
## [1] 0.95
```

Generate a plot of the posterior distribution of this heritability estimate:

```
plot(posterior.heritability1.1)
```

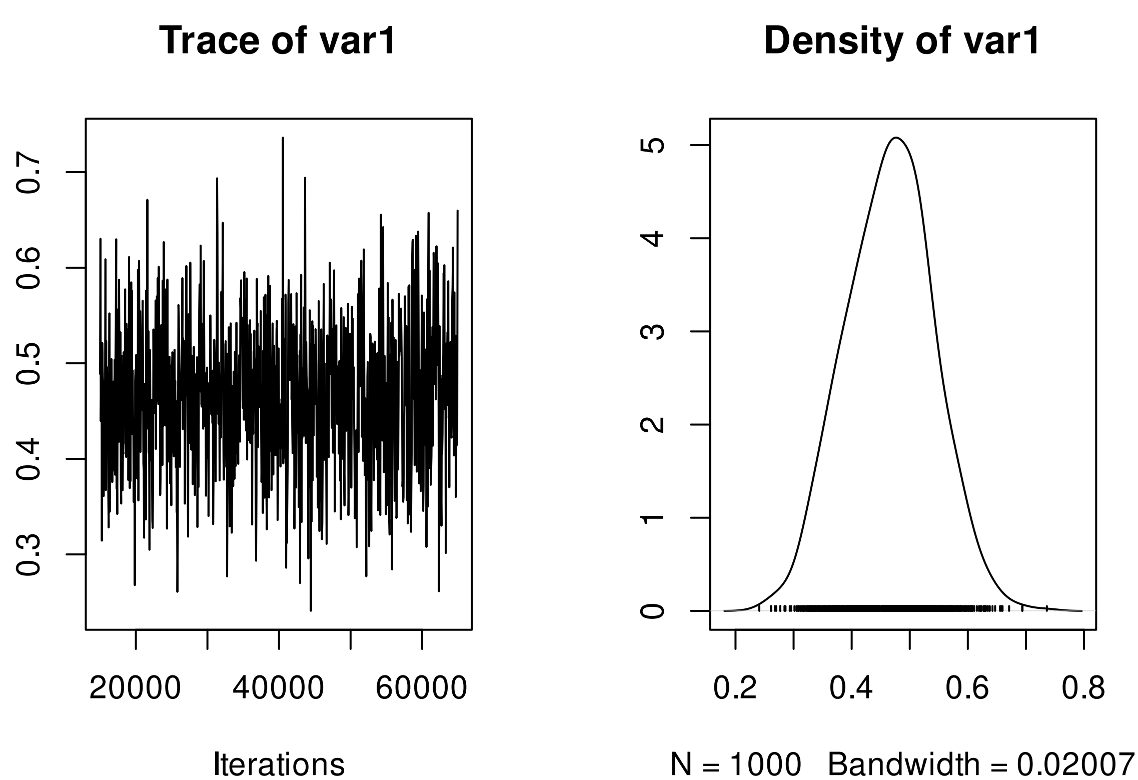


Figure 2.5: The posterior distributions the heritability from model 1.1

2.4.5 Adding fixed effects

To add effects to a univariate model, we simply modify the fixed effect part of the model specification:

```
model1.2 <- MCMCglmm(bwt ~ sex,
  random = ~animal, ginv = list(animal = Ainv),
  data = gryphon, prior = prior1.1,
  nitt = 65000, thin = 50, burnin = 15000, verbose = FALSE
)
summary(model1.2)
```

```
##
##  Iterations = 15001:64951
##  Thinning interval  = 50
##  Sample size  = 1000
##
##  DIC: 3719.3
##
##  G-structure:  ~animal
##
##        post.mean l-95% CI u-95% CI eff.samp
## animal     3.049    2.093    4.092    716.9
##
##  R-structure:  ~units
##
##       post.mean l-95% CI u-95% CI eff.samp
## units     2.974    2.168     3.74    775.5
##
##  Location effects: bwt ~ sex
##
##             post.mean l-95% CI u-95% CI eff.samp  pMCMC
## (Intercept)     6.053    5.726    6.359     1201 <0.001 ***
## sex2            2.214    1.895    2.536     1000 <0.001 ***
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

We can assess the significance of `sex` as a fixed effect by examining its posterior distribution. Important notes here, it is important to know how the model names their fixed effect level to call them properly.

```
posterior.mode(model1.2$Sol[, "sex2"])
```

```
##    var1
## 2.16871
```

```
HPDinterval(model1.2$Sol[, "sex2"], 0.95)
```

```
##        lower    upper
## var1 1.89504 2.536397
## attr(,"Probability")
## [1] 0.95
```

The posterior distribution of the `sex2` term does not overlap zero. Thus, we can infer that sex has an effect on birth weight (presence of a sexual dimorphism) in this model and is a useful addition to the model, for most purposes. It is also worth noting that the variance components have changed slightly:

```
posterior.mode(model1.2$VCV)
```

```
##   animal    units
## 2.960190 3.117091
```

In fact since sex effects were previously contributing to the residual variance of the model our estimate of V_R (denoted 'units' in the output) is now slightly lower than before. This has an important consequence for estimating heritability since if we calculate V_P as $V_A + V_R$ then as we include fixed effects we will soak up more residual variance driving V_P . Assuming that V_A is more or less unaffected by the fixed effects fitted then as V_P goes down we expect our estimate of h^2 will go up.

```
posterior.heritability1.2 <- model1.2$VCV[, "animal"] /
  (model1.2$VCV[, "animal"] + model1.2$VCV[, "units"])
posterior.mode(posterior.heritability1.2)
```

```
##      var1
## 0.4915129
```

```
HPDinterval(posterior.heritability1.2, 0.95)
```

```
##         lower     upper
## var1 0.364643 0.6437182
## attr(,"Probability")
## [1] 0.95
```

Here h^2 has increased slightly from 0.4829 to 0.5079 (again, your values may differ slightly due to Monte Carlo error). Which is the better estimate? It depends on what your question is. The first is an estimate of the proportion of variance in birth weight explained by additive effects, the latter is an estimate of the proportion of variance in birth weight after conditioning on sex that is explained by additive effects. An important piece of advice, each researcher should be consistent in how they name their estimates and always correctly describe which estimates they are using conditional or not (to avoid any confusion).

2.4.6 Adding random effects

This is done by simply modifying the model statement in the same way, but requires addition of a prior for the new random effect. For instance, we can fit an effect of birth year:

```
prior1.3 <- list(
  G = list(G1 = list(V = 1, nu = 0.002), G2 = list(V = 1, nu = 0.002)),
  R = list(V = 1, nu = 0.002)
)

model1.3 <- MCMCglmm(bwt ~ sex,
  random = ~ animal + byear, ginv = list(animal = Ainv),
  data = gryphon,
  nitt = 65000, thin = 50, burnin = 15000,
  prior = prior1.3, verbose = FALSE
)

posterior.mode(model1.3$VCV)
```

```
##    animal     byear     units
## 2.7656801 0.8753865 2.3439002
```

Here the variance in birth weight explained by birth year is 0.88. Note that although V_A has changed somewhat, most of what is now partitioned as a `birth year` effect was previously partitioned as V_R . Thus what we have really done here is to partition environmental effects into those arising from year to year differences versus everything else, and we do not really expect much change in h^2 (since now $h^2 = V_A/(V_A + V_{BY} + V_R)$). However, we get a somewhat different result if we also add a random effect of `mother` to test for maternal effects:

```
prior1.4 <- list(
  G = list(
    G1 = list(V = 1, nu = 0.002),
    G2 = list(V = 1, nu = 0.002),
    G3 = list(V = 1, nu = 0.002)
  ),
  R = list(V = 1, nu = 0.002)
)

model1.4 <- MCMCglmm(bwt ~ sex,
  random = ~ animal + byear + mother,
  ginv = list(animal = Ainv), data = gryphon,
  nitt = 65000, thin = 50, burnin = 15000,
  prior = prior1.4, verbose = FALSE
)

posterior.mode(model1.4$VCV)
```

```
##    animal     byear    mother     units
## 2.5454307 0.7545662 1.0474161 1.8486924
```

Here partitioning of significant maternal variance has resulted in a further decrease in V_R but also a decrease in V_A. The latter is because maternal effects of the sort we simulated (fixed differences between mothers) will have the consequence of increasing similarity among maternal siblings. Consequently they can look very much like an additive genetic effects and if present, but unmodelled, represent a type of 'common environment effect' that can - and will- cause upward bias in V_A and so h^2. Let's compare the estimates of heritability from each of models 1.2, 1.3 and 1.4:

```
posterior.heritability1.3 <- model1.3$VCV[, "animal"] /
  (model1.3$VCV[, "animal"] + model1.3$VCV[, "byear"] + model1.3$VCV[, "units"])
posterior.heritability1.4 <- model1.4$VCV[, "animal"] /
  (model1.4$VCV[, "animal"] + model1.4$VCV[, "byear"] + model1.4$VCV[, "mother"] + model1.
posterior.mode(posterior.heritability1.2)
```

```
##      var1
## 0.4915129
```

```
posterior.mode(posterior.heritability1.3)
```

```
##      var1
## 0.4536882
```

```
posterior.mode(posterior.heritability1.4)
```

```
##      var1
## 0.3790414
```

2.4.7 Testing significance of variance components

While testing the significance of fixed effects by evaluating whether or not their posterior distributions overlap zero was simple and valid, this approach does not work for variance components. Variance components are bounded to be positive (given a proper prior), and thus even when a random effect is not meaningful, its posterior distribution will never overlap zero. Model comparisons can be performed using the deviance information criterion (`DIC`), although it should be noted that the properties of DIC are not well understood and that the `DIC` may be focused at the wrong level for most people's intended level of inference - particularly with non-Gaussian responses. The implementation of `DIC` in MCMCglmm is further described in the reference manual. `DIC` values are calculated by MCMCglmm by default. Briefly, `DIC` like other information criteria balance model fit and model complexity simultaneously, and small values of DIC are preferred. We can compare `models 1.4` and `1.3`, i.e., models with and without the mother term:

```
model1.3$DIC
```

```
## [1] 3548.159
```

```
model1.4$DIC
```

```
## [1] 3327.724
```

`model 1.4` has a much lower DIC value. Since the maternal effect term is the only difference between the models, we can consider the inclusion of this term statistically justifiable. We should note however that DIC has a large sampling variance and should probably only be calculated based on much longer MCMC runs.

2.4.8 Further partitioning variance

A population can be further fragmented into different groups or categories (such as females and males, juveniles and adults or treated and untreated). Some scientific questions require further and deeper analysis of the variance. To avoid multiple model (one for each group), we can directly partition the variance between groups in a unique model. In addition, by doing so, we can also test if the variance are different between groups.

As example, we can partition the additive genetic variance and residual variance by sex. It is impossible to further partition the other variances but complexity an animal model requires sufficient sample size.

```
prior1.4.SEX <- list(
  G = list(G1 = list(V = diag(2), nu = 1.002), G2 = list(V = 1, nu = 0.002), G3 = list(V =
  R = list(V = diag(2), nu = 1.002)
)

model1.4.SEX <- MCMCglmm(bwt ~ sex,
  random = ~ idh(sex):animal + byear + mother,
  rcov = ~ idh(sex):units,
  ginv = list(animal = Ainv), data = gryphon, nitt = 65000, thin = 50, burnin = 15000,
  prior = prior1.4.SEX, verbose = FALSE
)

posterior.mode(model1.4.SEX$VCV)
```

```
## sex1.animal sex2.animal       byear      mother  sex1.units  sex2.units
##   1.2979861   1.6649978   0.7149751   1.2746095   2.4459575   0.9091363
```

```
posterior.heritability1.4.FEM <- model1.4.SEX$VCV[, "sex1.animal"] /
  (model1.4.SEX$VCV[, "sex1.animal"] + model1.4.SEX$VCV[, "byear"] +
    model1.4.SEX$VCV[, "mother"] + model1.4.SEX$VCV[, "sex1.units"])
```

```
posterior.heritability1.4.MAL <- model1.4.SEX$VCV[, "sex2.animal"] /
  (model1.4.SEX$VCV[, "sex2.animal"] + model1.4.SEX$VCV[, "byear"] +
    model1.4.SEX$VCV[, "mother"] + model1.4.SEX$VCV[, "sex2.units"])

posterior.mode(posterior.heritability1.4.FEM)
```

```
##      var1
## 0.2507729
```

```
HPDinterval(posterior.heritability1.4.FEM, 0.95)
```

```
##           lower     upper
## var1 0.04358691 0.4369285
## attr(,"Probability")
## [1] 0.95
```

```
posterior.mode(posterior.heritability1.4.MAL)
```

```
##      var1
## 0.4497827
```

```
HPDinterval(posterior.heritability1.4.MAL, 0.95)
```

```
##          lower     upper
## var1 0.1041657 0.6197678
## attr(,"Probability")
## [1] 0.95
```

Here, we can estimate the heritability for each sex. Both doesn't overlap with zero, so we can conclude both sexes have significant heritability. However due to their overlaps CIs, we can not conclude the heritability is not significantly different between sexes. An important quote to remember is "A difference in significance is not a significant difference"

```
h2.sex <- rbind(
  cbind(posterior.mode(posterior.heritability1.4.FEM), HPDinterval(posterior.heritability1
  cbind(posterior.mode(posterior.heritability1.4.MAL), HPDinterval(posterior.heritability1
)


plot(c(0.95, 1.05) ~ h2.sex[, 1], xlim = c(0, 0.8), ylim = c(0.5, 1.5), , xlab = "", ylab
arrows(y0 = 0.95, x0 = h2.sex[1, 2], y1 = 0.95, x1 = h2.sex[1, 3], code = 3, angle = 90, l
arrows(y0 = 1.05, x0 = h2.sex[2, 2], y1 = 1.05, x1 = h2.sex[2, 3], code = 3, angle = 90, l
mtext("Narrow-sense heritability (±CI)", side = 1, las = 1, adj = 0.4, line = 3, cex = 1.6
axis(2, at = 1, labels = c("birth weight"), las = 3, cex.axis = 1.6)
```

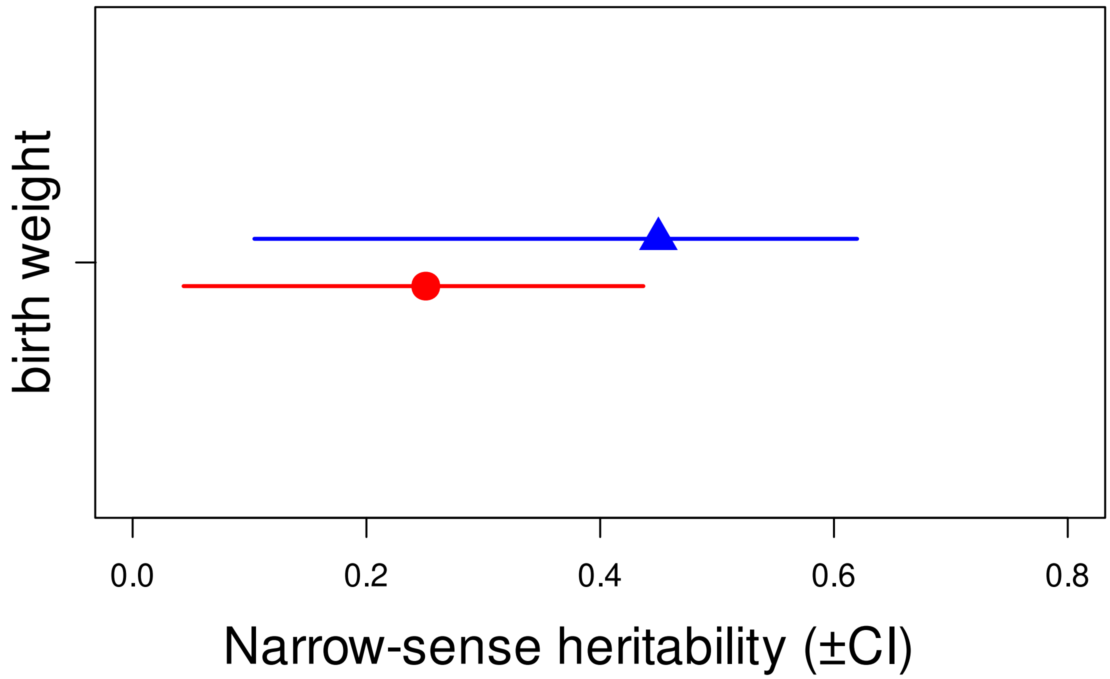


Figure 2.6: Female and male heritability of birth weight

2.4.9 Modification of model parameter

Unfortunately (to our knowledge), it is not possible to alter the variance matricesand refit them within the model.

2.4.10 Covariance between two random effects

Some research questions require to estimate the covariance between two random effects within a univariate model.To do so, we can use the argument `str`. A similar argument or linking.function `mm` can be used but it will forced the variance of `animal` and `mother` to be equal and the covariance to 1. As an example, we fit a model which estimate the covariance between the additive genetic variance and the mother variance. Both variances require to operate on the same level, thus `animal` and `mother` require to be associated to the pedigree information.The ginverse list name has to correspond to the first term in the argument or linking.function

2.5 brms

2.5.1 Running the model

First we need to load the `brms` library:

```
library(brms)
```

To be able to fit an animal model, `brms` needs the relativeness (relationship) matrix of the pedigree and not its inverse (as in other softwares). This can be estimated using the `nadiv` package created by Pr. Matthew Wolak (https://cran.r-project.org/web/packages/nadiv/index.html).

```
Amat <- as.matrix(nadiv::makeA(gryphonped))
```

We are now ready to specify our first model: The structure of a `bmrs` model is similar to `lme4`, thus the random effect is added to the model with the term `(1 | gr(animal, cov = Amat)` which associate the id animal to the matrix of relativeness. In addition to the synthase of `lme4`, we includes other features or parameters within the models such as `chain` which represent the number of Markov chains (defaults to 4), `core` which represents the number of cores to use when executing the chains in parallel and `iter` which represents the number of total iterations per chain. For more parameters such as `thin` or `warmup/burnin`, you can read the Cran R page of the package (https://cran.r-project.org/web/packages/brms/brms.pdf)

`bmrs` is a Bayesian Multilevel Models using Stan, doing so we can apply a prior to the model to better shape the distribution of the different variances estimated by the model. Given that `bmrs` fit the model using a Bayesian approach via the software `stan`, we need to specify priors for the model. Default priors in `brms` work relatively well, however we strongly suggest to carefully select an adequate prior for your analysis. In this tutorial we will use the default priors. To get the prior used by default, we can use the `get_prior()` function.

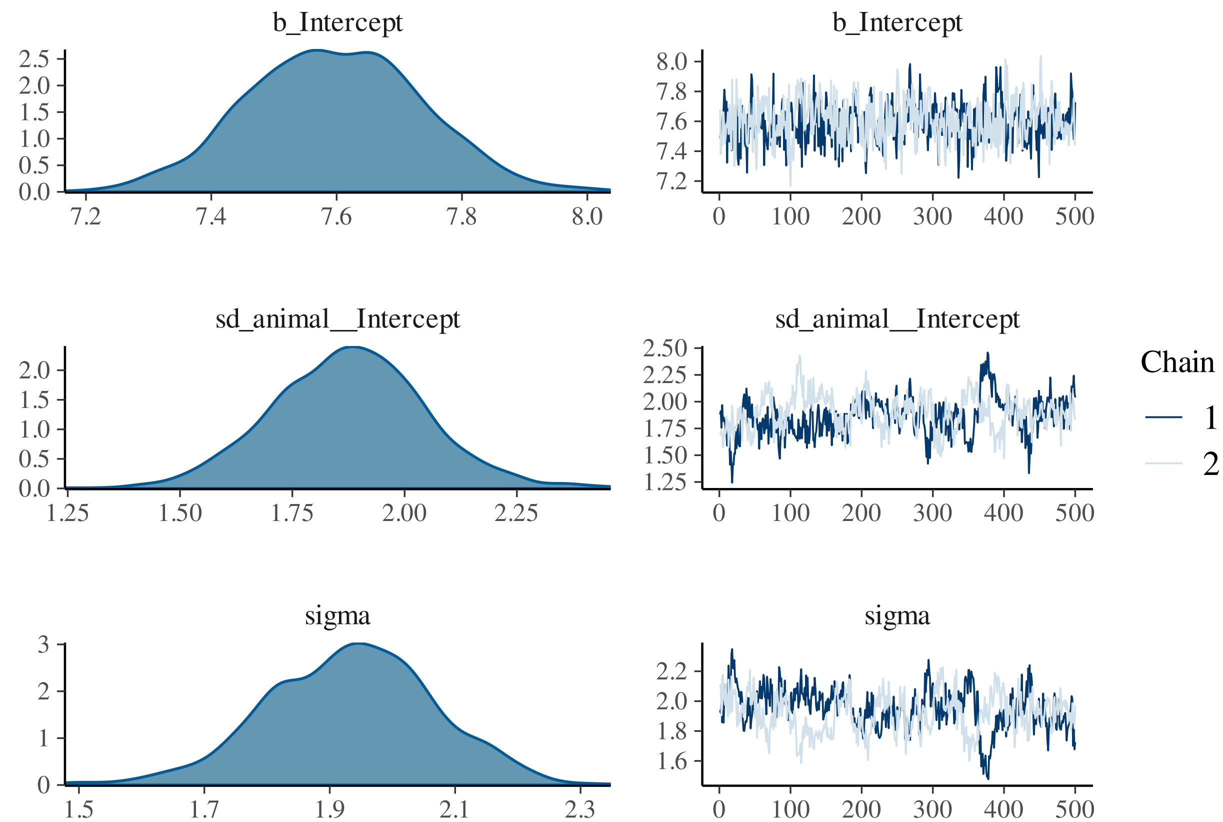
```
brms_m1.1 <- brm(
  bwt ~ 1 + (1 | gr(animal, cov = Amat)),
  data = gryphon,
  data2 = list(Amat = Amat),
  family = gaussian(),
  chains = 1, cores = 1, iter = 100
)

save(brms_m1.1, file = "data/brms_m1_1.rda")
```

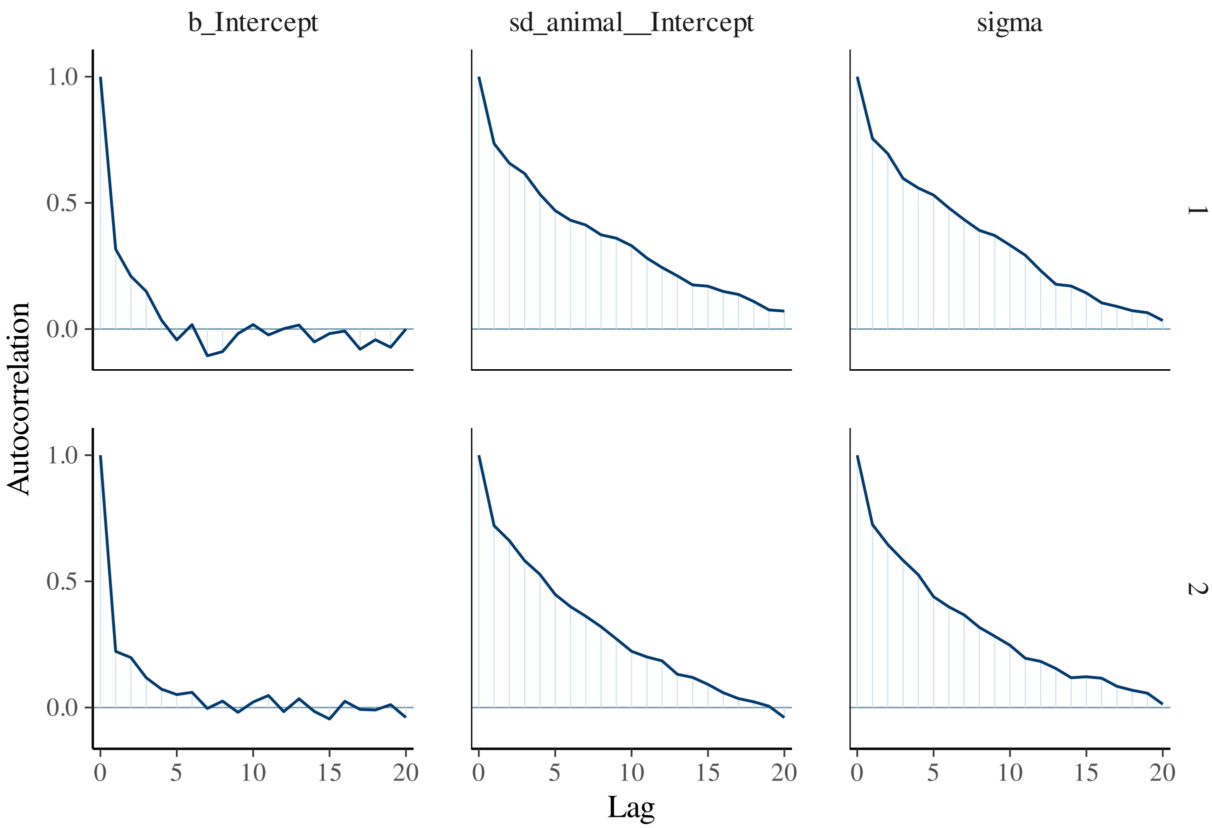
The result of the long model calculation is save in a spare file `brms_m1_1.rda"`. To help readers, we can directly reloading it. Two distinct plot can be produce to produce some diagnostics graphs `mcmc_plot`.Note, that `sigma` represents the residual standard deviation.

Next,we examine (or directly using the model) the variance estimate and their distributions (via `summary` or plot).

```
load("data/brms_m1_1.rda")
plot(brms_m1.1)
```




```
mcmc_plot(brms_m1.1, type = "acf")
```




```r
summary(brms_m1.1)
```

```
##  Family: gaussian
##   Links: mu = identity; sigma = identity
## Formula: bwt ~ 1 + (1 | gr(animal, cov = Amat))
##    Data: gryphon (Number of observations: 854)
##   Draws: 2 chains, each with iter = 1000; warmup = 500; thin = 1;
##          total post-warmup draws = 1000
##
## Group-Level Effects:
## ~animal (Number of levels: 854)
##               Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## sd(Intercept)     1.88      0.17     1.54     2.23 1.03       74       99
##
## Population-Level Effects:
##           Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## Intercept     7.60      0.14     7.33     7.86 1.01      428      727
##
## Family Specific Parameters:
##       Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## sigma     1.93      0.13     1.66     2.18 1.04       71      112
##
## Draws were sampled using sampling(NUTS). For each parameter, Bulk_ESS
```

```
## and Tail_ESS are effective sample size measures, and Rhat is the potential
## scale reduction factor on split chains (at convergence, Rhat = 1).
```

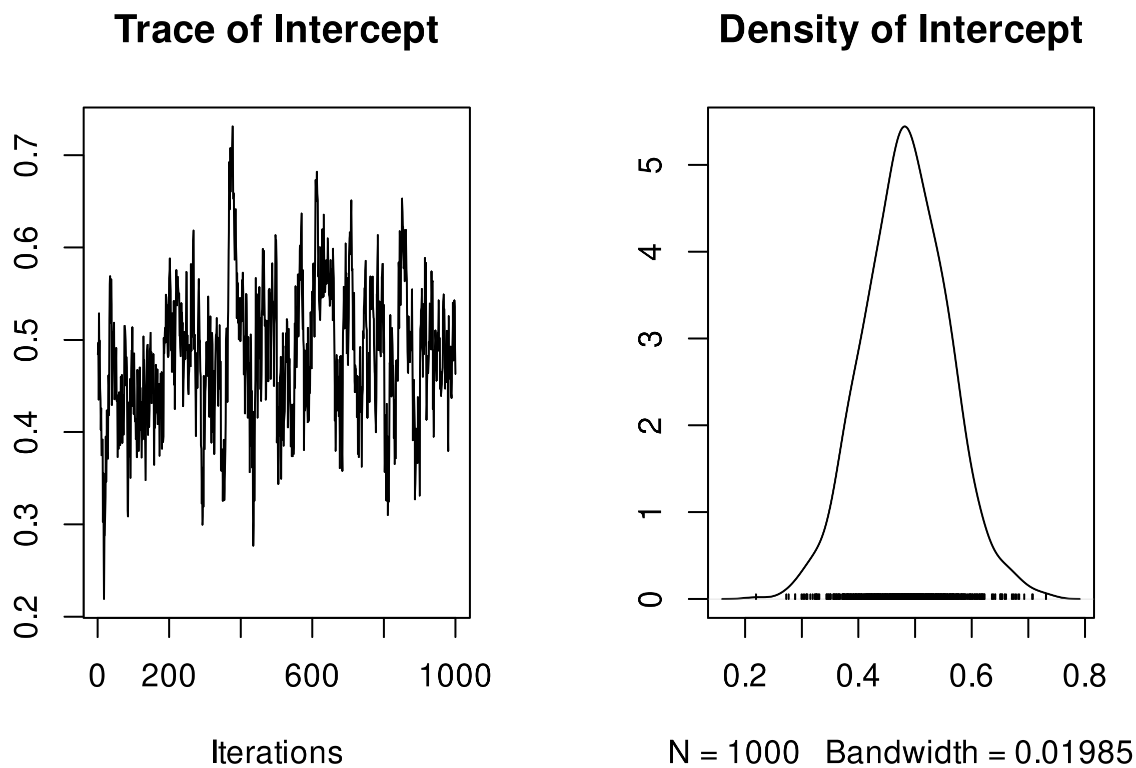
The `plot` of variance showed that the different variances have an normal distribution, the autocorrelation plot or 'acf' show that the autocorrelation is close to 0. The `summary` exposes the mean (Estimate) of each variance or fixed effect (here just the intercept) associated to their posterior distribution with standard deviation (Est.Error) and two-sided 95% Credible intervals. `Rhat` provides information on the estimate convergence. If it's greater than 1, the chains have not yet converged and it will be require to run more iterations and/or set stronger priors. `ESS` represents the Effective sample values as the number of independent samples from the posterior distribution. However, for the purpose of this guide, the Rhat values are acceptable.

It is also possible to calculate the heritability using the function 'as.mcmc'

```r
v_animal <- (VarCorr(brms_m1.1, summary = FALSE)$animal$sd)^2
v_r <- (VarCorr(brms_m1.1, summary = FALSE)$residual$sd)^2
h.bwt.1 <- as.mcmc(v_animal / (v_animal + v_r))
summary(h.bwt.1)
```

```
##
## Iterations = 1:1000
## Thinning interval = 1
## Number of chains = 1
## Sample size per chain = 1000
##
## 1. Empirical mean and standard deviation for each variable,
##    plus standard error of the mean:
##
##           Mean             SD       Naive SE Time-series SE
##       0.484221       0.074533       0.002357       0.009275
##
## 2. Quantiles for each variable:
##
##   2.5%    25%    50%    75%  97.5%
## 0.3433 0.4338 0.4841 0.5350 0.6369
```

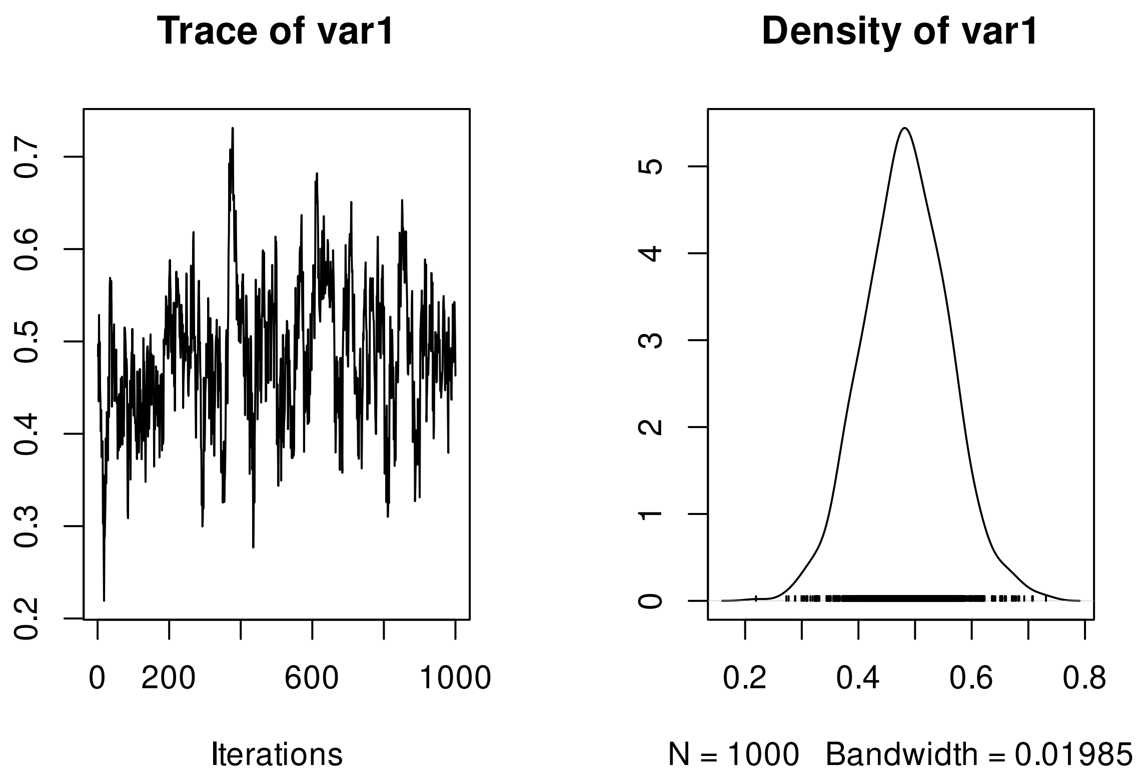
```r
plot(h.bwt.1)
```




```r
# or
Var.table <- as_draws_df(brms_m1.1)
Var.table$h.bwt.1 <- as.mcmc((Var.table$sd_animal__Intercept)^2 / ((Var.table$sd_animal__I
summary(Var.table$h.bwt.1)
```

```
##
## Iterations = 1:1000
## Thinning interval = 1
## Number of chains = 1
## Sample size per chain = 1000
##
## 1. Empirical mean and standard deviation for each variable,
##    plus standard error of the mean:
##
##           Mean             SD       Naive SE Time-series SE
##       0.484221       0.074533       0.002357       0.009275
##
## 2. Quantiles for each variable:
##
##   2.5%    25%    50%    75%  97.5%
## 0.3433 0.4338 0.4841 0.5350 0.6369
```

```
plot(Var.table$h.bwt.1)
```



2.5.2 Adding fixed effects

To add effects to a univariate model, we simply modify the priors and the fixed effect portion of the model specification:

```
brms_m1.2 <- brm(
  bwt ~ 1 + sex + (1 | gr(animal, cov = Amat)),
  data = gryphon,
  data2 = list(Amat = Amat),
  family = gaussian(),
  chains = 2, cores = 2, iter = 1000
)

save(brms_m1.2, file = "data/brms_m1_2.rda")
```

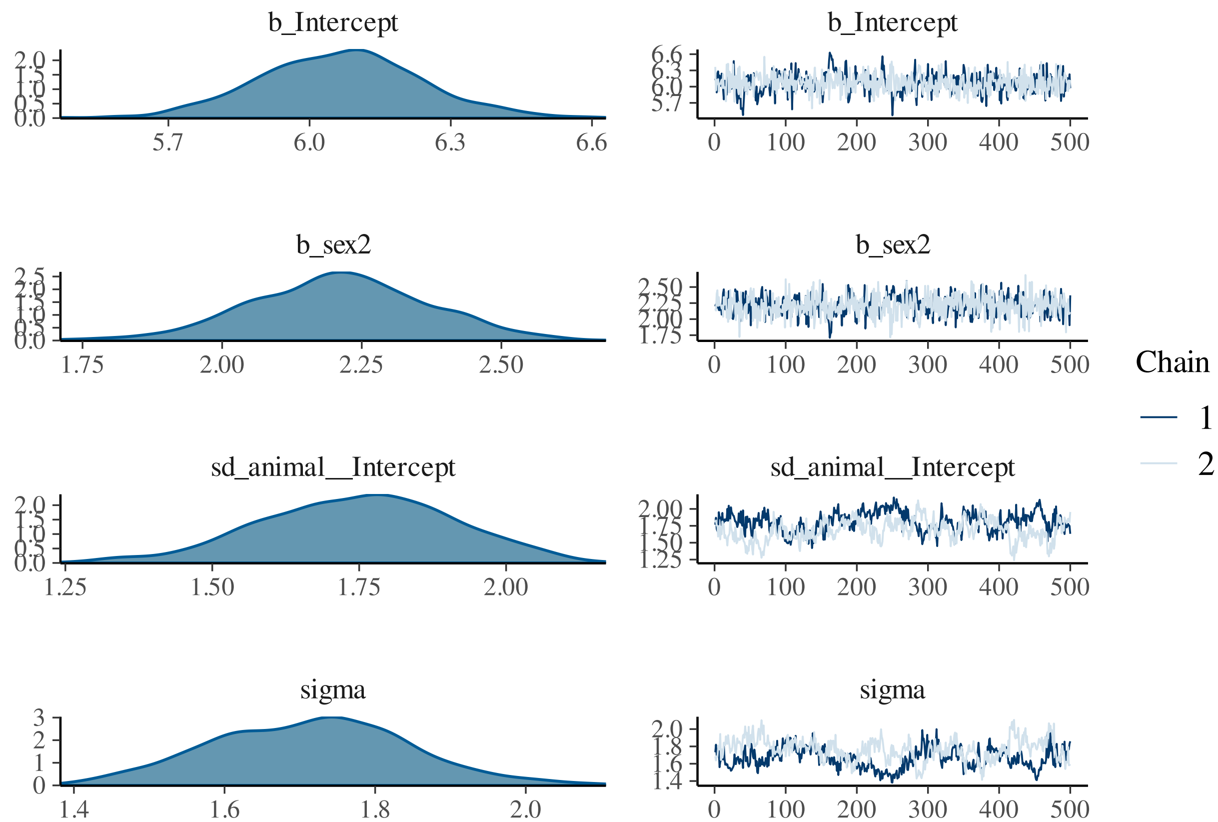
To save time, the results of the calculation is stored in the spare file `brms_m1_2.rda"`. We can assess the significance of `sex` as a fixed effect by examining its posterior distribution.

```
load("data/brms_m1_2.rda")
summary(brms_m1.2)
```

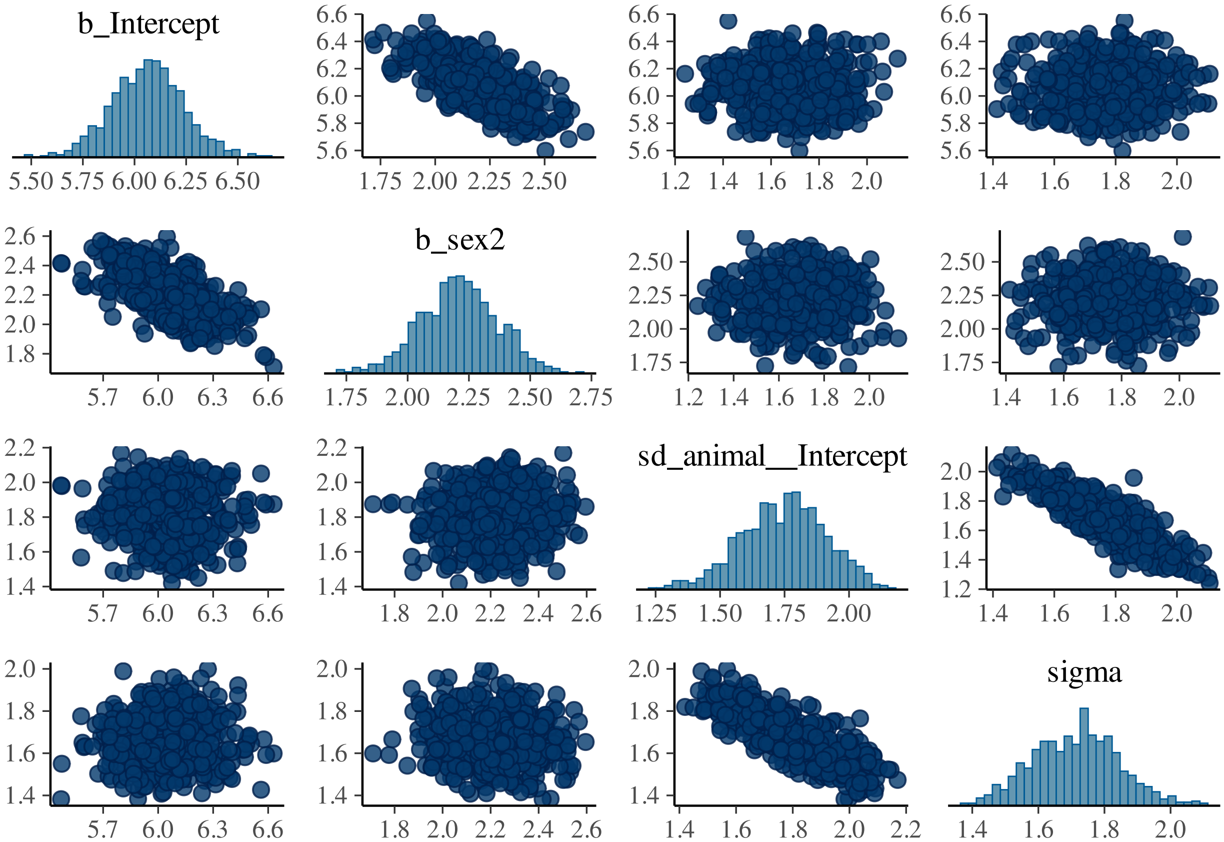
```
## Warning: Parts of the model have not converged (some Rhats are > 1.05). Be
## careful when analysing the results! We recommend running more iterations and/or
## setting stronger priors.
```

```
##  Family: gaussian
##   Links: mu = identity; sigma = identity
## Formula: bwt ~ 1 + sex + (1 | gr(animal, cov = Amat))
##    Data: gryphon (Number of observations: 854)
##   Draws: 2 chains, each with iter = 1000; warmup = 500; thin = 1;
##          total post-warmup draws = 1000
##
## Group-Level Effects:
## ~animal (Number of levels: 854)
##               Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## sd(Intercept)     1.75      0.16     1.42     2.05 1.13       13      113
##
## Population-Level Effects:
##           Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## Intercept     6.06      0.17     5.74     6.41 1.00      358      574
## sex2          2.21      0.16     1.90     2.52 1.00      723      657
##
## Family Specific Parameters:
##       Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## sigma     1.71      0.13     1.47     1.98 1.12       14       97
##
## Draws were sampled using sampling(NUTS). For each parameter, Bulk_ESS
## and Tail_ESS are effective sample size measures, and Rhat is the potential
## scale reduction factor on split chains (at convergence, Rhat = 1).
```

```
plot(brms_m1.2)
```




```r
mcmc_plot(brms_m1.2, type = "pairs")
```




```r
summary(brms_m1.2)$fixed
```

```
## Warning: Parts of the model have not converged (some Rhats are > 1.05). Be
## careful when analysing the results! We recommend running more iterations and/or
## setting stronger priors.

##            Estimate Est.Error l-95% CI u-95% CI     Rhat Bulk_ESS Tail_ESS
## Intercept 6.064853 0.1726459 5.735170 6.410117 1.002990 357.5666 574.2620
## sex2      2.210675 0.1574542 1.898645 2.520026 1.002313 722.8016 657.2121
```

```r
summary(brms_m1.2)$random
```

```
## Warning: Parts of the model have not converged (some Rhats are > 1.05). Be
## careful when analysing the results! We recommend running more iterations and/or
## setting stronger priors.

## $animal
##               Estimate Est.Error l-95% CI u-95% CI     Rhat Bulk_ESS Tail_ESS
## sd(Intercept) 1.747083 0.1632548 1.419377 2.050884 1.126639 13.10221 113.2445
```

The posterior distribution of the `sex2` term does not overlap zero. Thus, we can infer that sex has an effect on birth weight (presence of a sexual dimorphism) in this model and is a useful addition to the model, for most purposes. It is also worth noting that the variance components have changed slightly:

```r
summary(brms_m1.2)$random
```

```
## Warning: Parts of the model have not converged (some Rhats are > 1.05). Be
## careful when analysing the results! We recommend running more iterations and/or
## setting stronger priors.

## $animal
##               Estimate Est.Error l-95% CI u-95% CI     Rhat Bulk_ESS Tail_ESS
## sd(Intercept) 1.747083 0.1632548 1.419377 2.050884 1.126639 13.10221 113.2445
```

In fact since sex effects were previously contributing to the residual variance of the model our estimate of V_R (denoted 'units' in the output) is now slightly lower than before. This has an important consequence for estimating heritability since if we calculate V_P as $V_A + V_R$ then as we include fixed effects we will soak up more residual variance driving V_P . Assuming that V_A is more or less unaffected by the fixed effects fitted then as V_P goes down we expect our estimate of h^2 will go up.

```r
v_animal <- (VarCorr(brms_m1.2, summary = FALSE)$animal$sd)^2
v_r <- (VarCorr(brms_m1.2, summary = FALSE)$residual$sd)^2
h.bwt.2 <- as.mcmc(v_animal / (v_animal + v_r))

summary(h.bwt.2)
```

```
##
## Iterations = 1:1000
## Thinning interval = 1
## Number of chains = 1
## Sample size per chain = 1000
##
## 1. Empirical mean and standard deviation for each variable,
##    plus standard error of the mean:
##
##           Mean             SD       Naive SE Time-series SE
##       0.508677       0.080357       0.002541       0.011998
##
## 2. Quantiles for each variable:
##
##   2.5%    25%    50%    75%  97.5%
## 0.3427 0.4549 0.5107 0.5675 0.6576
```

```r
summary(h.bwt.1)
```

```
##
## Iterations = 1:1000
## Thinning interval = 1
## Number of chains = 1
```

```
## Sample size per chain = 1000
##
## 1. Empirical mean and standard deviation for each variable,
##    plus standard error of the mean:
##
##           Mean             SD       Naive SE Time-series SE
##       0.484221       0.074533       0.002357       0.009275
##
## 2. Quantiles for each variable:
##
##   2.5%    25%    50%    75%  97.5%
## 0.3433 0.4338 0.4841 0.5350 0.6369
```

Here h^2 has increased slightly from 0.5010 to 0.4192 (again, your values may differ slightly due to Monte Carlo error). Which is the better estimate? It depends on what your question is. The first is an estimate of the proportion of variance in birth weight explained by additive effects, the latter is an estimate of the proportion of variance in birth weight after conditioning on sex that is explained by additive effects. An important piece of advice, each researcher should be consistent in how they name their estimates and always correctly describe which estimates they are using conditional or not (to avoid any confusion).

2.5.3 Adding random effects

This is done by simply modifying the model statement in the same way, but requires addition of a prior for the new random effect. For instance, we can fit an effect of birth year:

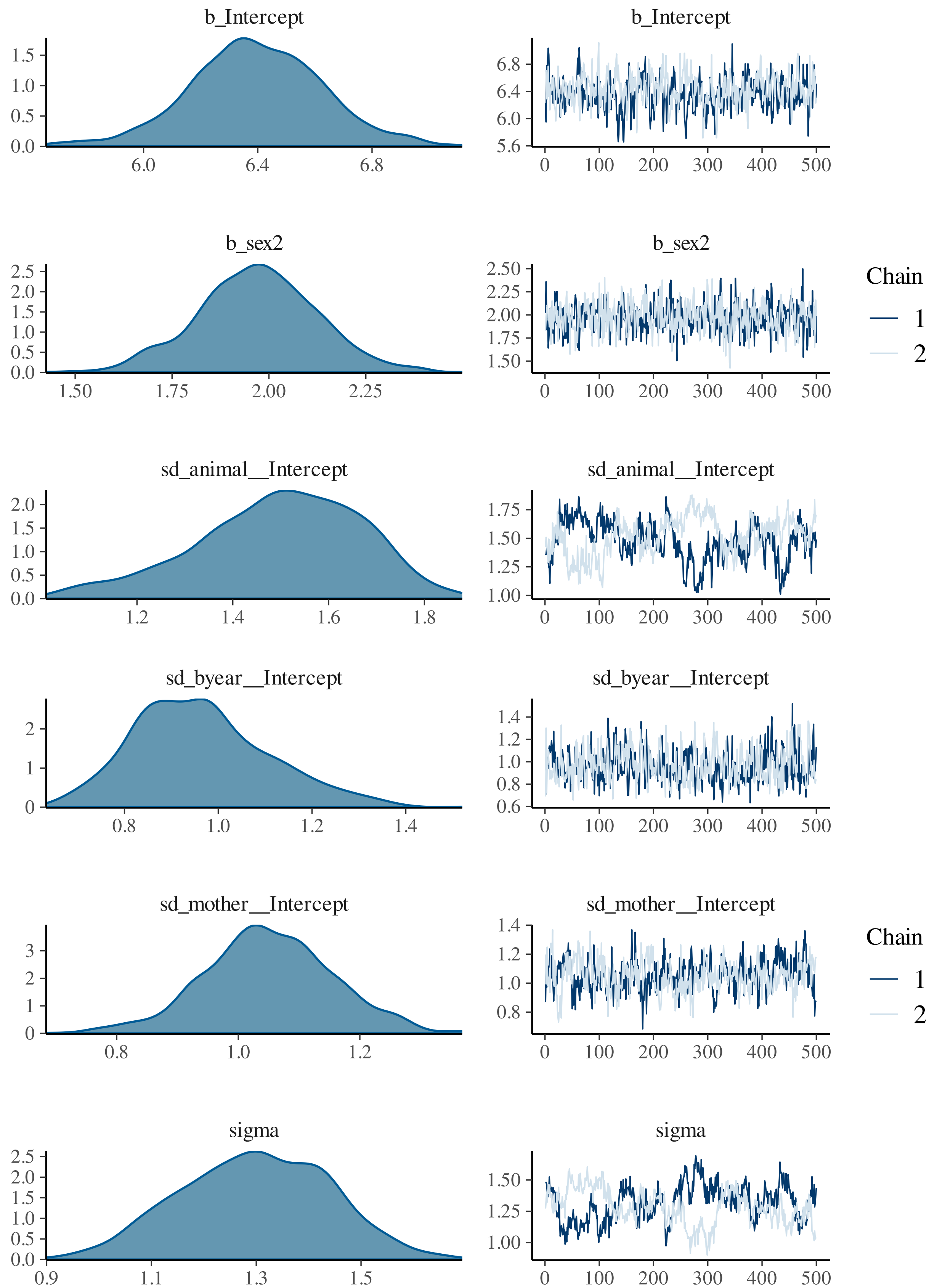
```
brms_m1.3 <- brm(
  bwt ~ 1 + sex + (1 | gr(animal, cov = Amat)) + (1 | byear) + (1 | mother),
  data = gryphon,
  data2 = list(Amat = Amat),
  family = gaussian(),
  chains = 2, cores = 2, iter = 1000
)

save(brms_m1.3, file = "data/brms_m1_3.rda")
```

To save time, the results of the calculation is stored in the spare file `brms_m1_3.rda"`. We can assess the significance of `sex` as a fixed effect by examining its posterior distribution.

```
load("data/brms_m1_3.rda")

plot(brms_m1.3, ask = FALSE, N = 3)
```


b_Intercept
1.5
1.0
0.5
0.0
6.0
6.4
6.8
b_Intercept
6.8
6.4
6.0
5.6
0
100
200
300
400
500
b_sex2
2.5
2.0
1.5
1.0
0.5
0.0
1.50
1.75
2.00
2.25
b_sex2
2.50
2.25
2.00
1.75
1.50
Chain
1
2
sd_animal__Intercept
2.0
1.5
1.0
0.5
0.0
1.2
1.4
1.6
1.8
sd_animal__Intercept
1.75
1.50
1.25
1.00
sd_byear__Intercept
2
1
0
0.8
1.0
1.2
1.4
sd_byear__Intercept
1.4
1.2
1.0
0.8
0.6
sd_mother__Intercept
3
2
1
0
0.8
1.0
1.2
sd_mother__Intercept
1.4
1.2
1.0
0.8
Chain
1
2
sigma
2.5
2.0
1.5
1.0
0.5
0.0
0.9
1.1
1.3
1.5
sigma
1.50
1.25
1.00
0
100
200
300
400
500

```
summary(brms_m1.3)$random
```

```
## Warning: Parts of the model have not converged (some Rhats are > 1.05). Be
## careful when analysing the results! We recommend running more iterations and/or
## setting stronger priors.

## $animal
##               Estimate Est.Error l-95% CI u-95% CI     Rhat Bulk_ESS Tail_ESS
## sd(Intercept) 1.496464 0.1708587 1.105797 1.782062 1.163193 9.153202 50.78299
##
## $byear
##                Estimate Est.Error  l-95% CI u-95% CI     Rhat Bulk_ESS Tail_ESS
## sd(Intercept) 0.9642702  0.144174 0.7147103 1.280642 1.002215 399.5806 642.4663
##
## $mother
##               Estimate Est.Error  l-95% CI u-95% CI     Rhat Bulk_ESS Tail_ESS
## sd(Intercept) 1.050225 0.1057319 0.8292744 1.258439 1.011062 192.6606 379.2063
```

Here partitioning of significant birth year and maternal variance has resulted in a further decrease in V_R but also a decrease in V_A. The latter is because maternal effects of the sort we simulated (fixed differences between mothers) will have the consequence of increasing similarity among maternal siblings. Consequently they can look very much like an additive genetic effects and if present, but unmodelled, represent a type of 'common environment effect' that can - and will- cause upward bias in V_A and so h^2. Let's compare the estimates of heritability from each of models 1.2, 1.3 and 1.4:

```
v_animal <- (VarCorr(brms_m1.3, summary = FALSE)$animal$sd)^2
v_byear <- (VarCorr(brms_m1.3, summary = FALSE)$byear$sd)^2
v_mother <- (VarCorr(brms_m1.3, summary = FALSE)$mother$sd)^2
v_r <- (VarCorr(brms_m1.3, summary = FALSE)$residual$sd)^2
h.bwt.3 <- as.mcmc(v_animal / (v_animal + v_byear + v_mother + v_r))
summary(h.bwt.3)
```

```
##
## Iterations = 1:1000
## Thinning interval = 1
## Number of chains = 1
## Sample size per chain = 1000
##
## 1. Empirical mean and standard deviation for each variable,
##    plus standard error of the mean:
##
##           Mean             SD       Naive SE Time-series SE
##       0.375509       0.078767       0.002491       0.012711
##
## 2. Quantiles for each variable:
```

```
##
##   2.5%    25%    50%    75%  97.5%
## 0.2140 0.3240 0.3764 0.4322 0.5182
```

```
summary(h.bwt.2)
```

```
##
## Iterations = 1:1000
## Thinning interval = 1
## Number of chains = 1
## Sample size per chain = 1000
##
## 1. Empirical mean and standard deviation for each variable,
##    plus standard error of the mean:
##
##           Mean             SD       Naive SE Time-series SE
##       0.508677       0.080357       0.002541       0.011998
##
## 2. Quantiles for each variable:
##
##   2.5%    25%    50%    75%  97.5%
## 0.3427 0.4549 0.5107 0.5675 0.6576
```

```
summary(h.bwt.1)
```

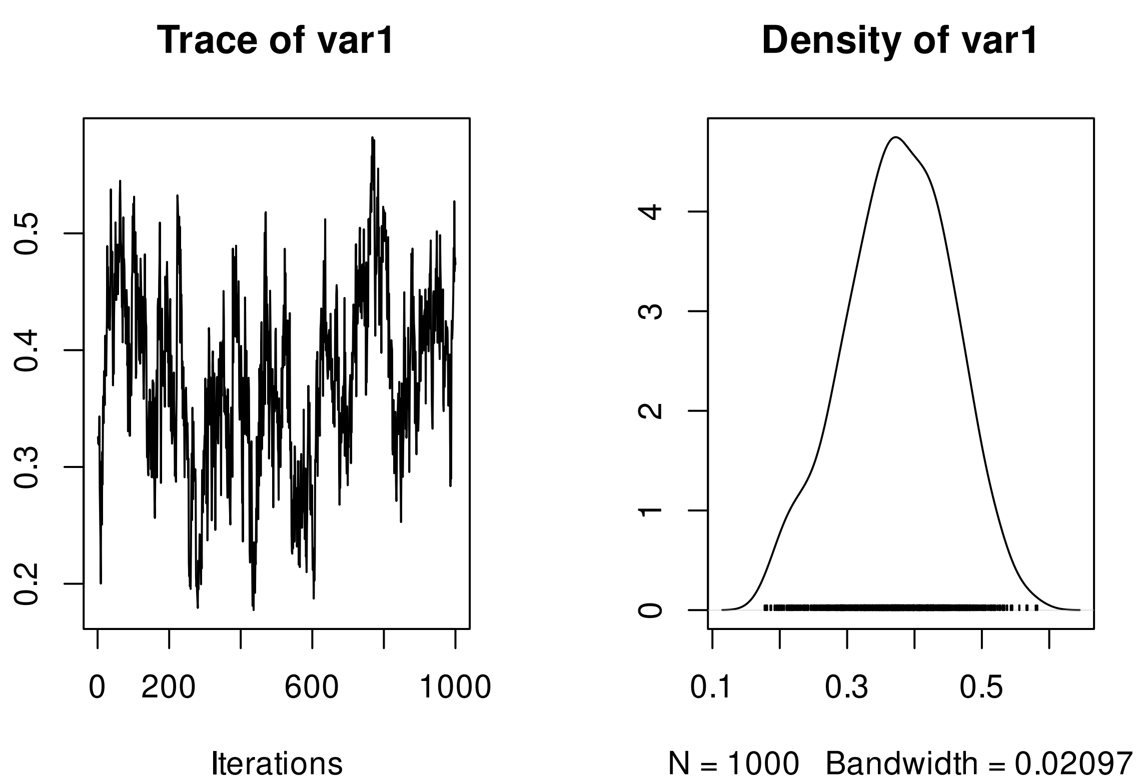
```
##
## Iterations = 1:1000
## Thinning interval = 1
## Number of chains = 1
## Sample size per chain = 1000
##
## 1. Empirical mean and standard deviation for each variable,
##    plus standard error of the mean:
##
##           Mean             SD       Naive SE Time-series SE
##       0.484221       0.074533       0.002357       0.009275
##
## 2. Quantiles for each variable:
##
##   2.5%    25%    50%    75%  97.5%
## 0.3433 0.4338 0.4841 0.5350 0.6369
```

```
# or
Var.table <- as_draws_df(brms_m1.3)
Var.table$h.bwt.3 <- as.mcmc((Var.table$sd_animal__Intercept)^2 / ((Var.table$sd_animal__I
```

```
summary(Var.table$h.bwt.3)
```

```
##
## Iterations = 1:1000
## Thinning interval = 1
## Number of chains = 1
## Sample size per chain = 1000
##
## 1. Empirical mean and standard deviation for each variable,
##    plus standard error of the mean:
##
##           Mean             SD       Naive SE Time-series SE
##       0.375509       0.078767       0.002491       0.012711
##
## 2. Quantiles for each variable:
##
##   2.5%    25%    50%    75%  97.5%
## 0.2140 0.3240 0.3764 0.4322 0.5182
```

```
plot(Var.table$h.bwt.3)
```



2.5.4 Testing significance of variance components

While testing the significance of fixed effects by evaluating whether or not their posterior distributions overlap zero was simple and valid, this approach does not work for variance components. Variance components are bounded to be positive (given a proper prior), and thus even when a random effect is not meaningful, its posterior distribution will never overlap zero.

Model comparisons can be performed using the function `loo_compare` using `waic` or weighted AIC.

```
brms_m1.3 <- add_criterion(brms_m1.3, "waic")
```

```
## Warning:
## 311 (36.4%) p_waic estimates greater than 0.4. We recommend trying loo instead.
```

```
brms_m1.1 <- add_criterion(brms_m1.1, "waic")
```

```
## Warning:
## 236 (27.6%) p_waic estimates greater than 0.4. We recommend trying loo instead.
```

```
loo_compare(brms_m1.3, brms_m1.1, criterion = "waic")
```

```
##           elpd_diff se_diff
## brms_m1.3    0.0       0.0
## brms_m1.1 -282.7      14.0
```

2.5.5 Further partitioning of the variance

Depending of the research question and the presence of different group within the dataset, `brms` allowed to partition the variance at different groups. Two distinct approch can be done to partition the different random effect: using an extra argument `by=sex` or by adding `(0+sex|)` before the `|`. Notes, here we used `||` which not estimate a possible covariance between groups (female and male) for the random effect.

```
brms_m1.4 <- brm(
  #  bwt ~ 1 +  sex + (1 | gr(animal, cov = Amat, by = sex))+ (1 | gr(byear, by = sex)) +
  bwt ~ 1 + sex + (0 + sex || gr(animal, cov = Amat)) + (0 + sex || byear) + (0 + sex || m
  data = gryphon,
  data2 = list(Amat = Amat),
  family = gaussian(),
  chains = 2, cores = 2, iter = 1000
)

save(brms_m1.4, file = "data/brms_m1_4.rda")
```

To save time, the results of the calculation is stored in the spare file `brms_m1_4.rda"`.

```
load("data/brms_m1_4.rda")
summary(brms_m1.4)
```

```
## Warning: Parts of the model have not converged (some Rhats are > 1.05). Be
## careful when analysing the results! We recommend running more iterations and/or
## setting stronger priors.

##  Family: gaussian
##   Links: mu = identity; sigma = identity
## Formula: bwt ~ 1 + sex + (0 + sex || gr(animal, cov = Amat)) + (0 + sex || byear) + (0 +
##    Data: gryphon (Number of observations: 854)
##   Draws: 2 chains, each with iter = 1000; warmup = 500; thin = 1;
##          total post-warmup draws = 1000
##
## Group-Level Effects:
## ~animal (Number of levels: 854)
##          Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## sd(sex1)     1.39      0.22     0.88     1.77 1.02       56      116
## sd(sex2)     1.06      0.31     0.35     1.57 1.06       29       63
##
## ~byear (Number of levels: 34)
##          Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## sd(sex1)     0.91      0.18     0.61     1.29 1.02      381      542
## sd(sex2)     1.09      0.20     0.77     1.56 1.01      310      626
##
## ~mother (Number of levels: 394)
##          Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## sd(sex1)     0.90      0.21     0.47     1.29 1.01      143      219
## sd(sex2)     1.34      0.16     1.00     1.65 1.01      143      396
##
## Population-Level Effects:
##           Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## Intercept     6.29      0.24     5.85     6.78 1.01      435      444
## sex2          2.03      0.35     1.31     2.69 1.00      568      679
##
## Family Specific Parameters:
##       Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## sigma     1.45      0.16     1.09     1.72 1.05       27       35
##
## Draws were sampled using sampling(NUTS). For each parameter, Bulk_ESS
## and Tail_ESS are effective sample size measures, and Rhat is the potential
## scale reduction factor on split chains (at convergence, Rhat = 1).
```

We can see the model estimate variance for both sexes. However, the residual level or sigma is not splitted by sexes. A futher and more complex code need to be performed, thus we can estimate the sex-specific heritability.

```
bf_m1.5 <- bf(
  bwt ~ 1 + sex + (0 + sex || gr(animal, cov = Amat)) + (0 + sex || mother) + (0 + sex ||
  sigma ~ sex - 1
)

brms_m1.5 <- brm(bf_m1.5,
  data = gryphon,
  data2 = list(Amat = Amat),
  family = gaussian(),
  chains = 1, cores = 1, iter = 1000
)

save(brms_m1.5, file = "data/brms_m1_5.rda")
```

To save time, the results of the calculation is stored in the spare file `brms_m1_4.rda`".

```
load("data/brms_m1_5.rda")
summary(brms_m1.5)
```

```
## Warning: Parts of the model have not converged (some Rhats are > 1.05). Be
## careful when analysing the results! We recommend running more iterations and/or
## setting stronger priors.

##  Family: gaussian
##   Links: mu = identity; sigma = log
## Formula: bwt ~ 1 + sex + (0 + sex || gr(animal, cov = Amat)) + (0 + sex || mother) + (0
##          sigma ~ sex - 1
##    Data: gryphon (Number of observations: 854)
##   Draws: 1 chains, each with iter = 1000; warmup = 500; thin = 1;
##          total post-warmup draws = 500
##
## Group-Level Effects:
## ~animal (Number of levels: 854)
##          Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## sd(sex1)     1.56      0.29     1.02     2.09 1.17        4       30
## sd(sex2)     1.61      0.41     0.52     2.08 1.36        2       21
##
## ~byear (Number of levels: 34)
##          Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## sd(sex1)     0.91      0.18     0.59     1.36 1.01      153      229
## sd(sex2)     1.06      0.20     0.75     1.49 1.00      170      143
##
## ~mother (Number of levels: 394)
##          Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## sd(sex1)     0.88      0.21     0.41     1.25 1.01       73      134
## sd(sex2)     1.27      0.18     0.88     1.59 1.01       31       64
```

```
##
## Population-Level Effects:
##            Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## Intercept      6.29      0.23     5.88     6.75 1.00      209      313
## sex2           2.02      0.31     1.49     2.66 1.00      127      296
## sigma_sex1     0.22      0.21    -0.25     0.54 1.15        5       12
## sigma_sex2    -0.20      0.40    -0.82     0.54 1.59        2       15
##
## Draws were sampled using sampling(NUTS). For each parameter, Bulk_ESS
## and Tail_ESS are effective sample size measures, and Rhat is the potential
## scale reduction factor on split chains (at convergence, Rhat = 1).
```

```
#
Var.table <- as_draws_df(brms_m1.5)
Var.table$h.bwt.f <- as.mcmc((Var.table$sd_animal__sex1)^2 / ((Var.table$sd_animal__sex1)^
Var.table$h.bwt.m <- as.mcmc((Var.table$sd_animal__sex2)^2 / ((Var.table$sd_animal__sex2)^
summary(Var.table$h.bwt.f)
```

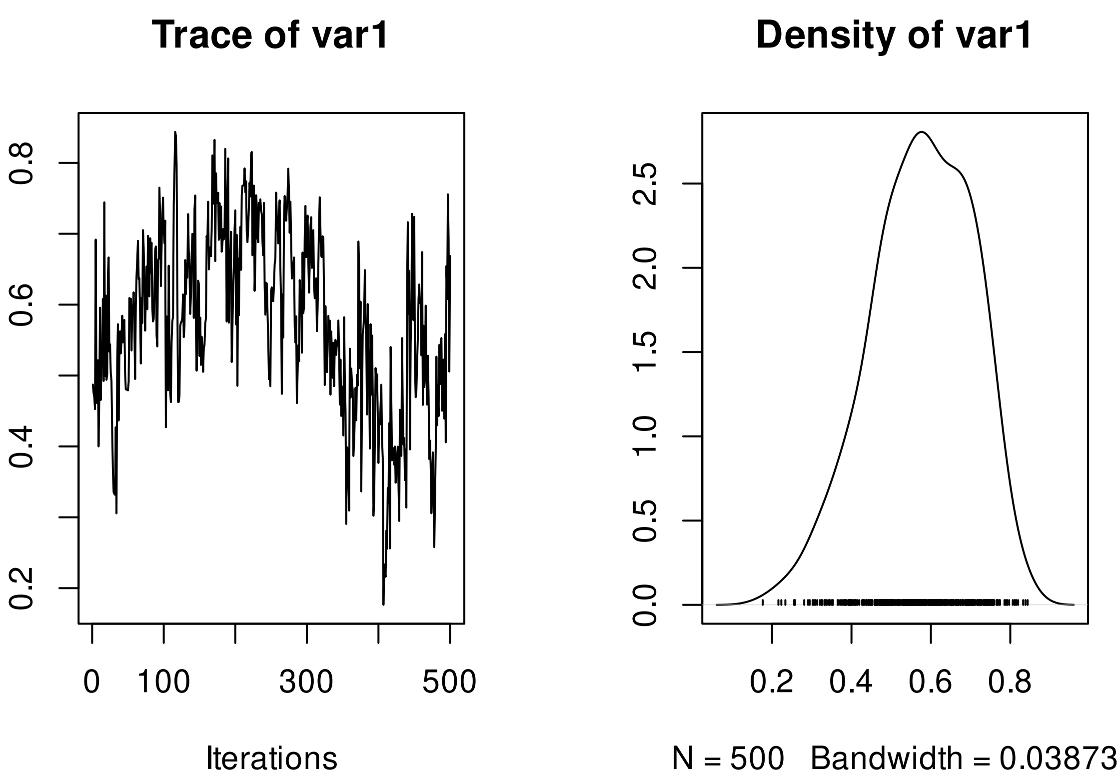
```
##
## Iterations = 1:500
## Thinning interval = 1
## Number of chains = 1
## Sample size per chain = 500
##
## 1. Empirical mean and standard deviation for each variable,
##    plus standard error of the mean:
##
##           Mean             SD       Naive SE Time-series SE
##       0.575443       0.126621       0.005663       0.031251
##
## 2. Quantiles for each variable:
##
##   2.5%    25%    50%    75%  97.5%
## 0.3075 0.4863 0.5811 0.6741 0.7800
```

```
summary(Var.table$h.bwt.m)
```

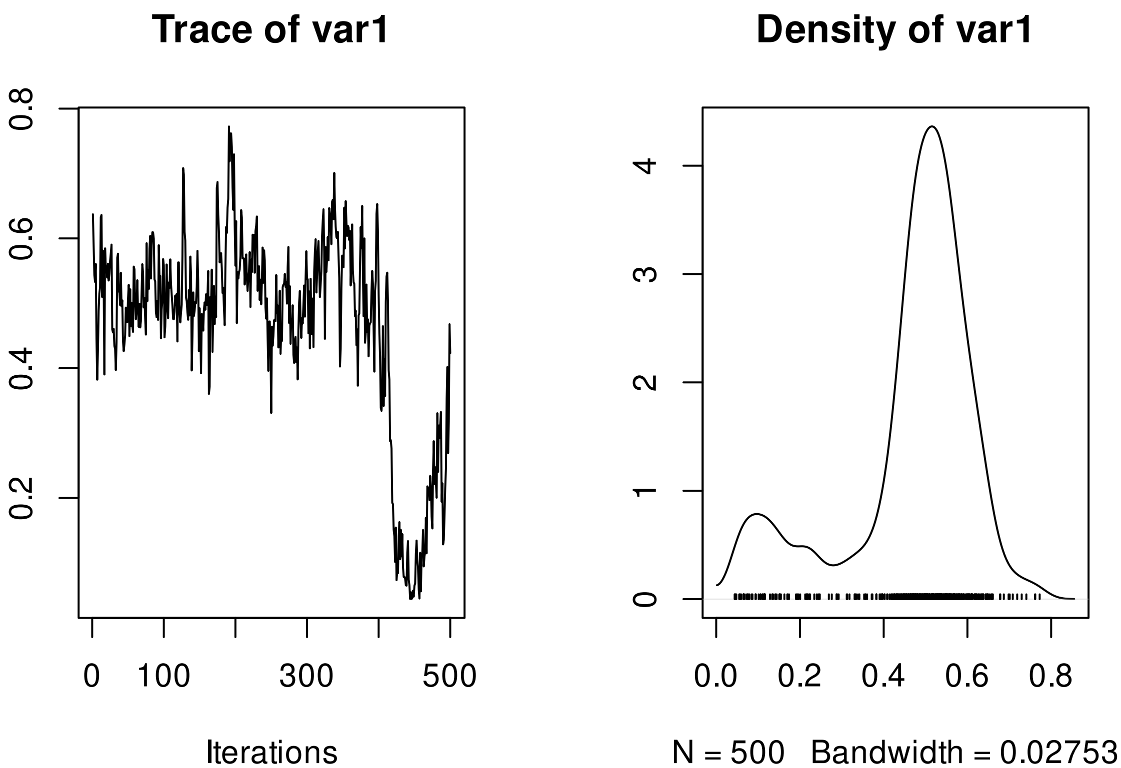
```
##
## Iterations = 1:500
## Thinning interval = 1
## Number of chains = 1
## Sample size per chain = 500
##
## 1. Empirical mean and standard deviation for each variable,
##    plus standard error of the mean:
##
```

```
##           Mean             SD       Naive SE Time-series SE
##       0.463879       0.155395       0.006949       0.078323
##
## 2. Quantiles for each variable:
##
##    2.5%     25%     50%     75%   97.5%
## 0.06693 0.43668 0.50150 0.55729 0.66016
```

```r
plot(Var.table$h.bwt.f)
```




```r
plot(Var.table$h.bwt.m)
```



Here, we can plot the point estimates of the h^2 which seems to differ between sexes, but their CI overlaps.

```
h2.sex <- rbind(
  cbind(summary(Var.table$h.bwt.f)$statistics[1], summary(Var.table$h.bwt.f)$quantiles[1],
  cbind(summary(Var.table$h.bwt.m)$statistics[1], summary(Var.table$h.bwt.m)$quantiles[1],
)

plot(c(0.95, 1.05) ~ h2.sex[, 1], xlim = c(0, 0.8), ylim = c(0.5, 1.5), , xlab = "", ylab
arrows(y0 = 0.95, x0 = h2.sex[1, 2], y1 = 0.95, x1 = h2.sex[1, 3], code = 3, angle = 90, l
arrows(y0 = 1.05, x0 = h2.sex[2, 2], y1 = 1.05, x1 = h2.sex[2, 3], code = 3, angle = 90, l
mtext("Narrow-sense heritability (±CI)", side = 1, las = 1, adj = 0.4, line = 3, cex = 1.6
axis(2, at = 1, labels = c("birth weight"), las = 3, cex.axis = 1.6)
```

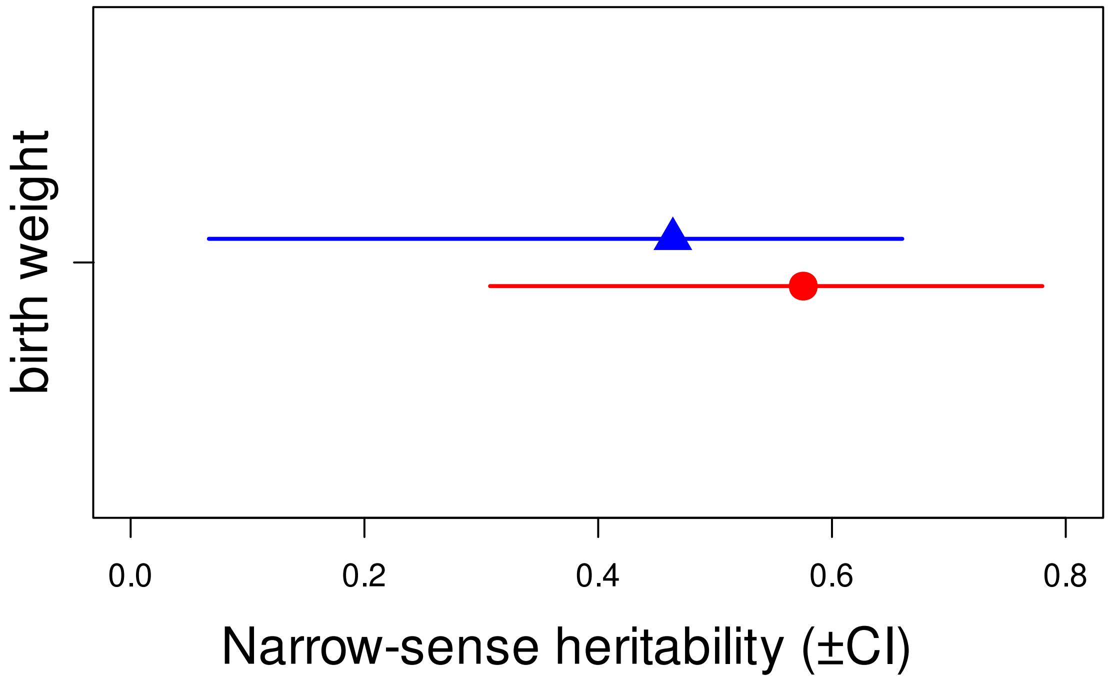


Figure 2.7: Female and male heritability of birth weight

2.5.6 Modification of model parameter

Unfortunately (to our knowledge), it is not possible to alter the variance matrices and refit them within the model.

2.5.7 Covariance between two random effects

Some research questions require to estimate the covariance between two random effects within a univariate model. Unfortunately (to our knowledge), it is not possible to create a covariance between distinct random effects (`https://github.com/paul-buerkner/brms/issues/502`). However,a multi-membership model can be fit using the linking.function `mm`, thus forcing the variance of two variables to be equal and the covariance to 1.

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Chapitre 3

Multivariate animal model

This tutorial will demonstrate how to run a multivariate animal model looking at birth weight and tarsus length of the phenomenal gryphons.

3.1 Scenario and data

3.1.1 Scenario

Since natural selection rarely acts on single traits, to understand how birth weight might evolve in our population of gryphons, we may also want to think about possible covariance with other traits. If tarsus length at fledging is also under positive selection, what implications does it have for birth weight and vice versa? If the two traits are positively genetically correlated then this will facilitate evolution of larger size (since response of one trait will induce a positively correlated response in the other). If there is negative genetic covariance then this could act as an evolutionary constraint.

Using multivariate models allows the estimation of parameters relating to each trait alone (*i.e.* V_A, h^2, etc), but also yields estimates of covariance components between traits. These include the (additive) genetic covariance COV_A which is often rescaled to give the additive genetic correlation r_A. However, covariance can also arise through other random effects (*e.g.* maternal covariance) and these sources can also be explicitly modeled in a bivariate analysis.

3.1.2 gryphon files

gryphonpedigree and phenotypic data files are the same as those used in tutorial 1 (*i.e*, `gryphonped.csv` and `gryphon.csv` respectively).

Reading the data

```
gryphon <- read.csv("data/gryphon.csv")
gryphon$animal <- as.factor(gryphon$animal)
gryphon$mother <- as.factor(gryphon$mother)
gryphon$byear <- as.factor(gryphon$byear)
gryphon$sex <- as.factor(gryphon$sex)
```

```
gryphon$bwt <- as.numeric(gryphon$bwt)
gryphon$tarsus <- as.numeric(gryphon$tarsus)
```

Reading the pedigree

```
gryphonped <- read.csv("data/gryphonped.csv")
gryphonped$id <- as.factor(gryphonped$id)
gryphonped$father <- as.factor(gryphonped$father)
gryphonped$mother <- as.factor(gryphonped$mother)
```

3.2 Asreml-R

3.2.1 Running the model

First we need to load the `asreml` library:

```
library(asreml)
```

For running multivariate analyses in ASReml-R, the code is slightly more complex than for the univariate case. This is because ASReml-R allows us to make different assumptions about the way in which traits might be related. We need to explicitly specify a covariance structure with difference covariance functions `us()`, `idh()` or `corgh()` which for example would estimate an unconstrained (co)variance matrix, an identity matrix and a variance and correlation matrix repestively. We can also specify some starting values for the variance matrices. These can be very approximate *guestimates* or not at all, but having reasonable starting values can help convergence. It is also possible to let the model running without specifying starting values. Finally, we have increased the default maximum number of iterations (`maxiter`) which can help to achieve convergence for more complicated models. Another way to increase the number of iteration will be to use the `update` function. Notes that if the `LogLik` is not stabilized after several iterations, it is good indication of the model require more iteration.

```
ainv <- ainverse(gryphonped)
modela <- asreml(
  fixed = cbind(bwt, tarsus) ~ trait,
  random = ~ us(trait, init = c(1, 0.1, 1)):vm(animal, ainv),
  residual = ~ id(units):us(trait, init = c(1, 0.1, 1)),
  data = gryphon,
  na.action = na.method(x = "include", y = "include"),
  maxit = 20
)
```

```
## Model fitted using the sigma parameterization.
## ASReml 4.1.0 Tue Nov 29 16:54:16 2022
```

```
##          LogLik        Sigma2     DF     wall    cpu
##  1     -7108.741         1.0   1535 16:54:16    0.0
##  2     -5837.803         1.0   1535 16:54:16    0.0
##  3     -4437.495         1.0   1535 16:54:16    0.0
##  4     -3459.378         1.0   1535 16:54:16    0.0
##  5     -2914.034         1.0   1535 16:54:16    0.0
##  6     -2729.131         1.0   1535 16:54:16    0.0
##  7     -2684.659         1.0   1535 16:54:16    0.0
##  8     -2679.838         1.0   1535 16:54:16    0.0
##  9     -2679.742         1.0   1535 16:54:16    0.0
## 10     -2679.741         1.0   1535 16:54:16    0.0
```

```
modela <- update(modela)
```

```
## Model fitted using the sigma parameterization.
## ASReml 4.1.0 Tue Nov 29 16:54:16 2022
##          LogLik        Sigma2     DF     wall    cpu
##  1     -2679.741         1.0   1535 16:54:16    0.0
##  2     -2679.741         1.0   1535 16:54:16    0.0
```

`modela` has fitted a bivariate model of `bwt` and `tarsus`, with the mean for each of the traits as a fixed effect (`trait`). The additive genetic variance-covariance matrix (**G**) is unstructured (`us`; *i.e.* all elements are free to vary) and the starting values for V_A for `bwt`, COV_A between `bwt` and `tarsus`, and V_A for `tarsus` are set to 1, 0.1 and 1, respectively. Similarly, the residual matrix is unstructured and uses the same starting values.

Note that the argument `na.action = na.method(x = "include", y = "include")` can be added to the model. In a bivariate model, it will help calculate the covariance between two traits with different missing information `NA` and so help imbalance phenotypage and save sample size. However, it is important to scale (mean =0, var =1) the two traits to correctly adjust the model(see Asreml-R manual for more information).

Let's have a look at the variance components, and notice that there are now seven (co)variance components reported in the table:

```
summary(modela)$varcomp
```

```
##                                               component std.error  z.ratio bound
## trait:vm(animal, ainv)!trait_bwt:bwt           3.368397 0.6348307 5.305977     P
## trait:vm(animal, ainv)!trait_tarsus:bwt        2.459809 1.0732644 2.291895     P
## trait:vm(animal, ainv)!trait_tarsus:tarsus 12.345792 3.0744285 4.015638     P
## units:trait!R                                  1.000000        NA       NA     F
## units:trait!trait_bwt:bwt                      3.849916 0.5200101 7.403541     P
## units:trait!trait_tarsus:bwt                   3.313282 0.9129234 3.629310     P
## units:trait!trait_tarsus:tarsus               17.646432 2.6670380 6.616491     P
##                                               %ch
## trait:vm(animal, ainv)!trait_bwt:bwt            0
```

```
## trait:vm(animal, ainv)!trait_tarsus:bwt      0
## trait:vm(animal, ainv)!trait_tarsus:tarsus   0
## units:trait!R                                0
## units:trait!trait_bwt:bwt                    0
## units:trait!trait_tarsus:bwt                 0
## units:trait!trait_tarsus:tarsus              0
```

The first three terms are related to the genetic matrix and, in order are $V_{A,bwt}$, COV_A, $V_{A,tarsus}$. Below is again a line where the `units:traitr!R` component equals to 1, which again can be ignored. The final three terms relate to the residual matrix and correspond to $V_{R,bwt}$, COV_R, $V_{R,tarsus}$. Based on our quick and dirty check (is `z.ratio` > 1.96?) all components look to be statistically significant.

We can calculate the genetic correlation as $COV_A/\sqrt{V_{A,bwt} \cdot V_{A,tarsus}}$. Thus this model gives an estimate of $r_A = 0.38$. It is also possible to estimate the residual correlation $r_{res} = 0.4$.

Both correlations are distinct in nature. The genetic correlation reflects how much the traits are linked by genetic via polygenic effect or linkage desequilibrium, whereas the residual correlation reflects the environmental correlation or errors measurement correlation.

Although we can calculate this by hand, we can also use `vpredict()`, which also provides an (approximate) standard error:

```r
vpredict(modela, r_A ~ V2 / sqrt(V1 * V3))
```

```
##      Estimate        SE
## r_A 0.3814436 0.1299759
```

```r
vpredict(modela, r_res ~ V6 / sqrt(V5 * V7))
```

```
##        Estimate         SE
## r_res 0.4019799 0.08607104
```

Of course we can also calculate the heritability of `bwt` and `tarsus` from this model:

```r
vpredict(modela, h2.bwt ~ V1 / (V1 + V5))
```

```
##        Estimate         SE
## h2.bwt 0.466646 0.07671533
```

```r
vpredict(modela, h2.tarsus ~ V3 / (V3 + V7))
```

```
##            Estimate         SE
## h2.tarsus 0.4116331 0.09305863
```

3.2.2 Adding fixed and random effects

Fixed and random effects can be added just as for the univariate case. Given that our full model of bwt from tutorial 1 had sex as a fixed effect as well as birth year and mother as random effects, we could specify a bivariate formulation with the same complexity:

```
modelb <- asreml(
  fixed = cbind(bwt, tarsus) ~ trait + at(trait):sex,
  random = ~ us(trait, init = c(1, 0.1, 1)):vm(animal, ainv) +
    us(trait, init = c(1, 0.1, 1)):byear +
    us(trait, init = c(1, 0.1, 1)):mother,
  residual = ~ id(units):us(trait, init = c(1, 0.1, 1)),
  data = gryphon,
  na.action = na.method(x = "include", y = "include"),
  maxit = 20
)
```

```
## Model fitted using the sigma parameterization.
## ASReml 4.1.0 Tue Nov 29 16:54:16 2022
##           LogLik        Sigma2     DF     wall    cpu
##  1     -4672.301           1.0   1533 16:54:16    0.0
##  2     -4005.615           1.0   1533 16:54:16    0.0
##  3     -3271.483           1.0   1533 16:54:16    0.0 (1 restrained)
##  4     -2761.414           1.0   1533 16:54:16    0.0 (1 restrained)
##  5     -2481.357           1.0   1533 16:54:17    0.0
##  6     -2395.858           1.0   1533 16:54:17    0.0
##  7     -2381.050           1.0   1533 16:54:17    0.0
##  8     -2380.251           1.0   1533 16:54:17    0.0
##  9     -2380.246           1.0   1533 16:54:17    0.0
```

```
modelb <- update(modelb)
```

```
## Model fitted using the sigma parameterization.
## ASReml 4.1.0 Tue Nov 29 16:54:17 2022
##           LogLik        Sigma2     DF     wall    cpu
##  1     -2380.246           1.0   1533 16:54:17    0.0
##  2     -2380.246           1.0   1533 16:54:17    0.0
```

Note that we have specified a covariance structure for each random effect and an estimate of the effect of sex on both birth weight and tarsus length.

There will now be thirteen (co)variance components reported after running the code:

```
summary(modelb)$varcomp
```

```
##                                          component std.error    z.ratio
## trait:byear!trait_bwt:bwt                0.9746385 0.2825727  3.4491602
```

```
## trait:byear!trait_tarsus:bwt                  0.1624076 0.4185079  0.3880635
## trait:byear!trait_tarsus:tarsus               3.7383721 1.2065992  3.0982716
## trait:mother!trait_bwt:bwt                    1.1445184 0.2302182  4.9714512
## trait:mother!trait_tarsus:bwt                -1.5567306 0.4051848 -3.8420260
## trait:mother!trait_tarsus:tarsus              4.8206132 1.3201300  3.6516202
## trait:vm(animal, ainv)!trait_bwt:bwt          1.9893546 0.4410246  4.5107569
## trait:vm(animal, ainv)!trait_tarsus:bwt       3.3170404 0.9032323  3.6724110
## trait:vm(animal, ainv)!trait_tarsus:tarsus 10.2294887 2.8077066  3.6433610
## units:trait!R                                 1.0000000        NA         NA
## units:trait!trait_bwt:bwt                     1.8443110 0.3443178  5.3564203
## units:trait!trait_tarsus:bwt                  4.0142841 0.7412540  5.4155308
## units:trait!trait_tarsus:tarsus              12.4845955 2.2893363  5.4533690
##                                              bound %ch
## trait:byear!trait_bwt:bwt                        P   0
## trait:byear!trait_tarsus:bwt                     P   0
## trait:byear!trait_tarsus:tarsus                  P   0
## trait:mother!trait_bwt:bwt                       P   0
## trait:mother!trait_tarsus:bwt                    P   0
## trait:mother!trait_tarsus:tarsus                 P   0
## trait:vm(animal, ainv)!trait_bwt:bwt             P   0
## trait:vm(animal, ainv)!trait_tarsus:bwt          P   0
## trait:vm(animal, ainv)!trait_tarsus:tarsus       P   0
## units:trait!R                                    F   0
## units:trait!trait_bwt:bwt                        P   0
## units:trait!trait_tarsus:bwt                     P   0
## units:trait!trait_tarsus:tarsus                  P   0
```

we can estimate the different correlations using `vpredict`:

```r
vpredict(modelb, r_byear ~ V2 / sqrt(V1 * V3))
```

```
##           Estimate        SE
## r_byear 0.08508312 0.2134209
```

```r
vpredict(modelb, r_M ~ V5 / sqrt(V4 * V6))
```

```
##       Estimate        SE
## r_M -0.6627518 0.2487963
```

```r
vpredict(modelb, r_A ~ V8 / sqrt(V7 * V9))
```

```
##      Estimate        SE
## r_A 0.7353053 0.1094747
```

```
vpredict(modelb, r_res ~ V12 / sqrt(V11 * V13))
```

```
##        Estimate         SE
## r_res 0.8365729 0.07366762
```

Now we can look at the fixed effects parameters and assess their significance with a conditional Wald F-test:

```
summary(modelb, coef = TRUE)$coef.fi
wald.asreml(modelb, denDF = "default", ssType = "conditional")$Wald
```

```
##                              solution std error    z.ratio
## at(trait, tarsus):sex_1  0.0000000        NA         NA
## at(trait, tarsus):sex_2 -0.0684413 0.3823448 -0.1790041
## at(trait, bwt):sex_1     0.0000000        NA         NA
## at(trait, bwt):sex_2     1.9502053 0.1480467 13.1729086
## trait_bwt                6.3844483 0.2328210 27.4221324
## trait_tarsus            20.5936436 0.5098944 40.3880569
```

```
## Model fitted using the sigma parameterization.
## ASReml 4.1.0 Tue Nov 29 16:54:17 2022
##          LogLik        Sigma2     DF     wall    cpu
##  1     -2380.246          1.0   1533 16:54:17    0.0
##  2     -2380.246          1.0   1533 16:54:17    0.0
## Calculating denominator DF
```

```
##
##                         Df denDF   F.inc   F.con Margin      Pr
## trait                    2  52.6 1396.00 1396.00        0.00000
## at(trait, bwt):sex       1 812.8  298.40  173.50      B 0.00000
## at(trait, tarsus):sex    1 747.9    0.03    0.03      B 0.85798
```

Note that it is possible to specify a fixed effect to a specific trait by adding the number of order within `cbind` inside the argument `at(trait,x)`. For example, here we apply the fixed effect `sex` only to the response variable `tarsus`.

```
modelb_2 <- asreml(
  fixed = cbind(bwt, tarsus) ~ trait + at(trait, 2):sex,
  random = ~ us(trait, init = c(1, 0.1, 1)):vm(animal, ainv) +
    us(trait, init = c(1, 0.1, 1)):byear +
    us(trait, init = c(1, 0.1, 1)):mother,
  residual = ~ id(units):us(trait, init = c(1, 0.1, 1)),
  data = gryphon,
  na.action = na.method(x = "include", y = "include"),
  maxit = 20
)
```

```
## Model fitted using the sigma parameterization.
## ASReml 4.1.0 Tue Nov 29 16:54:17 2022
##          LogLik        Sigma2     DF     wall    cpu
##  1     -4810.563          1.0   1534 16:54:18    0.1
##  2     -4129.799          1.0   1534 16:54:18    0.0
##  3     -3382.529          1.0   1534 16:54:18    0.0 (1 restrained)
##  4     -2864.076          1.0   1534 16:54:18    0.0
##  5     -2574.891          1.0   1534 16:54:18    0.0
##  6     -2478.879          1.0   1534 16:54:18    0.0
##  7     -2458.305          1.0   1534 16:54:18    0.0
##  8     -2456.425          1.0   1534 16:54:18    0.0
##  9     -2456.377          1.0   1534 16:54:18    0.0
## 10     -2456.376          1.0   1534 16:54:18    0.0
```

```
summary(modelb_2, coef = TRUE)$coef.fi
wald.asreml(modelb_2, denDF = "default", ssType = "conditional")$Wald
```

```
##                          solution std error   z.ratio
## at(trait, tarsus):sex_1  0.000000        NA        NA
## at(trait, tarsus):sex_2 -3.267042 0.2953279 -11.06242
## trait_bwt                7.636226 0.2389515  31.95722
## trait_tarsus            22.703658 0.4827348  47.03133
```

```
## Model fitted using the sigma parameterization.
## ASReml 4.1.0 Tue Nov 29 16:54:18 2022
##          LogLik        Sigma2     DF     wall    cpu
##  1     -2456.376          1.0   1534 16:54:18    0.0
##  2     -2456.376          1.0   1534 16:54:18    0.0
## Calculating denominator DF
```

```
##
##                         Df denDF  F.inc  F.con Margin          Pr
## trait                    2  50.7 1233.0 1233.0        0.00000e+00
## at(trait, tarsus):sex    1 522.9  122.4  122.4      B 1.02886e-25
```

3.2.3 Significance testing

Under the model above r_M is estimated as -0.66 and the `z.ratio` associated with the corresponding covariance (COV_M) is >2 (in absolute terms). We might therefore infer that there is evidence for a strong negative correlation between the traits with respect to the mother and that while maternal identity explains variance in both traits those mothers that tend to produce heavier offspring actually tend to produce offspring with shorter tarsus lengths.

To formally test if COV_M is significantly different from zero, we can compare the log-likelihood for this model:

```
modelb$loglik
```

```
## [1] -2380.246
```

to a model in which we specify that COV_M=0. Since this constraint reduces the number of parameters to be estimated by one, we can use a likelihood ratio test (LRT) with one degree of freedom. To run the constrained model, we modify the G structure defined for the `mother` random effect to diagonal (`diag`), which means we only estimate the variances (the diagonal of the matrix) but not the covariance (the covariance are fixed to 0):

```
modelc <- asreml(
  fixed = cbind(bwt, tarsus) ~ trait + at(trait):sex,
  random = ~ us(trait, init = c(1, 0.1, 1)):vm(animal, ainv) +
    us(trait, init = c(1, 0.1, 1)):byear +
    diag(trait, init = c(1, 1)):mother,
  residual = ~ id(units):us(trait, init = c(1, 0.1, 1)),
  data = gryphon,
  na.action = na.method(x = "include", y = "include"),
  maxit = 20
)
```

```
## Model fitted using the sigma parameterization.
## ASReml 4.1.0 Tue Nov 29 16:54:19 2022
##           LogLik        Sigma2     DF     wall    cpu
##  1     -4677.820           1.0   1533 16:54:19    0.0
##  2     -4010.442           1.0   1533 16:54:19    0.0
##  3     -3275.409           1.0   1533 16:54:19    0.0
##  4     -2763.519           1.0   1533 16:54:19    0.0
##  5     -2483.732           1.0   1533 16:54:19    0.0
##  6     -2400.242           1.0   1533 16:54:19    0.0
##  7     -2386.663           1.0   1533 16:54:19    0.0
##  8     -2386.049           1.0   1533 16:54:19    0.0
##  9     -2386.045           1.0   1533 16:54:19    0.0
```

You can run `summary(modelc)$varcomp` to confirm this worked. We can now obtain the log-likelihood of this model and compare this to that of `modelb` using a likelihood ratio test:

```
modelc$loglik
```

```
## [1] -2386.045
```

We can see that the model log-likelihood is now -2386.05. And comparing the models using a likelihood ratio test:

```
2 * (modelb$loglik - modelc$loglik)
```

```
## [1] 11.59835
```

So our chi-square test statistic is χ^2_1= 11.6. The p-value that goes with this is obtained by:

```
1 - pchisq(2 * (modelb$loglik - modelc$loglik), 1)
```

```
## [1] 0.0006601037
```

We would therefore conclude that the maternal covariance is significantly different from zero.

We could apply the same procedure to show that the residual (environmental) covariance and the genetic covariance estimates are significantly greater than zero (*i.e.*, heavier individuals tend to have longer tarsus lengths). In contrast, we should find that the byear covariance between the two traits is non-significant.

```
modeld <- asreml(
  fixed = cbind(bwt, tarsus) ~ trait + at(trait):sex,
  random = ~ us(trait, init = c(1, 0.1, 1)):vm(animal, ainv) +
    diag(trait, init = c(1, 1)):byear +
    us(trait, init = c(1, 0.1, 1)):mother,
  residual = ~ id(units):us(trait, init = c(1, 0.1, 1)),
  data = gryphon,
  na.action = na.method(x = "include", y = "include"),
  maxit = 20
)
```

```
## Model fitted using the sigma parameterization.
## ASReml 4.1.0 Tue Nov 29 16:54:19 2022
##           LogLik        Sigma2     DF     wall    cpu
##  1      -4672.708          1.0   1533 16:54:19    0.1
##  2      -4005.953          1.0   1533 16:54:19    0.0
##  3      -3271.737          1.0   1533 16:54:19    0.0 (1 restrained)
##  4      -2761.626          1.0   1533 16:54:19    0.0 (1 restrained)
##  5      -2481.649          1.0   1533 16:54:19    0.0
##  6      -2395.992          1.0   1533 16:54:19    0.0
##  7      -2381.136          1.0   1533 16:54:19    0.0
##  8      -2380.331          1.0   1533 16:54:19    0.0
##  9      -2380.326          1.0   1533 16:54:19    0.0
```

```
2 * (modelb$loglik - modeld$loglik)
```

```
## [1] 0.1600641
```

```
1 - pchisq(2 * (modelb$loglik - modeld$loglik), 1)
```

```
## [1] 0.6890975
```

3.2.4 Estimate directly the genetic correlation within the model

Within Asreml-r, different matrix structure can be specify such as `us`,`corg`, `diag`, etc (cf see the Asreml-r guide). Instead of the fitting an unstructured matrix with the argument `us` or a reduced model with no covariance with the argument `diag`, we can also directly estimate the genetic correlation between the `bwt` and `tarsus` with `corgh`.

Here we decide to estimate directly the additive genetic correlation.

```
modele <- asreml(
  fixed = cbind(bwt, tarsus) ~ trait + at(trait):sex,
  random = ~ corgh(trait, init = c(0.1, 1, 1)):vm(animal, ainv) +
    us(trait, init = c(1, 0.1, 1)):byear +
    us(trait, init = c(1, 0.1, 1)):mother,
  residual = ~ id(units):us(trait, init = c(1, 0.1, 1)),
  data = gryphon,
  na.action = na.method(x = "include", y = "include"),
  maxit = 20
)
```

```
## Model fitted using the sigma parameterization.
## ASReml 4.1.0 Tue Nov 29 16:54:20 2022
##          LogLik        Sigma2     DF     wall    cpu
##  1     -4672.301          1.0   1533 16:54:20    0.1
##  2     -4003.183          1.0   1533 16:54:20    0.0
##  3     -3266.521          1.0   1533 16:54:20    0.0 (1 restrained)
##  4     -2757.188          1.0   1533 16:54:20    0.0 (1 restrained)
##  5     -2479.293          1.0   1533 16:54:20    0.0
##  6     -2395.477          1.0   1533 16:54:20    0.0
##  7     -2381.026          1.0   1533 16:54:20    0.0
##  8     -2380.251          1.0   1533 16:54:20    0.0
##  9     -2380.246          1.0   1533 16:54:20    0.0
```

```
modele <- update(modele)
```

```
## Model fitted using the sigma parameterization.
## ASReml 4.1.0 Tue Nov 29 16:54:20 2022
##          LogLik        Sigma2     DF     wall    cpu
##  1     -2380.246          1.0   1533 16:54:20    0.0
##  2     -2380.246          1.0   1533 16:54:20    0.0
```

```
summary(modele)$varcomp
```

```
##                                                      component std.error
## trait:byear!trait_bwt:bwt                            0.9746386 0.2825728
## trait:byear!trait_tarsus:bwt                         0.1624071 0.4185082
```

```
## trait:byear!trait_tarsus:tarsus                      3.7383734 1.2066018
## trait:mother!trait_bwt:bwt                           1.1445186 0.2302183
## trait:mother!trait_tarsus:bwt                       -1.5567316 0.4051850
## trait:mother!trait_tarsus:tarsus                     4.8206154 1.3201324
## trait:vm(animal, ainv)!trait!tarsus:!trait!bwt.cor  0.7353061 0.1094807
## trait:vm(animal, ainv)!trait_bwt                     1.9893543 0.4410243
## trait:vm(animal, ainv)!trait_tarsus                 10.2294850 2.8077055
## units:trait!R                                        1.0000000        NA
## units:trait!trait_bwt:bwt                            1.8443112 0.3443178
## units:trait!trait_tarsus:bwt                         4.0142825 0.7412540
## units:trait!trait_tarsus:tarsus                     12.4845977 2.2893355
##                                                      z.ratio bound %ch
## trait:byear!trait_bwt:bwt                            3.449159     P   0
## trait:byear!trait_tarsus:bwt                         0.388062     P   0
## trait:byear!trait_tarsus:tarsus                      3.098266     P   0
## trait:mother!trait_bwt:bwt                           4.971450     P   0
## trait:mother!trait_tarsus:bwt                       -3.842027     P   0
## trait:mother!trait_tarsus:tarsus                     3.651615     P   0
## trait:vm(animal, ainv)!trait!tarsus:!trait!bwt.cor  6.716310     U   0
## trait:vm(animal, ainv)!trait_bwt                     4.510758     P   0
## trait:vm(animal, ainv)!trait_tarsus                  3.643361     P   0
## units:trait!R                                              NA     F   0
## units:trait!trait_bwt:bwt                            5.356422     P   0
## units:trait!trait_tarsus:bwt                         5.415529     P   0
## units:trait!trait_tarsus:tarsus                      5.453372     P   0
```

It is important to note that using `corgh` change the order of the estimate (co)variance/correlation. Thus, the initial values need to be reorder and all different calculation need to be adjust in consequence. It is also important to check the difference between the model with `us` and `corgh` to make sure any mistake are made.

```r
summary(modelb)$loglik
```

```
## [1] -2380.246
```

```r
summary(modele)$loglik
```

```
## [1] -2380.246
```

There two main advantages to use `corgh`: first, a direct estimation of correlation within the G matrix can avoid mistake in the `vpredict` calculation; second, it is possible to test if the correlation is significantly different than 0 (similar result as LRT with the covariance) but also to -1 and 1 which correspond of the correlation boundaries. The following code showed how to create a reduced model with the correlation close to 1 and compared to the initial model. Since we compared the correlation to its boundary, the degree of freedom is only half as a one tail LTR.

```r
MODEL_MODIF <- update.asreml(modele, start.values = T)
G_MOD <- MODEL_MODIF$vparameters.table[(1:9), ]
G_MOD[1, 2] <- 0.99999
G_MOD[1, 3] <- "F"
modele.red <- asreml(
  fixed = cbind(bwt, tarsus) ~ trait + at(trait):sex,
  random = ~ corgh(trait, init = c(0.1, 1, 1)):vm(animal, ainv) +
    us(trait, init = c(1, 0.1, 1)):byear +
    us(trait, init = c(1, 0.1, 1)):mother,
  residual = ~ id(units):us(trait, init = c(1, 0.1, 1)),
  data = gryphon,
  na.action = na.method(x = "include", y = "include"),
  maxit = 20,
  G.param = G_MOD
)
```

```
## Model fitted using the sigma parameterization.
## ASReml 4.1.0 Tue Nov 29 16:54:20 2022
##           LogLik        Sigma2     DF     wall    cpu
##  1     -2545.233           1.0   1533 16:54:20    0.0
##  2     -2483.883           1.0   1533 16:54:20    0.0
##  3     -2423.504           1.0   1533 16:54:21    0.0
##  4     -2392.509           1.0   1533 16:54:21    0.0
##  5     -2383.661           1.0   1533 16:54:21    0.0
##  6     -2383.084           1.0   1533 16:54:21    0.0
##  7     -2383.033           1.0   1533 16:54:21    0.0
##  8     -2383.022           1.0   1533 16:54:21    0.0
##  9     -2383.019           1.0   1533 16:54:21    0.1
## 10     -2383.019           1.0   1533 16:54:21    0.1
```

```r
2 * (modele$loglik - modele.red$loglik)
```

```
## [1] 5.544679
```

```r
1 - pchisq(2 * (modele$loglik - modele.red$loglik), df = 0.5)
```

```
## [1] 0.006598676
```

Here, the correlation is significantly different than 1 (~0.99999).

3.2.5 Visualisation of the correlation (aka BLUP extraction)

When estimating correlation between traits, having a visualization of it can help the interpretation. In addition, visualizing the correlation can spot outliers in the dataset. Thanks to mixed model, each breeding values is stored within the model and can be extract as BLUP (Best Linear Unbiased

Predictor).BLUP should be normaly distributed, if not you need to check the assumption of your animal model.

To simplify the following code, we rename the variable T1 and T2.

```
gryphon$T1 <- gryphon$bwt
gryphon$T2 <- gryphon$tarsus
############
modele <- asreml(
  fixed = cbind(T1, T2) ~ trait + at(trait):sex,
  random = ~ corgh(trait, init = c(0.1, 1, 1)):vm(animal, ainv) +
    us(trait, init = c(1, 0.1, 1)):byear +
    us(trait, init = c(1, 0.1, 1)):mother,
  residual = ~ id(units):us(trait, init = c(1, 0.1, 1)),
  data = gryphon,
  na.action = na.method(x = "include", y = "include"),
  maxit = 20
)
```

```
## Model fitted using the sigma parameterization.
## ASReml 4.1.0 Tue Nov 29 16:54:21 2022
##           LogLik        Sigma2     DF     wall    cpu
##  1     -4672.301           1.0   1533 16:54:21    0.1
##  2     -4003.183           1.0   1533 16:54:21    0.0
##  3     -3266.521           1.0   1533 16:54:21    0.0 (1 restrained)
##  4     -2757.188           1.0   1533 16:54:21    0.0 (1 restrained)
##  5     -2479.293           1.0   1533 16:54:21    0.0
##  6     -2395.477           1.0   1533 16:54:21    0.0
##  7     -2381.026           1.0   1533 16:54:21    0.0
##  8     -2380.251           1.0   1533 16:54:21    0.0
##  9     -2380.246           1.0   1533 16:54:22    0.0
```

```
modele <- update(modele)
```

```
## Model fitted using the sigma parameterization.
## ASReml 4.1.0 Tue Nov 29 16:54:22 2022
##           LogLik        Sigma2     DF     wall    cpu
##  1     -2380.246           1.0   1533 16:54:22    0.0
##  2     -2380.246           1.0   1533 16:54:22    0.0
```

```
summary(modele)$varcomp
```

```
##                                                component std.error   z.ratio
## trait:byear!trait_T1:T1                        0.9746386 0.2825728  3.449159
## trait:byear!trait_T2:T1                        0.1624071 0.4185082  0.388062
## trait:byear!trait_T2:T2                        3.7383734 1.2066018  3.098266
```

```
## trait:mother!trait_T1:T1                    1.1445186 0.2302183  4.971450
## trait:mother!trait_T2:T1                   -1.5567316 0.4051850 -3.842027
## trait:mother!trait_T2:T2                    4.8206154 1.3201324  3.651615
## trait:vm(animal, ainv)!trait!T2:!trait!T1.cor  0.7353061 0.1094807  6.716310
## trait:vm(animal, ainv)!trait_T1             1.9893543 0.4410243  4.510758
## trait:vm(animal, ainv)!trait_T2            10.2294850 2.8077055  3.643361
## units:trait!R                               1.0000000        NA        NA
## units:trait!trait_T1:T1                     1.8443112 0.3443178  5.356422
## units:trait!trait_T2:T1                     4.0142825 0.7412540  5.415529
## units:trait!trait_T2:T2                    12.4845977 2.2893355  5.453372
##                                            bound %ch
## trait:byear!trait_T1:T1                        P   0
## trait:byear!trait_T2:T1                        P   0
## trait:byear!trait_T2:T2                        P   0
## trait:mother!trait_T1:T1                       P   0
## trait:mother!trait_T2:T1                       P   0
## trait:mother!trait_T2:T2                       P   0
## trait:vm(animal, ainv)!trait!T2:!trait!T1.cor     U   0
## trait:vm(animal, ainv)!trait_T1                P   0
## trait:vm(animal, ainv)!trait_T2                P   0
## units:trait!R                                  F   0
## units:trait!trait_T1:T1                        P   0
## units:trait!trait_T2:T1                        P   0
## units:trait!trait_T2:T2                        P   0
```

```
############
DvsS <- data.frame(
  Trait = rownames(modele$coefficients$random),
  BLUP = modele$coefficients$random,
  SE = sqrt(modele$vcoeff$random * modele$sigma2)
)
DvsS$ID <- substr(DvsS$Trait, 27, 30)
DvsS$TRAIT <- substr(DvsS$Trait, 7, 8)
DvsS <- DvsS[927:3544, ] # keep only row associated to animal
summary(factor(DvsS$TRAIT)) # 1309 each
```

```
##   T1   T2
## 1309 1309
```

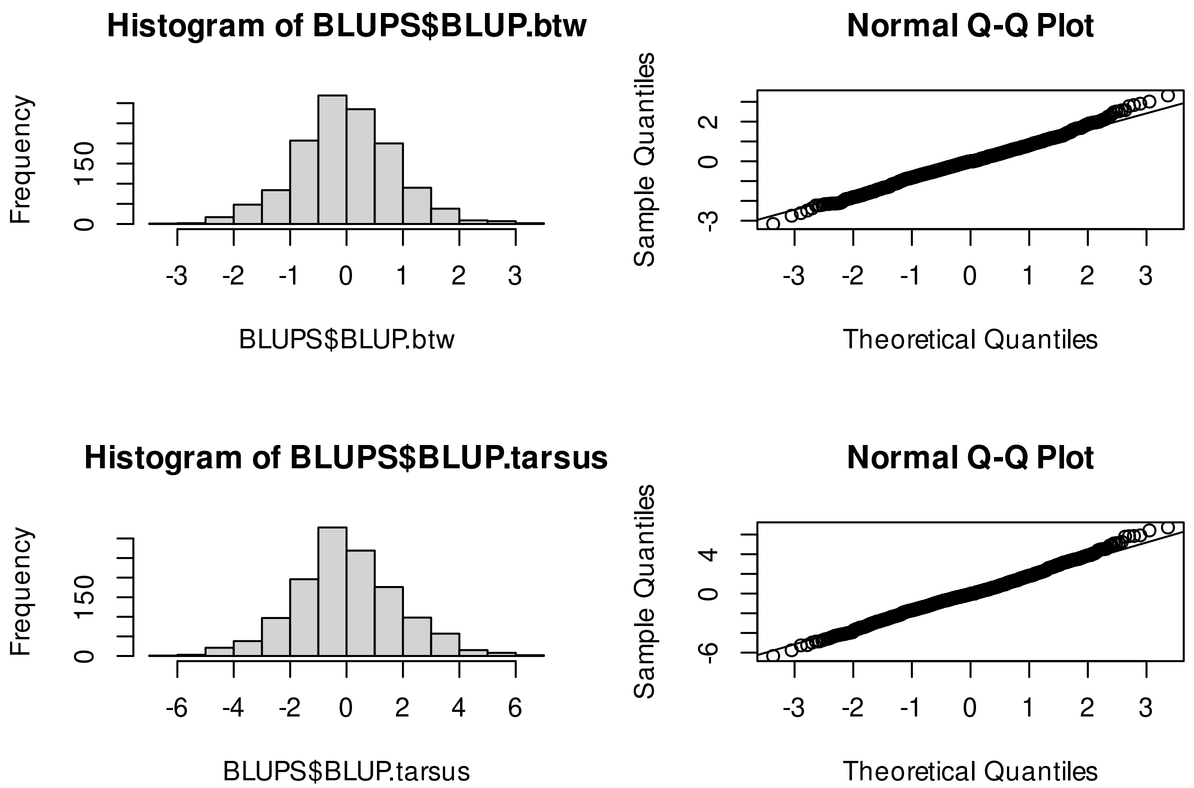
```
#
DvsS$Trait <- NULL
colnames(DvsS)[1] <- "BLUP"
BLUPS <- reshape(DvsS, v.names = c("BLUP", "SE"), idvar = "ID", timevar = "TRAIT", directi
nrow(BLUPS)
```

```
## [1] 1309
```

```
rownames(BLUPS) <- c()
colnames(BLUPS) <- c("ID", "BLUP.btw", "SE.btw", "BLUP.tarsus", "SE.tarsus")
summary(BLUPS)
```

```
##       ID               BLUP.btw             SE.btw        BLUP.tarsus
##  Length:1309        Min.   :-3.165474   Min.   :0.7984   Min.   :-6.34104
##  Class :character   1st Qu.:-0.559280   1st Qu.:0.9967   1st Qu.:-1.14428
##  Mode  :character   Median :-0.001912   Median :1.0367   Median :-0.02641
##                     Mean   :-0.009008   Mean   :1.0933   Mean   : 0.02134
##                     3rd Qu.: 0.533972   3rd Qu.:1.2210   3rd Qu.: 1.18107
##                     Max.   : 3.319657   Max.   :1.4377   Max.   : 6.71502
##    SE.tarsus
##  Min.   :1.928
##  1st Qu.:2.371
##  Median :2.451
##  Mean   :2.576
##  3rd Qu.:2.811
##  Max.   :3.287
```

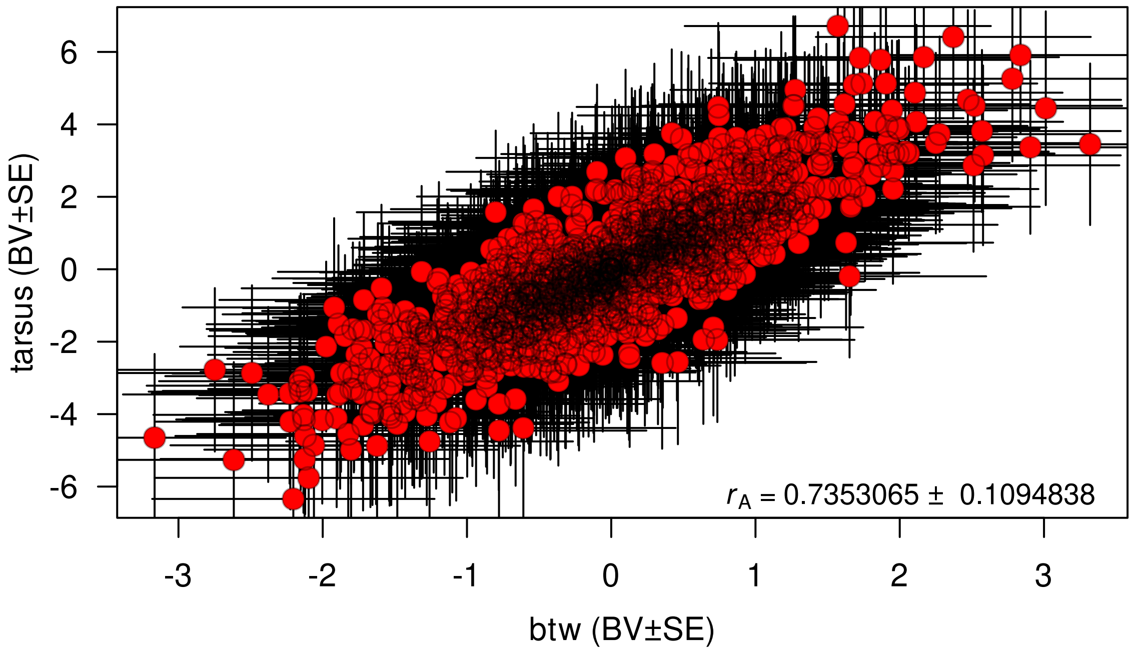
```
# write.csv(BLUPS,file="BLUPS_6x6.csv",row.names=F)
############
par(mfrow = c(2, 2))
hist(BLUPS$BLUP.btw)
qqnorm(BLUPS$BLUP.btw)
qqline(BLUPS$BLUP.btw)
hist(BLUPS$BLUP.tarsus)
qqnorm(BLUPS$BLUP.tarsus)
qqline(BLUPS$BLUP.tarsus)
```




```
#
```

Here, some simple code to plot the genetic correlation.

```
plot(BLUP.tarsus ~ BLUP.btw, BLUPS, xlab = "", ylab = "", las = 1.2, bty = "o", col = "whi
arrows(x0 = BLUPS$BLUP.btw, y0 = BLUPS$BLUP.tarsus - BLUPS$SE.tarsus, x1 = BLUPS$BLUP.btw,
arrows(x0 = BLUPS$BLUP.btw - BLUPS$SE.btw, y0 = BLUPS$BLUP.tarsus, x1 = BLUPS$BLUP.btw + B
points(BLUP.tarsus ~ BLUP.btw, BLUPS, pch = 16, col = "red", cex = 1.5)
points(BLUP.tarsus ~ BLUP.btw, BLUPS, pch = 1, col = rgb(0, 0, 0, 0.3), cex = c(1.5))
mtext("btw (BV±SE)", side = 1, line = 2.4)
mtext("tarsus (BV±SE)", side = 2, line = 2, las = 3)
mtext(expression(paste(italic(r)[A], " = 0.7353065 ±  0.1094838")), side = 1, line = -1, a
```



3.2.6 Partitionning (co)variance between groups

Similar to the univariate model, it is possible to partition the variance and also the covariance between different groups within the dataset. Here, we can estimate sex-specific genetic correlation. Note, to partition a correlation, it is require to have important sample size within each group. For this example, we simplify the model !

```
gryphon <- gryphon[order(gryphon$sex), ]
model_sex <- asreml(
  fixed = cbind(bwt, tarsus) ~ trait + at(trait):sex,
  random = ~ at(sex):us(trait, init = c(1, 0.1, 1)):vm(animal, ainv) +
    us(trait, init = c(1, 0.1, 1)):byear +
    us(trait, init = c(1, 0.1, 1)):mother,
  residual = ~ dsum(~ id(units):us(trait) | sex),
  data = gryphon,
  na.action = na.method(x = "include", y = "include"),
  maxit = 20
)
```

```
## Multi-section model using the sigma parameterization.
## ASReml 4.1.0 Tue Nov 29 16:54:23 2022
##          LogLik        Sigma2     DF     wall     cpu
##  1     -2522.729          1.0   1807 16:54:23    0.1 (1 restrained)
```

```
## Warning in asreml(fixed = cbind(bwt, tarsus) ~ trait + at(trait):sex, random
## = ~at(sex):us(trait, : US updates modified 1 times in iteration 2 to remain
## positive definite.

##  2     -2459.512           1.0   1807 16:54:23    0.1 (3 restrained)
##  3     -2408.940           1.0   1807 16:54:23    0.1
##  4     -2392.691           1.0   1807 16:54:23    0.2
##  5     -2388.962           1.0   1807 16:54:23    0.2
##  6     -2388.743           1.0   1807 16:54:24    0.1
##  7     -2388.736           1.0   1807 16:54:24    0.1
##  8     -2388.736           1.0   1807 16:54:24    0.1

## Warning in asreml(fixed = cbind(bwt, tarsus) ~ trait + at(trait):sex, random =
## ~at(sex):us(trait, : US variance structures were modified in 1 instances to make
## them positive definite
```

```
model_sex <- update(model_sex)
```

```
## Multi-section model using the sigma parameterization.
## ASReml 4.1.0 Tue Nov 29 16:54:24 2022
##           LogLik        Sigma2     DF     wall     cpu
##  1     -2388.736           1.0   1807 16:54:24    0.2
##  2     -2388.736           1.0   1807 16:54:24    0.1
```

```
summary(model_sex)$varcomp
```

```
##                                                      component std.error
## trait:byear!trait_bwt:bwt                            0.9858478 0.2863878
## trait:byear!trait_tarsus:bwt                         0.1525063 0.4334263
## trait:byear!trait_tarsus:tarsus                      3.9981983 1.2798747
## trait:mother!trait_bwt:bwt                           1.3312734 0.2484444
## trait:mother!trait_tarsus:bwt                       -1.6174228 0.4283851
## trait:mother!trait_tarsus:tarsus                     4.7542338 1.3546517
## at(sex, 1):trait:vm(animal, ainv)!trait_bwt:bwt      1.3402853 0.5670773
## at(sex, 1):trait:vm(animal, ainv)!trait_tarsus:bwt   2.3608392 1.1348473
## at(sex, 1):trait:vm(animal, ainv)!trait_tarsus:tarsus  6.0625993 3.1304394
## at(sex, 2):trait:vm(animal, ainv)!trait_bwt:bwt      1.8645998 0.8888206
## at(sex, 2):trait:vm(animal, ainv)!trait_tarsus:bwt   5.0954811 2.0684729
## at(sex, 2):trait:vm(animal, ainv)!trait_tarsus:tarsus 14.9771870 6.4479787
## sex_1!R                                              1.0000000        NA
## sex_1!trait_bwt:bwt                                  2.3079850 0.5015651
## sex_1!trait_tarsus:bwt                               4.4287898 1.0376370
## sex_1!trait_tarsus:tarsus                           13.4857819 2.9284922
## sex_2!R                                              1.0000000        NA
## sex_2!trait_bwt:bwt                                  1.7956612 0.7549779
## sex_2!trait_tarsus:bwt                               2.6340448 1.7685804
## sex_2!trait_tarsus:tarsus                            9.6094528 5.4917853
```

```
##                                                      z.ratio bound %ch
## trait:byear!trait_bwt:bwt                           3.4423530     P   0
## trait:byear!trait_tarsus:bwt                        0.3518622     P   0
## trait:byear!trait_tarsus:tarsus                     3.1238982     P   0
## trait:mother!trait_bwt:bwt                          5.3584371     P   0
## trait:mother!trait_tarsus:bwt                      -3.7756279     P   0
## trait:mother!trait_tarsus:tarsus                    3.5095618     P   0
## at(sex, 1):trait:vm(animal, ainv)!trait_bwt:bwt       2.3634965     P   0
## at(sex, 1):trait:vm(animal, ainv)!trait_tarsus:bwt    2.0803144     P   0
## at(sex, 1):trait:vm(animal, ainv)!trait_tarsus:tarsus 1.9366608     P   0
## at(sex, 2):trait:vm(animal, ainv)!trait_bwt:bwt       2.0978361     P   0
## at(sex, 2):trait:vm(animal, ainv)!trait_tarsus:bwt    2.4634024     P   0
## at(sex, 2):trait:vm(animal, ainv)!trait_tarsus:tarsus 2.3227724     P   0
## sex_1!R                                                    NA     F   0
## sex_1!trait_bwt:bwt                                 4.6015657     P   0
## sex_1!trait_tarsus:bwt                              4.2681493     P   0
## sex_1!trait_tarsus:tarsus                           4.6050257     P   0
## sex_2!R                                                    NA     F   0
## sex_2!trait_bwt:bwt                                 2.3784288     P   0
## sex_2!trait_tarsus:bwt                              1.4893554     P   0
## sex_2!trait_tarsus:tarsus                           1.7497867     P   0
```

we can estimate the different correlations using `vpredict`:

```
vpredict(model_sex, r_byear ~ V2 / sqrt(V1 * V3))
```

```
##           Estimate       SE
## r_byear 0.07681584 0.213141
```

```
vpredict(model_sex, r_M ~ V5 / sqrt(V4 * V6))
```

```
##       Estimate       SE
## r_M -0.6429092 0.248944
```

```
vpredict(model_sex, r_A.1 ~ V8 / sqrt(V7 * V9))
```

```
##        Estimate        SE
## r_A.1 0.8282059 0.1723596
```

```
vpredict(model_sex, r_A.2 ~ V11 / sqrt(V10 * V12))
```

```
##        Estimate        SE
## r_A.2 0.9642225 0.1241668
```

```
vpredict(model_sex, r_res.1 ~ V15 / sqrt(V14 * V16))
```

```
##          Estimate         SE
## r_res.1 0.7938355 0.07892634
```

```
vpredict(model_sex, r_res.2 ~ V19 / sqrt(V18 * V20))
```

```
##          Estimate        SE
## r_res.2 0.6341057 0.1894837
```

and the heritability too:

```
vpredict(model_sex, h2.bwt.1 ~ V7 / (V1 + V4 + V7 + V14))
```

```
##           Estimate         SE
## h2.bwt.1 0.2246768 0.09176827
```

```
vpredict(model_sex, h2.bwt.2 ~ V10 / (V1 + V4 + V10 + V18))
```

```
##           Estimate        SE
## h2.bwt.2 0.3119425 0.1442547
```

```
vpredict(model_sex, h2.tarsus.1 ~ V9 / (V3 + V6 + V9 + V16))
```

```
##             Estimate        SE
## h2.tarsus.1  0.21422 0.1070464
```

```
vpredict(model_sex, h2.tarsus.2 ~ V12 / (V3 + V6 + V12 + V20))
```

```
##              Estimate        SE
## h2.tarsus.2 0.4492383 0.1833858
```

Now we can look at the fixed effects parameters and assess their significance with a conditional Wald F-test:

```
summary(model_sex, coef = TRUE)$coef.fi
wald.asreml(model_sex, denDF = "default", ssType = "conditional")$Wald
```

```
##                            solution std error    z.ratio
## at(trait, tarsus):sex_1  0.0000000        NA         NA
## at(trait, tarsus):sex_2 -0.0554799 0.4758708 -0.1165861
## at(trait, bwt):sex_1     0.0000000        NA         NA
## at(trait, bwt):sex_2     1.9393688 0.1903239 10.1898321
```

```
## trait_bwt                6.3779149 0.2311766 27.5889321
## trait_tarsus            20.5838787 0.4942649 41.6454395
```

```
## Multi-section model using the sigma parameterization.
## ASReml 4.1.0 Tue Nov 29 16:54:25 2022
##           LogLik        Sigma2     DF     wall    cpu
##  1     -2388.736           1.0   1807 16:54:25    0.2
##  2     -2388.736           1.0   1807 16:54:25    0.1
## Calculating denominator DF
```

```
##
##                         Df denDF   F.inc   F.con Margin      Pr
## trait                    2  44.8 1522.00 1522.00        0.00000
## at(trait, bwt):sex       1 137.5  220.90  103.80      B 0.00000
## at(trait, tarsus):sex  1 138.6    0.01    0.01      B 0.90737
```

To assess the significant of the covariance, a LTR test can be done with a reduced model where a specific covariance can be fixed to 0 (for example the female covariance, following code).

```
model_modif <- update.asreml(model_sex, start.values = T)
G <- model_modif$vparameters[(1:12), ]
G$Constraint[(2)] <- "F"
G$Value[(2)] <- 0
#
reduc.model_sex <- asreml(
  fixed = cbind(bwt, tarsus) ~ trait + at(trait):sex,
  random = ~ at(sex):us(trait, init = c(1, 0.1, 1)):vm(animal, ainv) +
    us(trait, init = c(1, 0.1, 1)):byear +
    us(trait, init = c(1, 0.1, 1)):mother,
  residual = ~ dsum(~ id(units):us(trait) | sex),
  data = gryphon,
  na.action = na.method(x = "include", y = "include"),
  maxit = 20,
  G.param = G
)
```

```
## Multi-section model using the sigma parameterization.
## ASReml 4.1.0 Tue Nov 29 16:54:26 2022
```

```
## Warning in asreml(fixed = cbind(bwt, tarsus) ~ trait + at(trait):sex, random
## = ~at(sex):us(trait, : US updates modified 1 times in iteration 1 to remain
## positive definite.
```

```
##           LogLik        Sigma2     DF     wall    cpu
##  1     -2474.972           1.0   1807 16:54:26    0.1 (3 restrained)
##  2     -2406.283           1.0   1807 16:54:26    0.1
##  3     -2394.010           1.0   1807 16:54:27    0.1
##  4     -2391.718           1.0   1807 16:54:27    0.1
##  5     -2391.480           1.0   1807 16:54:27    0.1
```

```
## 6     -2391.477           1.0   1807 16:54:27    0.1
```

```
## Warning in asreml(fixed = cbind(bwt, tarsus) ~ trait + at(trait):sex, random =
## ~at(sex):us(trait, : US variance structures were modified in 1 instances to make
## them positive definite
```

```r
reduc.model_sex <- update(reduc.model_sex)
```

```
## Multi-section model using the sigma parameterization.
## ASReml 4.1.0 Tue Nov 29 16:54:27 2022
##           LogLik        Sigma2     DF     wall     cpu
##  1     -2391.476           1.0   1807 16:54:27    0.2
##  2     -2391.476           1.0   1807 16:54:27    0.1
```

```r
summary(reduc.model_sex)$varcomp
```

```
##                                                       component std.error
## trait:byear!trait_bwt:bwt                             0.9794331 0.2848997
## trait:byear!trait_tarsus:bwt                          0.1428995 0.4322719
## trait:byear!trait_tarsus:tarsus                       4.0021595 1.2818624
## trait:mother!trait_bwt:bwt                            1.4956509 0.2568074
## trait:mother!trait_tarsus:bwt                        -1.2460057 0.4438357
## trait:mother!trait_tarsus:tarsus                      5.3945609 1.4035705
## at(sex, 1):trait:vm(animal, ainv)!trait_bwt:bwt       0.5265716 0.3579555
## at(sex, 1):trait:vm(animal, ainv)!trait_tarsus:bwt    0.0000000        NA
## at(sex, 1):trait:vm(animal, ainv)!trait_tarsus:tarsus  1.4223969 1.9103795
## at(sex, 2):trait:vm(animal, ainv)!trait_bwt:bwt       1.5835813 0.8671365
## at(sex, 2):trait:vm(animal, ainv)!trait_tarsus:bwt    4.4288714 2.0173971
## at(sex, 2):trait:vm(animal, ainv)!trait_tarsus:tarsus 12.9349047 6.2946996
## sex_1!R                                               1.0000000        NA
## sex_1!trait_bwt:bwt                                   2.9539767 0.4196755
## sex_1!trait_tarsus:bwt                                6.3138301 0.6802598
## sex_1!trait_tarsus:tarsus                            17.3577089 2.4730547
## sex_2!R                                               1.0000000        NA
## sex_2!trait_bwt:bwt                                   1.9341439 0.7416691
## sex_2!trait_tarsus:bwt                                2.9467290 1.7370018
## sex_2!trait_tarsus:tarsus                            10.7245912 5.4025888
##                                                         z.ratio bound %ch
## trait:byear!trait_bwt:bwt                             3.4378175     P   0
## trait:byear!trait_tarsus:bwt                          0.3305778     P   0
## trait:byear!trait_tarsus:tarsus                       3.1221444     P   0
## trait:mother!trait_bwt:bwt                            5.8240170     P   0
## trait:mother!trait_tarsus:bwt                        -2.8073580     P   0
## trait:mother!trait_tarsus:tarsus                      3.8434556     P   0
## at(sex, 1):trait:vm(animal, ainv)!trait_bwt:bwt       1.4710530     P   0
## at(sex, 1):trait:vm(animal, ainv)!trait_tarsus:bwt           NA     F  NA
```

```
## at(sex, 1):trait:vm(animal, ainv)!trait_tarsus:tarsus  0.7445625     P   0
## at(sex, 2):trait:vm(animal, ainv)!trait_bwt:bwt        1.8262193     P   0
## at(sex, 2):trait:vm(animal, ainv)!trait_tarsus:bwt     2.1953395     P   0
## at(sex, 2):trait:vm(animal, ainv)!trait_tarsus:tarsus  2.0548883     P   0
## sex_1!R                                                       NA     F   0
## sex_1!trait_bwt:bwt                                    7.0387165     P   0
## sex_1!trait_tarsus:bwt                                 9.2814981     P   0
## sex_1!trait_tarsus:tarsus                              7.0187323     P   0
## sex_2!R                                                       NA     F   0
## sex_2!trait_bwt:bwt                                    2.6078261     P   0
## sex_2!trait_tarsus:bwt                                 1.6964455     P   0
## sex_2!trait_tarsus:tarsus                              1.9850837     P   0
```

```
2 * (model_sex$loglik - reduc.model_sex$loglik)
```

```
## [1] 5.481033
```

```
1 - pchisq(2 * (model_sex$loglik - reduc.model_sex$loglik), df = 1)
```

```
## [1] 0.0192239
```

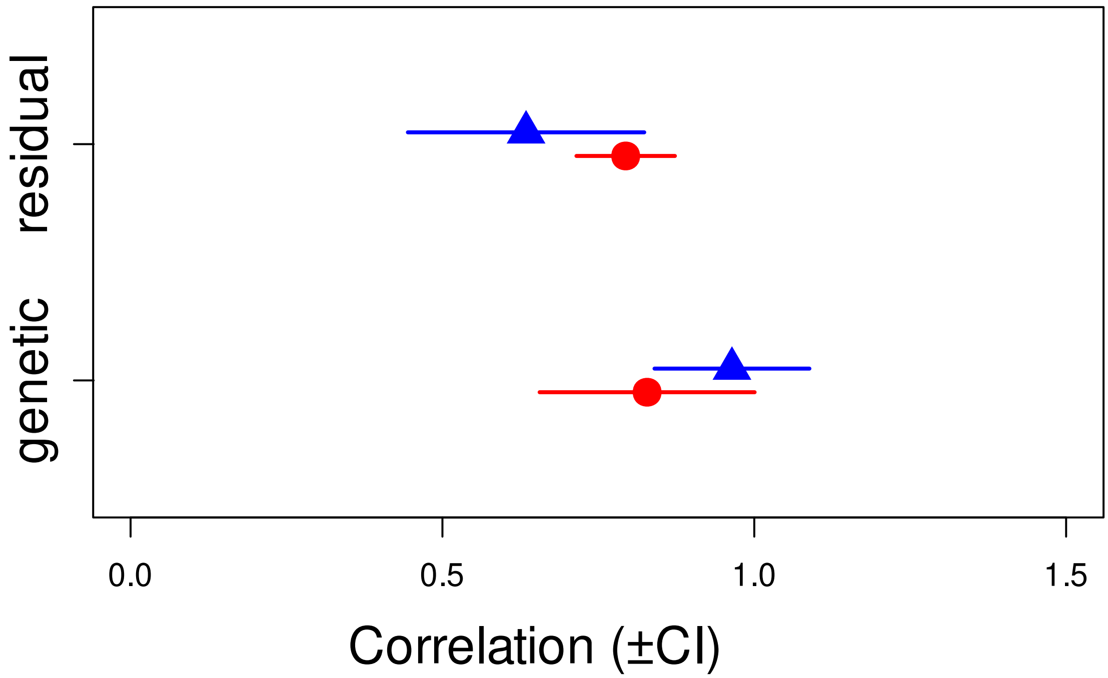
In addition, it is also possible to test the sexesif sexes has significant differences with another reduced model where both covariance are fixed to their average values.

```
# code provided as an example for the moment since the model cannot run on this data
model_modif <- update.asreml(model_sex, start.values = T)
G <- model_modif$vparameters[(1:12), ]
G$fac <- factor(
  c(
    1, 2, 3, 4, 2, 6, # Additive genetic matrix  2 =5
    7, 8, 9, # byear  matrix
    10, 11, 12 # mother matrix
  )
)
Modif <- vcm.lm(~fac, data = G)
attr(Modif, "assign") <- NULL
attr(Modif, "contrasts") <- NULL
#
reduc.model_sex_2 <- asreml(
  fixed = cbind(bwt, tarsus) ~ trait + at(trait):sex,
  random = ~ at(sex):us(trait, init = c(1, 0.1, 1)):vm(animal, ainv) +
    us(trait, init = c(1, 0.1, 1)):byear +
    us(trait, init = c(1, 0.1, 1)):mother,
  residual = ~ dsum(~ id(units):us(trait) | sex),
  data = gryphon,
```

```
  na.action = na.method(x = "include", y = "include"),
  maxit = 20,
  G.param = G, vcm = Modif
)
reduc.model_sex_2 <- update(reduc.model_sex_2)
summary(reduc.model_sex_2)$varcomp




2 * (model_sex$loglik - reduc.model_sex_2$loglik)
1 - pchisq(2 * (model_sex$loglik - reduc.model_sex_2$loglik), df = 2)
```

Here a plot to visualize the overlaps of covariances.

```
genetic.correlation.F <- vpredict(model_sex, r_A.1 ~ V8 / sqrt(V7 * V9))
genetic.correlation.M <- vpredict(model_sex, r_A.2 ~ V11 / sqrt(V10 * V12))
residual.correlation.F <- vpredict(model_sex, r_res.1 ~ V15 / sqrt(V14 * V16))
residual.correlation.M <- vpredict(model_sex, r_res.2 ~ V19 / sqrt(V18 * V20))
cor.est <- rbind(genetic.correlation.F, genetic.correlation.M, residual.correlation.F, res

plot(c(0.95, 1.05, 1.95, 2.05) ~ cor.est[, 1], xlim = c(0, 1.5), ylim = c(0.5, 2.5), xlab
arrows(y0 = 0.95, x0 = cor.est[1, 1] - cor.est[1, 2], y1 = 0.95, x1 = cor.est[1, 1] + cor.
arrows(y0 = 1.05, x0 = cor.est[2, 1] - cor.est[2, 2], y1 = 1.05, x1 = cor.est[2, 1] + cor.
arrows(y0 = 1.95, x0 = cor.est[3, 1] - cor.est[3, 2], y1 = 1.95, x1 = cor.est[3, 1] + cor.
arrows(y0 = 2.05, x0 = cor.est[4, 1] - cor.est[4, 2], y1 = 2.05, x1 = cor.est[4, 1] + cor.
mtext("Correlation (±CI)", side = 1, las = 1, adj = 0.4, line = 3, cex = 1.6)
axis(2, at = 1, labels = c("genetic"), las = 3, cex.axis = 1.6)
axis(2, at = 2, labels = c("residual"), las = 3, cex.axis = 1.6)
```



By using `corgh`, we can extract the BLUPs and plot the sex-specific correlation.

```
gryphon$T1 <- gryphon$bwt
gryphon$T2 <- gryphon$tarsus
###
model_sex <- asreml(
  fixed = cbind(T1, T2) ~ trait + at(trait):sex,
  random = ~ at(sex):corgh(trait, init = c(0.1, 1, 1)):vm(animal, ainv) +
    us(trait, init = c(1, 0.1, 1)):byear +
    us(trait, init = c(1, 0.1, 1)):mother,
  residual = ~ dsum(~ id(units):us(trait) | sex),
  data = gryphon,
  na.action = na.method(x = "include", y = "include"),
  maxit = 20
)
```

```
## Multi-section model using the sigma parameterization.
## ASReml 4.1.0 Tue Nov 29 16:54:27 2022
##           LogLik        Sigma2     DF      wall     cpu
##  1      -2522.729          1.0   1807  16:54:28     0.1 (2 restrained)
##  2      -2457.755          1.0   1807  16:54:28     0.1 (2 restrained)
##  3      -2407.462          1.0   1807  16:54:28     0.1 (2 restrained)
##  4      -2394.143          1.0   1807  16:54:28     0.1 (1 restrained)
```

```
## 5     -2389.368           1.0   1807 16:54:28    0.1
## 6     -2388.741           1.0   1807 16:54:28    0.1
## 7     -2388.736           1.0   1807 16:54:28    0.1
```

```
model_sex <- update(model_sex)
```

```
## Multi-section model using the sigma parameterization.
## ASReml 4.1.0 Tue Nov 29 16:54:28 2022
##           LogLik        Sigma2     DF      wall     cpu
## 1     -2388.736           1.0   1807 16:54:28    0.1
## 2     -2388.736           1.0   1807 16:54:29    0.1
```

```
DvsS <- data.frame(
  Trait = rownames(model_sex$coefficients$random),
  BLUP = model_sex$coefficients$random,
  SE = sqrt(model_sex$vcoeff$random * model_sex$sigma2)
)
DvsS$ID <- substr(DvsS$Trait, 38, 40)
DvsS$TRAIT <- substr(DvsS$Trait, 18, 19)
DvsS$SEX <- substr(DvsS$Trait, 9, 9)
DvsS <- DvsS[927:6162, ] # keep only row associated to animal
summary(factor(DvsS$TRAIT)) # 1309 each
```

```
##   T1   T2
## 2618 2618
```

```
#
DvsS$Trait <- NULL
colnames(DvsS)[1] <- "BLUP"
BLUPS <- reshape(DvsS, v.names = c("BLUP", "SE"), idvar = c("ID", "SEX"), timevar = "TRAIT
```

```
## Warning in reshapeWide(data, idvar = idvar, timevar = timevar, varying =
## varying, : multiple rows match for TRAIT=T1: first taken

## Warning in reshapeWide(data, idvar = idvar, timevar = timevar, varying =
## varying, : multiple rows match for TRAIT=T2: first taken
```

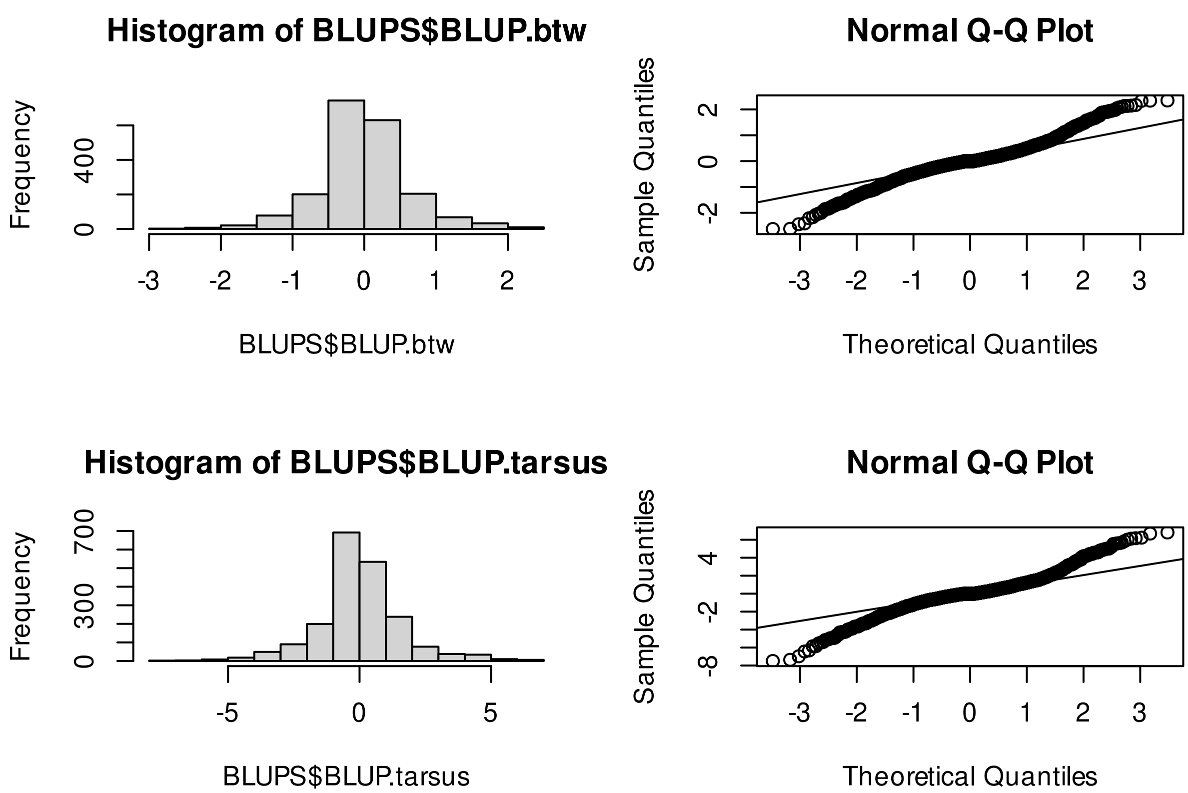
```
nrow(BLUPS)
```

```
## [1] 1998
```

```
rownames(BLUPS) <- c()
colnames(BLUPS) <- c("ID", "SEX", "BLUP.btw", "SE.btw", "BLUP.tarsus", "SE.tarsus")
summary(BLUPS)
```

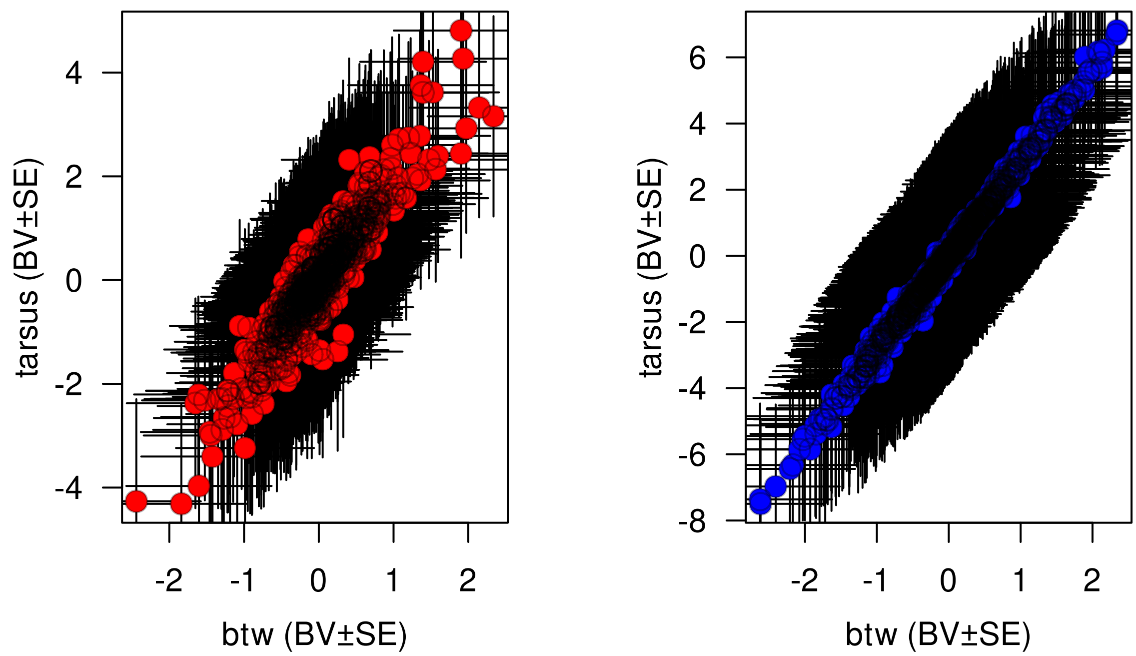
```
##        ID                 SEX                BLUP.btw              SE.btw
##  Length:1998        Length:1998        Min.   :-2.625088   Min.   :0.8383
##  Class :character   Class :character   1st Qu.:-0.281979   1st Qu.:0.9412
##  Mode  :character   Mode  :character   Median : 0.000000   Median :1.1018
##                                        Mean   : 0.008687   Mean   :1.0931
##                                        3rd Qu.: 0.293571   3rd Qu.:1.1777
##                                        Max.   : 2.344440   Max.   :1.3650
##   BLUP.tarsus         SE.tarsus
##  Min.   :-7.49444   Min.   :1.829
##  1st Qu.:-0.66206   1st Qu.:2.345
##  Median : 0.00000   Median :2.462
##  Mean   : 0.02557   Mean   :2.730
##  3rd Qu.: 0.71508   3rd Qu.:3.326
##  Max.   : 6.80950   Max.   :3.868
```

```r
# write.csv(BLUPS,file="BLUPS_6x6_SEX.csv",row.names=F)
############
par(mfrow = c(2, 2))
hist(BLUPS$BLUP.btw)
qqnorm(BLUPS$BLUP.btw)
qqline(BLUPS$BLUP.btw)
hist(BLUPS$BLUP.tarsus)
qqnorm(BLUPS$BLUP.tarsus)
qqline(BLUPS$BLUP.tarsus)
```



Here, some simple codes to plot the genetic correlation.

```
FEM <- subset(BLUPS, SEX == "1")
MAL <- subset(BLUPS, SEX == "2")
#
par(mfrow = c(1, 2))
#
plot(BLUP.tarsus ~ BLUP.btw, FEM, xlab = "", ylab = "", las = 1.2, bty = "o", col = "white
arrows(x0 = FEM$BLUP.btw, y0 = FEM$BLUP.tarsus - FEM$SE.tarsus, x1 = FEM$BLUP.btw, y1 = FE
arrows(x0 = FEM$BLUP.btw - FEM$SE.btw, y0 = FEM$BLUP.tarsus, x1 = FEM$BLUP.btw + FEM$SE.bt
points(BLUP.tarsus ~ BLUP.btw, FEM, pch = 16, col = "red", cex = 1.5)
points(BLUP.tarsus ~ BLUP.btw, FEM, pch = 1, col = rgb(0, 0, 0, 0.3), cex = c(1.5))
mtext("btw (BV±SE)", side = 1, line = 2.4)
mtext("tarsus (BV±SE)", side = 2, line = 2, las = 3)
#
plot(BLUP.tarsus ~ BLUP.btw, MAL, xlab = "", ylab = "", las = 1.2, bty = "o", col = "white
arrows(x0 = MAL$BLUP.btw, y0 = MAL$BLUP.tarsus - MAL$SE.tarsus, x1 = MAL$BLUP.btw, y1 = MA
arrows(x0 = MAL$BLUP.btw - MAL$SE.btw, y0 = MAL$BLUP.tarsus, x1 = MAL$BLUP.btw + MAL$SE.bt
points(BLUP.tarsus ~ BLUP.btw, MAL, pch = 16, col = "blue", cex = 1.5)
points(BLUP.tarsus ~ BLUP.btw, MAL, pch = 1, col = rgb(0, 0, 0, 0.3), cex = c(1.5))
mtext("btw (BV±SE)", side = 1, line = 2.4)
mtext("tarsus (BV±SE)", side = 2, line = 2, las = 3)
```



3.2.7 Between groups (co)variances and the B-matrix

Animal models are amazing model. With different group within a population, it is also possible to estimate how much the different groups shared the same genetic via the cross-group genetic covariance. This covariance is essential to understand ontogenic or sexual conflict, which can constraint or enhanced response to evolution. As an example, we estimate the cross-sex genetic correlation `r_{fm}`

First, we need to dissociate the trait values for females and males into distinct variables. Then, we use a bivariate model (for one trait: `tarsus`) and a multivariate model (for various traits: `tarsus` and `bwt`). With a multivariate model, the cross-sex-cross trait covariance matrixis also named `B matrix`.

The coding is a bit complex but pretty straightforward. It is important to modify the covariance matrix at the residual level to avoid the calculation of a cross-sex residual covariance (no individual switched sex during the experiment).

```
gryphon$bwt.1 <- NA
gryphon$tarsus.1 <- NA
animal <- gryphon[gryphon$sex == "1", ]$animal
for (i in unique(animal)) {
  gryphon$bwt.1[which(gryphon$animal == i)] <- gryphon$bwt[which(gryphon$animal == i)]
  gryphon$tarsus.1[which(gryphon$animal == i)] <- gryphon$tarsus[which(gryphon$animal == i
```

```
}
#
gryphon$bwt.2 <- NA
gryphon$tarsus.2 <- NA
animal <- gryphon[gryphon$sex == "2", ]$animal
for (i in unique(animal)) {
  gryphon$bwt.2[which(gryphon$animal == i)] <- gryphon$bwt[which(gryphon$animal == i)]
  gryphon$tarsus.2[which(gryphon$animal == i)] <- gryphon$tarsus[which(gryphon$animal == i
}

###########
temp <- asreml(cbind(tarsus.1, tarsus.2) ~ trait,
  random = ~ us(trait):vm(animal, ainv) +
    diag(trait):byear + diag(trait):mother,
  residual = ~ units:us(trait),
  data = gryphon, na.action = na.method(y = "include", x = "include"), maxiter = 20,
  start.values = T
)
G <- temp$vparameters[(1:7), ]
R <- temp$vparameters[-(1:7), ]
#
G$Constraint <- "U"
R$Value[3] <- 0
R$Constraint[3] <- "F"
#
model.BiV_Sex <- asreml(cbind(tarsus.1, tarsus.2) ~ trait,
  random = ~ us(trait):vm(animal, ainv) +
    diag(trait):byear + diag(trait):mother,
  residual = ~ units:us(trait),
  data = gryphon, na.action = na.method(y = "include", x = "include"), maxiter = 20,
  G.param = G, R.param = R
)
```

```
## Model fitted using the sigma parameterization.
## ASReml 4.1.0 Tue Nov 29 16:54:30 2022
##          LogLik        Sigma2     DF     wall    cpu
##  1     -1494.807          1.0    681 16:54:30    0.0 (1 restrained)
##  2     -1484.793          1.0    681 16:54:30    0.0 (1 restrained)
##  3     -1475.726          1.0    681 16:54:30    0.0 (1 restrained)
##  4     -1471.905          1.0    681 16:54:30    0.0 (1 restrained)
##  5     -1470.716          1.0    681 16:54:30    0.0
##  6     -1468.154          1.0    681 16:54:30    0.0
##  7     -1467.969          1.0    681 16:54:30    0.0
##  8     -1467.967          1.0    681 16:54:30    0.0
```

```
model.BiV_Sex <- update.asreml(model.BiV_Sex)
```

```
## Model fitted using the sigma parameterization.
## ASReml 4.1.0 Tue Nov 29 16:54:30 2022
##          LogLik        Sigma2     DF     wall    cpu
##  1     -1467.967          1.0    681 16:54:30    0.0
##  2     -1467.967          1.0    681 16:54:30    0.0
```

```
#
summary(model.BiV_Sex)$varcomp
```

```
##                                               component std.error   z.ratio
## trait:byear!trait_tarsus.1                     3.280319  1.532909 2.1399299
## trait:byear!trait_tarsus.2                     4.743134  1.891252 2.5079332
## trait:mother!trait_tarsus.1                    1.875132  2.424092 0.7735398
## trait:mother!trait_tarsus.2                    4.314158  2.785254 1.5489283
## trait:vm(animal, ainv)!trait_tarsus.1:tarsus.1  6.582654  3.636467 1.8101781
## trait:vm(animal, ainv)!trait_tarsus.2:tarsus.1  8.396245  3.278591 2.5609306
## trait:vm(animal, ainv)!trait_tarsus.2:tarsus.2 12.898424  8.038362 1.6046084
## units:trait!R                                  1.000000        NA        NA
## units:trait!trait_tarsus.1:tarsus.1           14.872757  3.637545 4.0886803
## units:trait!trait_tarsus.2:tarsus.1            0.000000        NA        NA
## units:trait!trait_tarsus.2:tarsus.2           10.760849  6.294585 1.7095406
##                                               bound %ch
## trait:byear!trait_tarsus.1                        U   0
## trait:byear!trait_tarsus.2                        U   0
## trait:mother!trait_tarsus.1                       U   0
## trait:mother!trait_tarsus.2                       U   0
## trait:vm(animal, ainv)!trait_tarsus.1:tarsus.1    U   0
## trait:vm(animal, ainv)!trait_tarsus.2:tarsus.1    U   0
## trait:vm(animal, ainv)!trait_tarsus.2:tarsus.2    U   0
## units:trait!R                                     F   0
## units:trait!trait_tarsus.1:tarsus.1               P   0
## units:trait!trait_tarsus.2:tarsus.1               F  NA
## units:trait!trait_tarsus.2:tarsus.2               P   0
```

The cross-sex genetic correlation can estimate form the output of the model. For tarsus length at fledging, sexes shared a lot of genetic variance which is commun for a trait with low sexual dimorphism. If the selection is antagonistic between males and females, sexes can not evolve freely form the other sexes and a sexual conflict appears.

```
vpredict(model.BiV_Sex, r_fm ~ V6 / sqrt(V5 * V7))
```

```
##       Estimate        SE
## r_fm 0.9112054 0.4229764
```

We can estimate directly the correlation and plot the cross-sex genetic correlation

```
temp <- asreml(cbind(tarsus.1, tarsus.2) ~ trait,
  random = ~ corgh(trait):vm(animal, ainv) +
    diag(trait):byear + diag(trait):mother,
  residual = ~ units:corgh(trait),
  data = gryphon, na.action = na.method(y = "include", x = "include"), maxiter = 20,
  start.values = T
)
G <- temp$vparameters[(1:7), ]
R <- temp$vparameters[-(1:7), ]
#
G$Constraint <- "U"
R$Value[2] <- 0
R$Constraint[2] <- "F"
#
model.BiV_Sex <- asreml(cbind(tarsus.1, tarsus.2) ~ trait,
  random = ~ corgh(trait):vm(animal, ainv) +
    diag(trait):byear + diag(trait):mother,
  residual = ~ units:corgh(trait),
  data = gryphon, na.action = na.method(y = "include", x = "include"), maxiter = 20,
  G.param = G, R.param = R
)
```

```
## Model fitted using the sigma parameterization.
## ASReml 4.1.0 Tue Nov 29 16:54:30 2022
##          LogLik        Sigma2     DF     wall    cpu
##  1     -1494.323          1.0    681 16:54:31    0.1 (1 restrained)
##  2     -1482.996          1.0    681 16:54:31    0.0 (1 restrained)
##  3     -1472.827          1.0    681 16:54:31    0.0 (1 restrained)
##  4     -1468.707          1.0    681 16:54:31    0.0
##  5     -1467.984          1.0    681 16:54:31    0.0
##  6     -1467.968          1.0    681 16:54:31    0.0
##  7     -1467.967          1.0    681 16:54:31    0.0
```

```
model.BiV_Sex <- update.asreml(model.BiV_Sex)
```

```
## Model fitted using the sigma parameterization.
## ASReml 4.1.0 Tue Nov 29 16:54:31 2022
##          LogLik        Sigma2     DF     wall    cpu
##  1     -1467.967          1.0    681 16:54:31    0.1
##  2     -1467.967          1.0    681 16:54:31    0.0
```

```
#
summary(model.BiV_Sex)$varcomp
```

```
##                                                       component std.error
## trait:byear!trait_tarsus.1                            3.2803263 1.5329224
## trait:byear!trait_tarsus.2                            4.7431679 1.8913244
## trait:mother!trait_tarsus.1                           1.8751274 2.4240942
## trait:mother!trait_tarsus.2                           4.3141262 2.7852550
## trait:vm(animal, ainv)!trait!tarsus.2:!trait!tarsus.1.cor  0.9111864 0.4230261
## trait:vm(animal, ainv)!trait_tarsus.1                 6.5826478 3.6364929
## trait:vm(animal, ainv)!trait_tarsus.2                12.8988848 8.0388517
## units:trait!R                                         1.0000000        NA
## units:trait!trait!tarsus.2:!trait!tarsus.1.cor        0.0000000        NA
## units:trait!trait_tarsus.1                           14.8727602 3.6375549
## units:trait!trait_tarsus.2                           10.7604420 6.2948051
##                                                        z.ratio bound %ch
## trait:byear!trait_tarsus.1                           2.1399167     U   0
## trait:byear!trait_tarsus.2                           2.5078553     U   0
## trait:mother!trait_tarsus.1                          0.7735373     U   0
## trait:mother!trait_tarsus.2                          1.5489160     U   0
## trait:vm(animal, ainv)!trait!tarsus.2:!trait!tarsus.1.cor 2.1539720     U   0
## trait:vm(animal, ainv)!trait_tarsus.1                1.8101638     U   0
## trait:vm(animal, ainv)!trait_tarsus.2                1.6045681     U   0
## units:trait!R                                               NA     F   0
## units:trait!trait!tarsus.2:!trait!tarsus.1.cor              NA     F  NA
## units:trait!trait_tarsus.1                           4.0886696     P   0
## units:trait!trait_tarsus.2                           1.7094162     P   0
```

```
###########
DvsS <- data.frame(
  Trait = rownames(model.BiV_Sex$coefficients$random),
  BLUP = model.BiV_Sex$coefficients$random,
  SE = sqrt(model.BiV_Sex$vcoeff$random * model.BiV_Sex$sigma2)
)
DvsS$ID <- substr(DvsS$Trait, 33, 35)
DvsS$TRAIT <- substr(DvsS$Trait, 7, 14)
DvsS <- DvsS[927:3544, ] # keep only row associated to animal
summary(factor(DvsS$TRAIT))
```

```
## tarsus.1 tarsus.2
##     1309     1309
```

```
#
DvsS$Trait <- NULL
colnames(DvsS)[1] <- "BLUP"
BLUPS <- reshape(DvsS, v.names = c("BLUP", "SE"), idvar = "ID", timevar = "TRAIT", directi
```

```
## Warning in reshapeWide(data, idvar = idvar, timevar = timevar, varying =
## varying, : multiple rows match for TRAIT=tarsus.1: first taken
```

```
## Warning in reshapeWide(data, idvar = idvar, timevar = timevar, varying =
## varying, : multiple rows match for TRAIT=tarsus.2: first taken
```

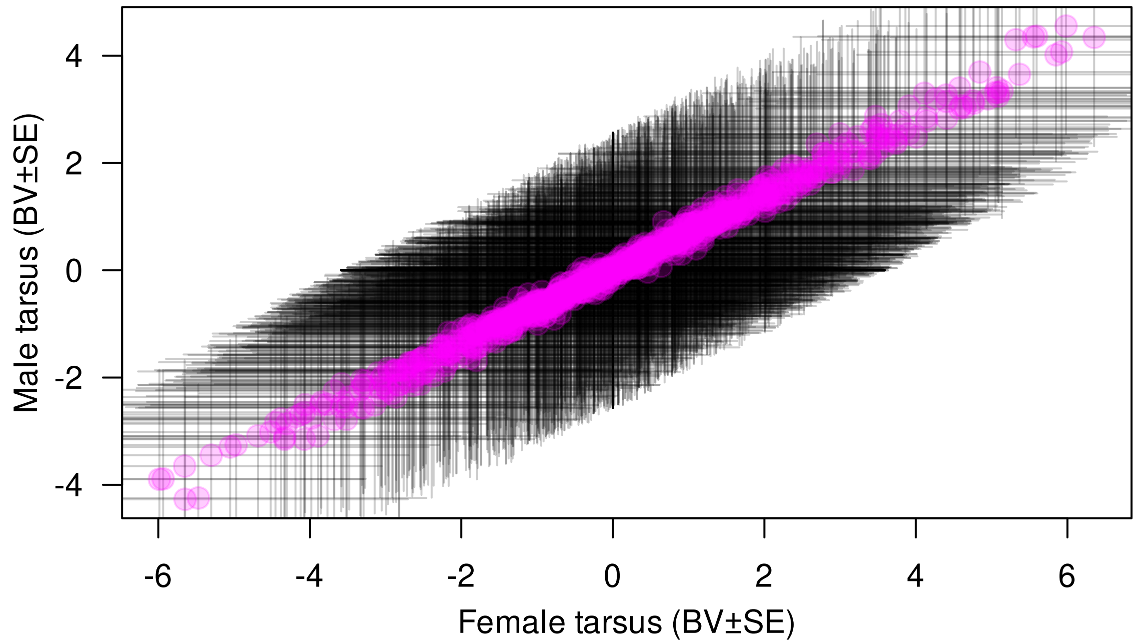
```r
nrow(BLUPS)
```

```
## [1] 999
```

```r
rownames(BLUPS) <- c()
colnames(BLUPS) <- c("ID", "BLUP.1", "SE.1", "BLUP.2", "SE.2")
summary(BLUPS)
```

```
##       ID                BLUP.1               SE.1            BLUP.2
##  Length:999         Min.   :-4.27022   Min.   :1.724   Min.   :-5.98516
##  Class :character   1st Qu.:-0.69816   1st Qu.:2.010   1st Qu.:-0.99808
##  Mode  :character   Median : 0.00000   Median :2.143   Median : 0.00000
##                     Mean   : 0.05588   Mean   :2.204   Mean   : 0.06904
##                     3rd Qu.: 0.84250   3rd Qu.:2.426   3rd Qu.: 1.13426
##                     Max.   : 4.55405   Max.   :2.567   Max.   : 6.35309
##       SE.2
##  Min.   :2.375
##  1st Qu.:2.677
##  Median :3.055
##  Mean   :3.047
##  3rd Qu.:3.378
##  Max.   :3.591
```

```r
###########
Y <- BLUPS$BLUP.1
X <- BLUPS$BLUP.2
se.Y <- BLUPS$SE.1
se.X <- BLUPS$SE.2

plot(X, Y, xlab = "", ylab = "", las = 1.2, bty = "o", col = "white")
arrows(x0 = X, y0 = Y - se.Y, x1 = X, y1 = Y + se.Y, col = rgb(0, 0, 0, 0.2), code = 3, an
arrows(x0 = X - se.X, y0 = Y, x1 = X + se.X, y1 = Y, col = rgb(0, 0, 0, 0.2), code = 3, an
points(X, Y, pch = 1, col = rgb(1, 0, 1, 0.2), cex = 1.5)
points(X, Y, pch = 16, col = rgb(1, 0, 1, 0.2), cex = 1.5)
# abline(v=0,lty=3);abline(h=0,lty=3)
mtext("Male tarsus (BV±SE)", side = 2, line = 2, las = 3)
mtext("Female tarsus (BV±SE)", side = 1, line = 2.2)
```



The B matrix used the same code but in a multivariate animal model framework. Here some example code, however due to the nature of the dataset, the cross-sex genetic covariance for birth weight is hard to estimate making difficulty to fit this multivariate animal model.

```
temp <- asreml(cbind(tarsus.1, bwt.1, tarsus.2, bwt.2) ~ trait,
  random = ~ us(trait):vm(animal, ainv) +
    diag(trait):byear + diag(trait):mother,
  residual = ~ units:us(trait),
  data = gryphon, na.action = na.method(y = "include", x = "include"), maxiter = 20,
  start.values = T
)
G <- temp$vparameters[(1:18), ]
R <- temp$vparameters[-(1:18), ]
#
G$Constraint <- "U"
R$Value[5:6] <- 0
R$Constraint[5:6] <- "F"
R$Value[8:9] <- 0
R$Constraint[8:9] <- "F"
#
# model.MultV_Sex<-asreml(cbind(tarsus.1,bwt.1,tarsus.2,bwt.2)~trait,
#          random=~us(trait):vm(animal,ainv)+
#          diag(trait):byear +   diag(trait):mother,
```

```
#          residual = ~units:us(trait),
#          data=gryphon,na.action=na.method(y="include",x="include"),maxiter=20,
#      G.param=G,R.param=R)
# model.MultV_Sex<-update.asreml(model.MultV_Sex)
#
# summary(model.MultV_Sex)$varcomp
```

3.3 gremlin

No in the development plans

Meanwhile

Figure 3.1: Keep it dry and do no feed after midnight.

3.4 MCMCglmm

`MCMCglmm` has the advantage to keep automatically keep the lines with missing data and will try to fit the model use latent variables for missing data. We will remove the missing values from the data before fitting the model.

```
gryphon2 <- subset(gryphon, !is.na(bwt) & !is.na(tarsus))
```

First load MCMCglmm:

```
library(MCMCglmm)
Ainv <- inverseA(gryphonped)$Ainv
```

3.4.1 Fitting the model

Fitting a multivariate model in MCMCglmm involves several new consideration above those for fitting univariate models. First, we have to fit multivariate priors; second, we have to specify the ways in which effects on different traits may covary, including the nature of residual (co)variation; and third, we will have to be a little more specific when specifying to MCMCglmm what type of distributions from which we assume our data are drawn. Our most basic model can be specified as:

```
prior2.1 <- list(
  G = list(G1 = list(V = diag(2), nu = 1.002)),
  R = list(V = diag(2), nu = 1.002)
)

model2.1 <- MCMCglmm(cbind(bwt, tarsus) ~ trait - 1,
  random = ~ us(trait):animal,
  rcov = ~ us(trait):units,
  family = c("gaussian", "gaussian"),
  ginv = list(animal = Ainv),
  data = gryphon2, prior = prior2.1, verbose = FALSE
)
summary(model2.1)
```

```
##
##  Iterations = 3001:12991
##  Thinning interval  = 10
##  Sample size  = 1000
##
##  DIC: 7156.888
##
##  G-structure:  ~us(trait):animal
##
##                                  post.mean l-95% CI u-95% CI eff.samp
## traitbwt:traitbwt.animal             3.236  1.98774    4.656   117.84
## traittarsus:traitbwt.animal          2.045 -0.02795    4.612    97.11
## traitbwt:traittarsus.animal          2.045 -0.02795    4.612    97.11
## traittarsus:traittarsus.animal      11.357  5.21354   17.365    65.68
##
##  R-structure:  ~us(trait):units
##
```

```
##                                     post.mean l-95% CI u-95% CI eff.samp
## traitbwt:traitbwt.units                 3.951    2.790    5.074    154.3
## traittarsus:traitbwt.units              3.641    1.736    5.841    115.4
## traitbwt:traittarsus.units              3.641    1.736    5.841    115.4
## traittarsus:traittarsus.units          18.646   13.084   24.144    102.7
##
##  Location effects: cbind(bwt, tarsus) ~ trait - 1
##
##             post.mean l-95% CI u-95% CI eff.samp  pMCMC
## traitbwt        7.483    7.166    7.749    609.9 <0.001 ***
## traittarsus    20.424   19.784   20.972   1000.0 <0.001 ***
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

```r
plot(model2.1$VCV[, "traittarsus:traittarsus.animal"])
```

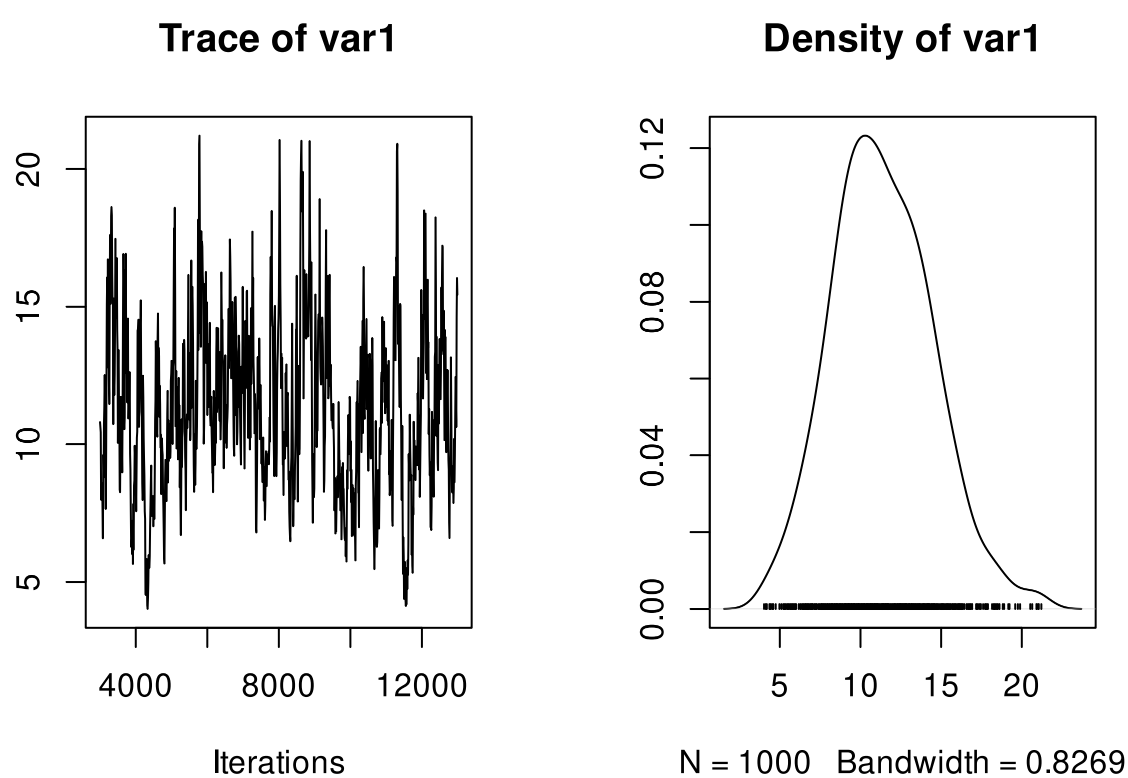


Figure 3.2: The posterior distribution of the additive genetic effect for tarsus length in a MCMCglmm run with default values

```r
autocorr.diag(model2.1$VCV)[, "traittarsus:traittarsus.animal"][2]
```

```
##    Lag 10
## 0.8199896
```

We have constructed the prior similarly to the those in the univariate models in tutorial 1, only we are specifying a 2x2 covariance matrix rather than a single variance. In order to provide proper priors, we have set the degree of belief parameter to greater than 1 (1.002). Those priors are not necessarily weak or uninformative in all circumstances. We will consider them adequate nonetheless for this tutorial. Please the vignette of the MCMCglmm packages (**?**) for more information on priors. In tutorial 1, we used full autocorrelation tables to evaluate the validity of the posterior distribution. Note that we have not done this here.

For a bivariate model this table can become very complex. Nonetheless, it is worth evaluating, rather it is simply to large to include here. It can be viewed in the console as before. Here we have displayed only the autocorrelation for estimates of additive genetic effects for tarsus length with a lag of one samples (10 iterations given this MCMCglmm run with default values). This lag of 0.8199896 is clearly unacceptable. The posterior distribution of the additive genetic effect on tarsus length is shown in Figure 4, note the autocorrelation evident in the left-hand plot.

We will opt to run the analysis for longer. This longer run could be run using the following code (including a line to save the output):

```
model2.1 <- MCMCglmm(cbind(bwt, tarsus) ~ trait - 1,
  random = ~ us(trait):animal,
  rcov = ~ us(trait):units,
  family = c("gaussian", "gaussian"),
  ginv = list(animal = Ainv),
  data = gryphon2,
  nitt = 130000, thin = 100, burnin = 30000,
  prior = prior2.1, verbose = FALSE
)
save(model2.1, file = "data/MCMCglmm_model2_1_LongRun.rda")
```

However, this run might take as long as an hour. For the purpose of this tutorial we have provided an output for such a run. It can be obtained and manipulated as follows, assuming that the file `MCMCglmm_model2_1_LongRun.rda` is available at the specified location:

```
load(file = "data/MCMCglmm_model2_1_LongRun.rda")
autocorr.diag(model2.1$VCV)[, "traittarsus:traittarsus.animal"][2]
```

```
##   Lag 100
## 0.2805747
```

This level of autocorrelation is more acceptable, at least for the purpose of demonstration in this tutorial. We can recover variance components, heritabilities, and genetic correlations from the posterior distribution of this model:

```
posterior.mode(model2.1$VCV)
```

```
##       traitbwt:traitbwt.animal    traittarsus:traitbwt.animal
##                       3.147319                       2.390698
##    traitbwt:traittarsus.animal traittarsus:traittarsus.animal
##                       2.390698                      10.863567
##        traitbwt:traitbwt.units     traittarsus:traitbwt.units
##                       3.823107                       4.044831
##     traitbwt:traittarsus.units  traittarsus:traittarsus.units
##                       4.044831                      17.734520
```

```
heritability.bwt2.1 <- model2.1$VCV[, "traitbwt:traitbwt.animal"] / (model2.1$VCV[, "trait
posterior.mode(heritability.bwt2.1)
```

```
##      var1
## 0.4999336
```

```
heritability.tarsus2.1 <- model2.1$VCV[, "traittarsus:traittarsus.animal"] / (model2.1$VCV
posterior.mode(heritability.tarsus2.1)
```

```
##      var1
## 0.3698826
```

```
genetic.correlation2.1 <- model2.1$VCV[, "traitbwt:traittarsus.animal"] / sqrt(model2.1$VC
posterior.mode(genetic.correlation2.1)
```

```
##      var1
## 0.3815069
```

3.4.2 Adding fixed and random effects

Fixed and random effects can be added just as for the univariate case. Given that our full model of bwt from tutorial 1 had sex as a fixed effect as well as random effects of byear and mother, we could specify a bivariate formulation of this using the following code (including a line to save the output):

```
prior2.2 <- list(
  G = list(
    G1 = list(V = diag(2), nu = 1.002),
    G2 = list(V = diag(2), nu = 1.002),
    G3 = list(V = diag(2), nu = 1.002)
  ),
  R = list(V = diag(2), nu = 1.002)
```

```
)
model2.2 <- MCMCglmm(cbind(bwt, tarsus) ~ trait - 1 + trait:sex,
  random = ~ us(trait):animal + us(trait):byear + us(trait):mother,
  rcov = ~ us(trait):units,
  family = c("gaussian", "gaussian"),
  ginv = list(animal = Ainv), data = gryphon2,
  nitt = 130000, thin = 100, burnin = 30000,
  prior = prior2.2, verbose = FALSE
)
save(model2.2, file = "data/MCMCglmm_model2_2_LongRun.rda")
```

Again we have provided the data from one such run. It can be accessed using the code:

```
load(file = "data/MCMCglmm_model2_2_LongRun.rda")
summary(model2.2)
```

```
##
##  Iterations = 30001:129901
##  Thinning interval  = 100
##  Sample size  = 1000
##
##  DIC: 5832.952
##
##  G-structure:  ~us(trait):animal
##
##                                 post.mean l-95% CI u-95% CI eff.samp
## traitbwt:traitbwt.animal            1.558   0.5616    2.488    230.8
## traittarsus:traitbwt.animal         2.290   0.3241    4.264    274.8
## traitbwt:traittarsus.animal         2.290   0.3241    4.264    274.8
## traittarsus:traittarsus.animal      8.083   0.9063   13.599    228.1
##
##                ~us(trait):byear
##
##                                post.mean l-95% CI u-95% CI eff.samp
## traitbwt:traitbwt.byear          0.96775   0.4124   1.5053     1000
## traittarsus:traitbwt.byear       0.07332  -0.8100   0.9791     1000
## traitbwt:traittarsus.byear       0.07332  -0.8100   0.9791     1000
## traittarsus:traittarsus.byear    3.80720   1.6291   6.3986     1000
##
##                ~us(trait):mother
##
##                                 post.mean l-95% CI u-95% CI eff.samp
## traitbwt:traitbwt.mother            1.335   0.8564   1.8090    871.2
## traittarsus:traitbwt.mother        -1.508  -2.1667  -0.8288    648.6
## traitbwt:traittarsus.mother        -1.508  -2.1667  -0.8288    648.6
```

```
## traittarsus:traittarsus.mother     4.292   2.2380   6.6336    796.0
##
##  R-structure:  ~us(trait):units
##
##                                post.mean l-95% CI u-95% CI eff.samp
## traitbwt:traitbwt.units             2.13    1.304    2.939    469.2
## traittarsus:traitbwt.units          4.81    3.111    6.568    414.7
## traitbwt:traittarsus.units          4.81    3.111    6.568    414.7
## traittarsus:traittarsus.units     14.51    9.419   19.892    261.3
##
##  Location effects: cbind(bwt, tarsus) ~ trait - 1 + trait:sex
##
##                   post.mean l-95% CI u-95% CI eff.samp  pMCMC
## traitbwt             6.2734   5.8152   6.7272     1205 <0.001 ***
## traittarsus         20.3985  19.4021  21.4106     1000 <0.001 ***
## traitbwt:sex2        2.0354   1.7347   2.3529     1000 <0.001 ***
## traittarsus:sex2     0.0705  -0.6949   0.7686     1000  0.868
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

```
autocorr(model2.2$VCV)[, , "traittarsus:traittarsus.animal"][3, 4]
```

```
## [1] 0.1026744
```

We can evaluate the fixed effect, their Ci evaluate their significance.

```
posterior.mode(model2.2$Sol)
```

```
##         traitbwt      traittarsus    traitbwt:sex2 traittarsus:sex2
##       6.26902047      20.35816977       2.06048779      -0.06501522
```

```
HPDinterval(model2.2$Sol, 0.95)
```

```
##                       lower      upper
## traitbwt          5.8151983  6.7272503
## traittarsus      19.4021008 21.4106029
## traitbwt:sex2     1.7347121  2.3528879
## traittarsus:sex2 -0.6948574  0.7686074
## attr(,"Probability")
## [1] 0.95
```

```
plot(model2.2$Sol)
```

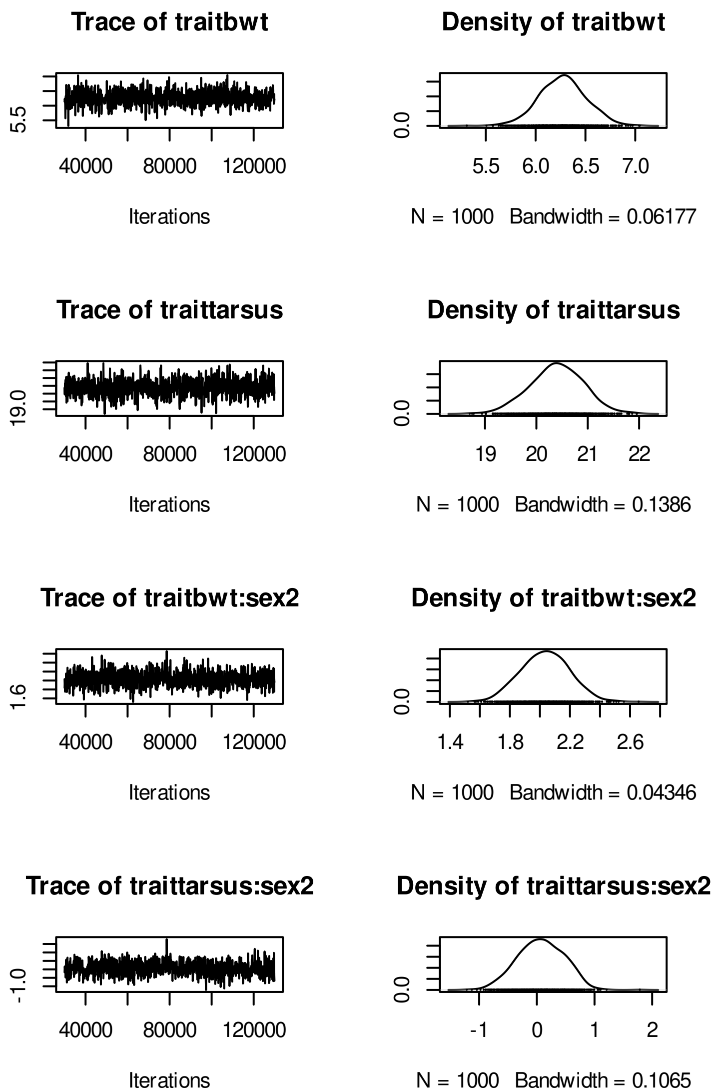


Figure 3.3: Posterior trace and distribution for the fixed effects in model 2.2

As before we can obtain the raw variance component estimates and genetic correlations for the random effects:

```
posterior.mode(model2.2$VCV)
```

```
##       traitbwt:traitbwt.animal    traittarsus:traitbwt.animal
##                      1.3294950                      2.0622374
##    traitbwt:traittarsus.animal traittarsus:traittarsus.animal
##                      2.0622374                      8.3900676
##        traitbwt:traitbwt.byear     traittarsus:traitbwt.byear
##                      0.8118565                      0.2327381
##     traitbwt:traittarsus.byear  traittarsus:traittarsus.byear
##                      0.2327381                      3.7375906
```

```
##      traitbwt:traitbwt.mother    traittarsus:traitbwt.mother
##                     1.4089440                     -1.4963686
##    traitbwt:traittarsus.mother traittarsus:traittarsus.mother
##                    -1.4963686                      3.9386669
##       traitbwt:traitbwt.units     traittarsus:traitbwt.units
##                     2.2353960                      4.3432849
##     traitbwt:traittarsus.units  traittarsus:traittarsus.units
##                     4.3432849                     15.0853981
```

```
genetic.correlation2.2 <- model2.2$VCV[, "traitbwt:traittarsus.animal"] / sqrt(model2.2$VC
maternal.correlation2.2 <- model2.2$VCV[, "traitbwt:traittarsus.mother"] / sqrt(model2.2$V
posterior.mode(genetic.correlation2.2)
```

```
##      var1
## 0.6932486
```

```
posterior.mode(maternal.correlation2.2)
```

```
##       var1
## -0.7431221
```

Evaluation of the statistical support for these genetic and maternal correlations is straightforward. Because we imposed no constraint on their estimation, we can evaluate the extent to which the posterior distributions overlap zero:

```
HPDinterval(genetic.correlation2.2, 0.95)
```

```
##          lower     upper
## var1 0.3062932 0.9197543
## attr(,"Probability")
## [1] 0.95
```

```
HPDinterval(maternal.correlation2.2, 0.95)
```

```
##           lower      upper
## var1 -0.9432297 -0.3210149
## attr(,"Probability")
## [1] 0.95
```

Neither or these posterior distributions overlaps zero, so we can consider them both statistically supported.

3.4.3 Direct estimate of the correlation instead of the covariance.

For this example, we just estimate the correlation at the genetic level, the covariance for the other random effect (`mother` and `byear`) and the residual level was not estimate to help the model to converge and compute faster. The prior will be the same but we change the `pr` argument to be `TRUE` to keep the posterior distribution of random effects. To simplify the following code and facilitate the BLUP extraction, we rename the variable T1 and T2 and estimate correlation only for the additive genetic and residual matrices.

```
gryphon2$T1 <- gryphon2$bwt
gryphon2$T2 <- gryphon2$tarsus
#
model2.3 <- MCMCglmm(cbind(T1, T2) ~ trait - 1 + trait:sex,
  random = ~ corg(trait):animal + corg(trait):byear + corg(trait):mother,
  rcov = ~ corg(trait):units,
  family = c("gaussian", "gaussian"),
  ginv = list(animal = Ainv), data = gryphon2,
  nitt = 130000, thin = 100, burnin = 30000,
  prior = prior2.2, verbose = FALSE, pr = TRUE,
)

save(model2.3, file = "data/MCMCglmm_model2_3_LongRun.rda")
```

Again we have provided the data from one such run. It can be accessed using the code:

```
load(file = "data/MCMCglmm_model2_3_LongRun.rda")
summary(model2.3)
```

```
##
##  Iterations = 30001:129901
##  Thinning interval  = 100
##  Sample size  = 1000
##
##  DIC: 972.9044
##
##  G-structure:  ~corg(trait):animal
##
##                        post.mean l-95% CI u-95% CI eff.samp
## traitT1:traitT1.animal         1        1        1        0
## traitT2:traitT1.animal        -1       -1       -1        0
## traitT1:traitT2.animal        -1       -1       -1        0
## traitT2:traitT2.animal         1        1        1        0
##
##                ~corg(trait):byear
##
##                       post.mean l-95% CI u-95% CI eff.samp
## traitT1:traitT1.byear    1.0000  1.00000    1.000        0
## traitT2:traitT1.byear    0.2436 -0.09388    0.588     1000
## traitT1:traitT2.byear    0.2436 -0.09388    0.588     1000
## traitT2:traitT2.byear    1.0000  1.00000    1.000        0
```

```
##
##                ~corg(trait):mother
##
##                       post.mean l-95% CI u-95% CI eff.samp
## traitT1:traitT1.mother         1        1        1        0
## traitT2:traitT1.mother        -1       -1       -1        0
## traitT1:traitT2.mother        -1       -1       -1        0
## traitT2:traitT2.mother         1        1        1        0
##
##  R-structure:  ~corg(trait):units
##
##                      post.mean l-95% CI u-95% CI eff.samp
## traitT1:traitT1.units         1        1        1        0
## traitT2:traitT1.units         1        1        1        0
## traitT1:traitT2.units         1        1        1        0
## traitT2:traitT2.units         1        1        1        0
##
##  Location effects: cbind(T1, T2) ~ trait - 1 + trait:sex
##
##              post.mean l-95% CI u-95% CI eff.samp  pMCMC
## traitT1        6.29252  5.79418  6.77846     1000 <0.001 ***
## traitT2       20.53149 20.04183 21.00833     1000 <0.001 ***
## traitT1:sex2   2.07254  1.83815  2.32478     1000 <0.001 ***
## traitT2:sex2   0.02657 -0.21610  0.26411     1000  0.864
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

```
autocorr(model2.3$VCV)[, , "traitT2:traitT1.animal"][3, 4]
```

```
## [1] NaN
```

Here we can plot the genetic correlation by extraction the breeding values or BLUP. Just to remember it is an example, the correlation is close to 1 due to a weak prior and model parameters.

```
DvsS <- data.frame(
  Trait = colnames(model2.3$Sol),
  BLUP = posterior.mode(model2.3$Sol),
  CI = HPDinterval((model2.3$Sol))
)
DvsS <- DvsS[5:2622, ] # keep only rows associated with animal

DvsS$ID <- substr(DvsS$Trait, 16, 19)
DvsS$TRAIT <- substr(DvsS$Trait, 6, 7)
summary(factor(DvsS$TRAIT))
```

```
##   T1   T2
```

```
## 1309 1309
```

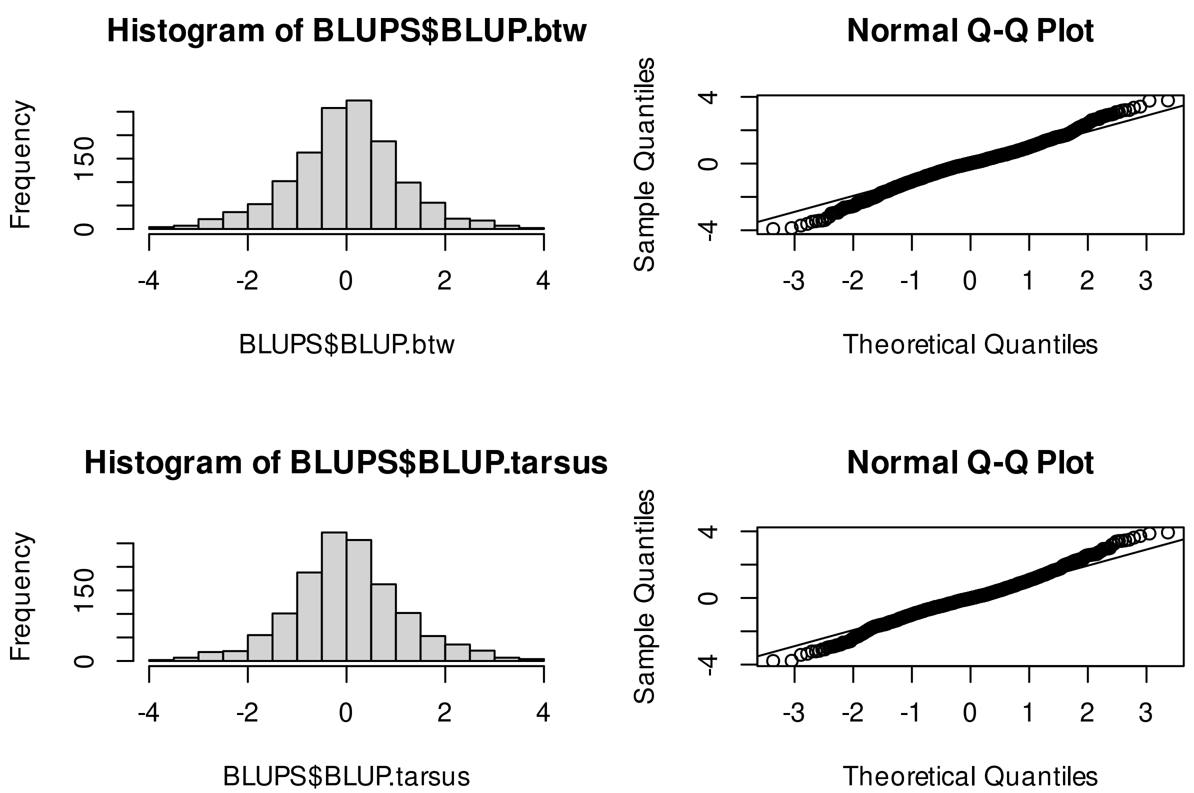
```
DvsS$Trait <- NULL
BLUPS <- reshape(DvsS, v.names = c("BLUP", "CI.lower", "CI.upper"), idvar = "ID", timevar
nrow(BLUPS)
```

```
## [1] 1309
```

```
rownames(BLUPS) <- c()
colnames(BLUPS) <- c("ID", "BLUP.btw", "CI.L.btw", "CI.U.btw", "BLUP.tarsus", "CI.L.tarsus
summary(BLUPS)
```

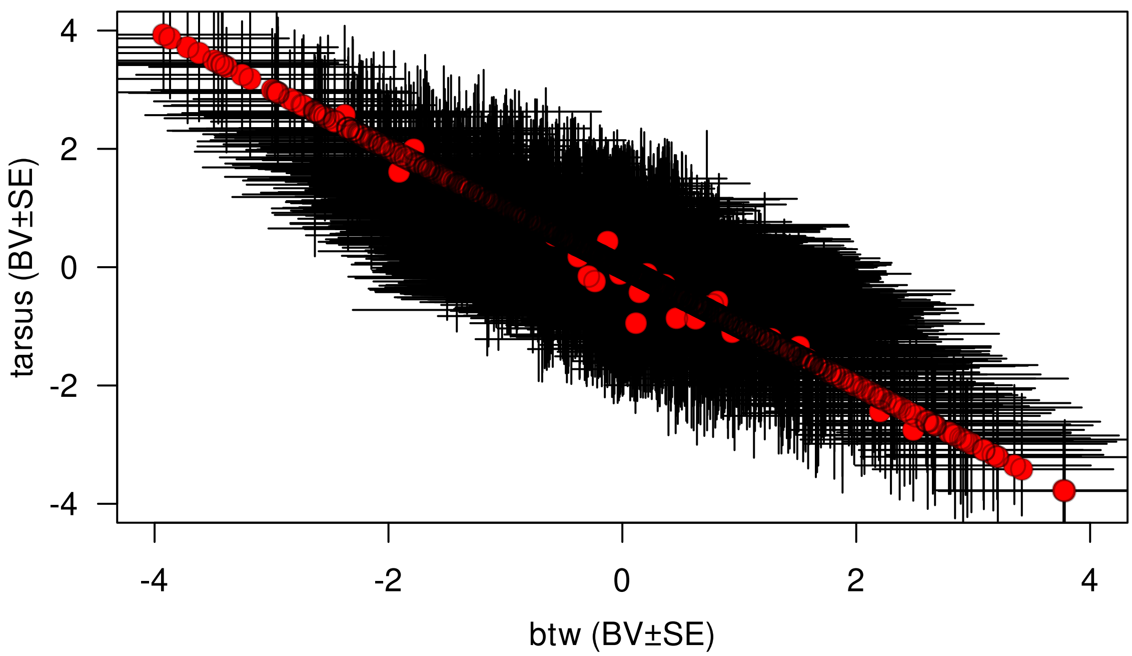
```
##       ID               BLUP.btw          CI.L.btw          CI.U.btw
##  Length:1309        Min.   :-3.92390   Min.   :-5.0229   Min.   :-3.0062
##  Class :character   1st Qu.:-0.65954   1st Qu.:-2.1218   1st Qu.: 0.7462
##  Mode  :character   Median : 0.01183   Median :-1.5472   Median : 1.5745
##                     Mean   :-0.02007   Mean   :-1.4347   Mean   : 1.3860
##                     3rd Qu.: 0.63842   3rd Qu.:-0.7509   3rd Qu.: 2.1033
##                     Max.   : 3.78330   Max.   : 2.7030   Max.   : 4.7851
##   BLUP.tarsus         CI.L.tarsus       CI.U.tarsus
##  Min.   :-3.78353   Min.   :-4.6656   Min.   :-2.6778
##  1st Qu.:-0.64453   1st Qu.:-2.1033   1st Qu.: 0.7505
##  Median :-0.02336   Median :-1.5741   Median : 1.5477
##  Mean   : 0.01820   Mean   :-1.3864   Mean   : 1.4343
##  3rd Qu.: 0.65947   3rd Qu.:-0.7485   3rd Qu.: 2.1219
##  Max.   : 3.93053   Max.   : 3.0061   Max.   : 5.0231
```

```
#
par(mfrow = c(2, 2))
hist(BLUPS$BLUP.btw)
qqnorm(BLUPS$BLUP.btw)
qqline(BLUPS$BLUP.btw)
hist(BLUPS$BLUP.tarsus)
qqnorm(BLUPS$BLUP.tarsus)
qqline(BLUPS$BLUP.tarsus)
```



Here the code to plot the genetic correlation.

```
plot(BLUP.tarsus ~ BLUP.btw, BLUPS, xlab = "", ylab = "", las = 1.2, bty = "o", col = "whi
arrows(x0 = BLUPS$BLUP.btw, y0 = BLUPS$CI.L.tarsus, x1 = BLUPS$BLUP.btw, y1 = BLUPS$CI.U.t
arrows(x0 = BLUPS$CI.L.btw, y0 = BLUPS$BLUP.tarsus, x1 = BLUPS$CI.U.btw, y1 = BLUPS$BLUP.t
points(BLUP.tarsus ~ BLUP.btw, BLUPS, pch = 16, col = "red", cex = 1.5)
points(BLUP.tarsus ~ BLUP.btw, BLUPS, pch = 1, col = rgb(0, 0, 0, 0.3), cex = c(1.5))
mtext("btw (BV±SE)", side = 1, line = 2.4)
mtext("tarsus (BV±SE)", side = 2, line = 2, las = 3)
```



3.4.4 Partitioning (co)variances

As in the tutorial 1, it is possible to partition the variance-covariance matrix between groups (here sex) Note: the model is simplified without sex-specific covariance for the `byear` and `mother` random effect.

```
gryphon2 <- gryphon2[order(gryphon2$sex), ]


prior2.3 <- list(
  G = list(
    G1 = list(V = diag(2), nu = 1.002),
    G2 = list(V = diag(2), nu = 1.002),
    G3 = list(V = diag(2), nu = 1.002),
    G4 = list(V = diag(2), nu = 1.002)
  ),
  R = list(
    V1 = list(V = diag(2), nu = 1.002),
    V2 = list(V = diag(2), nu = 1.002)
  )
)
```

```r
model2.4 <- MCMCglmm(cbind(bwt, tarsus) ~ trait - 1 + trait:sex,
  random = ~ us(at.level(sex, "1"):trait):animal + us(at.level(sex, "2"):trait):animal + i
  rcov = ~ us(at.level(sex, "1"):trait):units + us(at.level(sex, "2"):trait):units,
  family = c("gaussian", "gaussian"),
  ginv = list(animal = Ainv), data = gryphon2,
  nitt = 130000, thin = 100, burnin = 30000,
  prior = prior2.3, verbose = FALSE, pr = TRUE,
)
save(model2.4, file = "data/MCMCglmm_model2_4_LongRun.rda")
```

Again we have provided the data from one such run. It can be accessed using the code:

```r
load(file = "data/MCMCglmm_model2_4_LongRun.rda")
summary(model2.4)
```

```
##
##  Iterations = 30001:129901
##  Thinning interval  = 100
##  Sample size  = 1000
##
##  DIC: 5576.328
##
##  G-structure:  ~us(at.level(sex, "1"):trait):animal
##
##                                                                post.mean
## at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.animal         1.122
## at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.animal      1.127
## at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.animal      1.127
## at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.animal    3.379
##                                                                l-95% CI
## at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.animal        0.1602
## at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.animal    -0.6531
## at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.animal    -0.6531
## at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.animal   0.1844
##                                                                u-95% CI
## at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.animal          2.359
## at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.animal       3.496
## at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.animal       3.496
## at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.animal    8.918
##                                                                eff.samp
## at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.animal          167.5
## at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.animal       119.3
## at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.animal       119.3
## at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.animal    102.6
##
```

```
##                ~us(at.level(sex, "2"):trait):animal
##
##                                                                       post.mean
## at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.animal            1.598
## at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.animal         3.099
## at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.animal         3.099
## at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.animal     10.218
##                                                                       l-95% CI
## at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.animal          0.1895
## at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.animal      -0.5506
## at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.animal      -0.5506
## at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.animal    0.2127
##                                                                       u-95% CI
## at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.animal           3.305
## at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.animal        7.864
## at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.animal        7.864
## at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.animal    24.230
##                                                                       eff.samp
## at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.animal           57.28
## at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.animal        42.01
## at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.animal        42.01
## at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.animal     37.21
##
##                ~idh(trait):byear
##
##                   post.mean l-95% CI u-95% CI eff.samp
## traitbwt.byear       0.9309   0.4614    1.463     1000
## traittarsus.byear    4.0310   1.9268    6.724     1000
##
##                ~idh(trait):mother
##
##                    post.mean l-95% CI u-95% CI eff.samp
## traitbwt.mother        1.924    1.406    2.398    667.6
## traittarsus.mother     7.093    4.626    9.681    698.5
##
##  R-structure:  ~us(at.level(sex, "1"):trait):units
##
##                                                                      post.mean
## at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.units            2.090
## at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.units         4.533
## at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.units         4.533
## at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.units     14.113
##                                                                     l-95% CI
## at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.units          0.9958
## at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.units       2.4185
## at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.units       2.4185
## at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.units    8.1848
```

```
##                                                                   u-95% CI
## at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.units        3.128
## at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.units     6.875
## at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.units     6.875
## at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.units 18.935
##                                                                   eff.samp
## at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.units        207.2
## at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.units     168.4
## at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.units     168.4
## at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.units  185.3
##
##                ~us(at.level(sex, "2"):trait):units
##
##                                                                   post.mean
## at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.units         1.782
## at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.units      3.697
## at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.units      3.697
## at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.units  12.437
##                                                                   l-95% CI
## at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.units       0.2776
## at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.units   -0.3141
## at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.units   -0.3141
## at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.units 0.1776
##                                                                   u-95% CI
## at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.units        3.115
## at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.units     7.218
## at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.units     7.218
## at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.units 21.903
##                                                                   eff.samp
## at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.units        52.55
## at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.units     51.90
## at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.units     51.90
## at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.units  39.20
##
##  Location effects: cbind(bwt, tarsus) ~ trait - 1 + trait:sex
##
##                   post.mean l-95% CI u-95% CI eff.samp  pMCMC
## traitbwt            6.30098  5.89218  6.78834   1000.0 <0.001 ***
## traittarsus        20.45577 19.53577 21.34719   1129.8 <0.001 ***
## traitbwt:sex2       2.01306  1.63662  2.38011    887.4 <0.001 ***
## traittarsus:sex2   0.05817 -0.86635  0.89119   1016.6  0.896
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

```r
autocorr(model2.4$VCV)
```

```
## , , at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.animal
##
##          at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.animal
## Lag 0                                                        1.00000000
## Lag 100                                                      0.64694479
## Lag 500                                                      0.18648179
## Lag 1000                                                     0.10392219
## Lag 5000                                                    -0.04275072
##          at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.animal
## Lag 0                                                           0.84704874
## Lag 100                                                         0.60161240
## Lag 500                                                         0.20180692
## Lag 1000                                                        0.10068129
## Lag 5000                                                       -0.03878312
##          at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.animal
## Lag 0                                                           0.84704874
## Lag 100                                                         0.60161240
## Lag 500                                                         0.20180692
## Lag 1000                                                        0.10068129
## Lag 5000                                                       -0.03878312
##          at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.animal
## Lag 0                                                              0.53041407
## Lag 100                                                            0.39413485
## Lag 500                                                            0.16964194
## Lag 1000                                                           0.11264314
## Lag 5000                                                          -0.01013697
##          at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.animal
## Lag 0                                                       -0.07132000
## Lag 100                                                     -0.09608251
## Lag 500                                                     -0.05360431
## Lag 1000                                                    -0.02600414
## Lag 5000                                                    -0.02326421
##          at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.animal
## Lag 0                                                          -0.07404287
## Lag 100                                                        -0.08742103
## Lag 500                                                        -0.05376905
## Lag 1000                                                       -0.03219125
## Lag 5000                                                        0.02771727
##          at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.animal
## Lag 0                                                          -0.07404287
## Lag 100                                                        -0.08742103
## Lag 500                                                        -0.05376905
## Lag 1000                                                       -0.03219125
## Lag 5000                                                        0.02771727
```

```
##           at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.animal
## Lag 0                                                              -0.06663301
## Lag 100                                                            -0.07398282
## Lag 500                                                            -0.03873715
## Lag 1000                                                           -0.03346102
## Lag 5000                                                            0.06535632
##           traitbwt.byear traittarsus.byear traitbwt.mother traittarsus.mother
## Lag 0       -0.002044905        0.06061428     -0.13681757        0.063034744
## Lag 100     -0.029101625        0.04741082     -0.09232454        0.062553003
## Lag 500     -0.025891155        0.04101237     -0.01510511       -0.026837884
## Lag 1000     0.029398462        0.02792539     -0.02514900        0.009578198
## Lag 5000    -0.016122661        0.03081539      0.04189460       -0.039791141
##           at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.units
## Lag 0                                                      -0.842319278
## Lag 100                                                    -0.569203867
## Lag 500                                                    -0.167844469
## Lag 1000                                                   -0.114647645
## Lag 5000                                                   -0.002132053
##           at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.units
## Lag 0                                                         -0.708901550
## Lag 100                                                       -0.517998161
## Lag 500                                                       -0.167589741
## Lag 1000                                                      -0.110500558
## Lag 5000                                                       0.002914291
##           at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.units
## Lag 0                                                         -0.708901550
## Lag 100                                                       -0.517998161
## Lag 500                                                       -0.167589741
## Lag 1000                                                      -0.110500558
## Lag 5000                                                       0.002914291
##           at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.units
## Lag 0                                                            -0.438123204
## Lag 100                                                          -0.337083166
## Lag 500                                                          -0.129292647
## Lag 1000                                                         -0.103678560
## Lag 5000                                                         -0.001926232
##           at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.units
## Lag 0                                                        0.07807105
## Lag 100                                                      0.10707885
## Lag 500                                                      0.05568856
## Lag 1000                                                     0.02521629
## Lag 5000                                                     0.01402475
##           at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.units
## Lag 0                                                           0.06679340
## Lag 100                                                         0.08704308
## Lag 500                                                         0.05892190
## Lag 1000                                                        0.02676188
```

```
## Lag 5000                                                    -0.03056683
##          at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.units
## Lag 0                                                        0.06679340
## Lag 100                                                      0.08704308
## Lag 500                                                      0.05892190
## Lag 1000                                                     0.02676188
## Lag 5000                                                    -0.03056683
##          at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.units
## Lag 0                                                           0.04797898
## Lag 100                                                         0.05730717
## Lag 500                                                         0.04727555
## Lag 1000                                                        0.02677473
## Lag 5000                                                       -0.06608227
##
## , , at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.animal
##
##          at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.animal
## Lag 0                                                     0.847048735
## Lag 100                                                   0.596411029
## Lag 500                                                   0.228550625
## Lag 1000                                                  0.137616124
## Lag 5000                                                  0.009429906
##          at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.animal
## Lag 0                                                         1.00000000
## Lag 100                                                       0.71730236
## Lag 500                                                       0.27616079
## Lag 1000                                                      0.13795063
## Lag 5000                                                      0.01144749
##          at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.animal
## Lag 0                                                         1.00000000
## Lag 100                                                       0.71730236
## Lag 500                                                       0.27616079
## Lag 1000                                                      0.13795063
## Lag 5000                                                      0.01144749
##          at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.animal
## Lag 0                                                              0.7989970
## Lag 100                                                            0.6014134
## Lag 500                                                            0.2515262
## Lag 1000                                                           0.1354306
## Lag 5000                                                           0.0136445
##          at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.animal
## Lag 0                                                    -0.069644149
## Lag 100                                                  -0.094348331
## Lag 500                                                  -0.069174874
## Lag 1000                                                 -0.030980734
## Lag 5000                                                 -0.001770693
##          at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.animal
```

```
## Lag 0                                                               -0.09266557
## Lag 100                                                             -0.10417316
## Lag 500                                                             -0.06908668
## Lag 1000                                                            -0.04934221
## Lag 5000                                                             0.03968797
##          at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.animal
## Lag 0                                                               -0.09266557
## Lag 100                                                             -0.10417316
## Lag 500                                                             -0.06908668
## Lag 1000                                                            -0.04934221
## Lag 5000                                                             0.03968797
##          at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.animal
## Lag 0                                                                  -0.10219567
## Lag 100                                                                -0.10740690
## Lag 500                                                                -0.05829130
## Lag 1000                                                               -0.05667648
## Lag 5000                                                                0.08311412
##          traitbwt.byear traittarsus.byear traitbwt.mother traittarsus.mother
## Lag 0       -0.03731153        0.05572330     -0.12626725         0.06865980
## Lag 100     -0.04492620        0.05076637     -0.08142219         0.05404288
## Lag 500     -0.03460527        0.03246607     -0.03107773        -0.02899561
## Lag 1000     0.01459594        0.01717445     -0.05078674         0.01110690
## Lag 5000    -0.01688700        0.03883380      0.02698184        -0.03307579
##          at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.units
## Lag 0                                                        -0.73143141
## Lag 100                                                      -0.52689086
## Lag 500                                                      -0.22551523
## Lag 1000                                                     -0.12616708
## Lag 5000                                                     -0.04647821
##          at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.units
## Lag 0                                                           -0.82495927
## Lag 100                                                         -0.60990914
## Lag 500                                                         -0.24464022
## Lag 1000                                                        -0.12721295
## Lag 5000                                                        -0.03841367
##          at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.units
## Lag 0                                                           -0.82495927
## Lag 100                                                         -0.60990914
## Lag 500                                                         -0.24464022
## Lag 1000                                                        -0.12721295
## Lag 5000                                                        -0.03841367
##          at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.units
## Lag 0                                                              -0.64394327
## Lag 100                                                            -0.48995337
## Lag 500                                                            -0.19725633
## Lag 1000                                                           -0.10852446
## Lag 5000                                                           -0.02105523
```

```
##          at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.units
## Lag 0                                                       0.082481767
## Lag 100                                                     0.105417000
## Lag 500                                                     0.073280263
## Lag 1000                                                    0.028355398
## Lag 5000                                                   -0.006019758
##          at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.units
## Lag 0                                                          0.09308370
## Lag 100                                                        0.10680733
## Lag 500                                                        0.07810010
## Lag 1000                                                       0.04359553
## Lag 5000                                                      -0.04726853
##          at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.units
## Lag 0                                                          0.09308370
## Lag 100                                                        0.10680733
## Lag 500                                                        0.07810010
## Lag 1000                                                       0.04359553
## Lag 5000                                                      -0.04726853
##          at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.units
## Lag 0                                                             0.08843633
## Lag 100                                                           0.09343376
## Lag 500                                                           0.06886426
## Lag 1000                                                          0.05338682
## Lag 5000                                                         -0.09185034
##
## , , at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.animal
##
##          at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.animal
## Lag 0                                                        0.847048735
## Lag 100                                                      0.596411029
## Lag 500                                                      0.228550625
## Lag 1000                                                     0.137616124
## Lag 5000                                                     0.009429906
##          at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.animal
## Lag 0                                                           1.00000000
## Lag 100                                                         0.71730236
## Lag 500                                                         0.27616079
## Lag 1000                                                        0.13795063
## Lag 5000                                                        0.01144749
##          at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.animal
## Lag 0                                                           1.00000000
## Lag 100                                                         0.71730236
## Lag 500                                                         0.27616079
## Lag 1000                                                        0.13795063
## Lag 5000                                                        0.01144749
##          at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.animal
## Lag 0                                                              0.7989970
```

```
## Lag 100                                                           0.6014134
## Lag 500                                                           0.2515262
## Lag 1000                                                          0.1354306
## Lag 5000                                                          0.0136445
##          at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.animal
## Lag 0                                                      -0.069644149
## Lag 100                                                    -0.094348331
## Lag 500                                                    -0.069174874
## Lag 1000                                                   -0.030980734
## Lag 5000                                                   -0.001770693
##          at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.animal
## Lag 0                                                         -0.09266557
## Lag 100                                                       -0.10417316
## Lag 500                                                       -0.06908668
## Lag 1000                                                      -0.04934221
## Lag 5000                                                       0.03968797
##          at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.animal
## Lag 0                                                         -0.09266557
## Lag 100                                                       -0.10417316
## Lag 500                                                       -0.06908668
## Lag 1000                                                      -0.04934221
## Lag 5000                                                       0.03968797
##          at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.animal
## Lag 0                                                            -0.10219567
## Lag 100                                                          -0.10740690
## Lag 500                                                          -0.05829130
## Lag 1000                                                         -0.05667648
## Lag 5000                                                          0.08311412
##          traitbwt.byear traittarsus.byear traitbwt.mother traittarsus.mother
## Lag 0       -0.03731153        0.05572330     -0.12626725         0.06865980
## Lag 100     -0.04492620        0.05076637     -0.08142219         0.05404288
## Lag 500     -0.03460527        0.03246607     -0.03107773        -0.02899561
## Lag 1000     0.01459594        0.01717445     -0.05078674         0.01110690
## Lag 5000    -0.01688700        0.03883380      0.02698184        -0.03307579
##          at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.units
## Lag 0                                                       -0.73143141
## Lag 100                                                     -0.52689086
## Lag 500                                                     -0.22551523
## Lag 1000                                                    -0.12616708
## Lag 5000                                                    -0.04647821
##          at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.units
## Lag 0                                                          -0.82495927
## Lag 100                                                        -0.60990914
## Lag 500                                                        -0.24464022
## Lag 1000                                                       -0.12721295
## Lag 5000                                                       -0.03841367
##          at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.units
```

```
## Lag 0                                                   -0.82495927
## Lag 100                                                 -0.60990914
## Lag 500                                                 -0.24464022
## Lag 1000                                                -0.12721295
## Lag 5000                                                -0.03841367
##          at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.units
## Lag 0                                                     -0.64394327
## Lag 100                                                   -0.48995337
## Lag 500                                                   -0.19725633
## Lag 1000                                                  -0.10852446
## Lag 5000                                                  -0.02105523
##          at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.units
## Lag 0                                                 0.082481767
## Lag 100                                               0.105417000
## Lag 500                                               0.073280263
## Lag 1000                                              0.028355398
## Lag 5000                                             -0.006019758
##          at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.units
## Lag 0                                                      0.09308370
## Lag 100                                                    0.10680733
## Lag 500                                                    0.07810010
## Lag 1000                                                   0.04359553
## Lag 5000                                                  -0.04726853
##          at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.units
## Lag 0                                                      0.09308370
## Lag 100                                                    0.10680733
## Lag 500                                                    0.07810010
## Lag 1000                                                   0.04359553
## Lag 5000                                                  -0.04726853
##          at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.units
## Lag 0                                                        0.08843633
## Lag 100                                                      0.09343376
## Lag 500                                                      0.06886426
## Lag 1000                                                     0.05338682
## Lag 5000                                                    -0.09185034
##
## , , at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.animal
##
##          at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.animal
## Lag 0                                                    0.5304141
## Lag 100                                                  0.3737195
## Lag 500                                                  0.1441203
## Lag 1000                                                 0.1503417
## Lag 5000                                                 0.1187940
##          at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.animal
## Lag 0                                                       0.7989970
## Lag 100                                                     0.5706521
```

```
## Lag 500                                                          0.2430451
## Lag 1000                                                         0.1680830
## Lag 5000                                                         0.1259980
##          at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.animal
## Lag 0                                                            0.7989970
## Lag 100                                                          0.5706521
## Lag 500                                                          0.2430451
## Lag 1000                                                         0.1680830
## Lag 5000                                                         0.1259980
##          at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.animal
## Lag 0                                                              1.00000000
## Lag 100                                                            0.73196692
## Lag 500                                                            0.31335783
## Lag 1000                                                           0.18501263
## Lag 5000                                                           0.08438218
##          at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.animal
## Lag 0                                                        -0.01785209
## Lag 100                                                      -0.03508025
## Lag 500                                                      -0.04733762
## Lag 1000                                                     -0.01709422
## Lag 5000                                                     -0.01586047
##          at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.animal
## Lag 0                                                          -0.038020441
## Lag 100                                                        -0.045171003
## Lag 500                                                        -0.050004069
## Lag 1000                                                       -0.054183547
## Lag 5000                                                       -0.004955516
##          at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.animal
## Lag 0                                                          -0.038020441
## Lag 100                                                        -0.045171003
## Lag 500                                                        -0.050004069
## Lag 1000                                                       -0.054183547
## Lag 5000                                                       -0.004955516
##          at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.animal
## Lag 0                                                             -0.05447207
## Lag 100                                                           -0.05998184
## Lag 500                                                           -0.06158778
## Lag 1000                                                          -0.08267333
## Lag 5000                                                           0.02065741
##          traitbwt.byear traittarsus.byear traitbwt.mother traittarsus.mother
## Lag 0      -0.060159939        0.06450755   -0.0973321863       -0.009350685
## Lag 100    -0.043720033        0.03483594   -0.0765923141       -0.006212912
## Lag 500    -0.052466217        0.02987272   -0.0662772868       -0.030465249
## Lag 1000   -0.001034192        0.03110963   -0.0728720391        0.009855596
## Lag 5000   -0.034160786        0.05472996    0.0008533055        0.003426058
##          at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.units
## Lag 0                                                        -0.4637838
```

```
## Lag 100                                                   -0.3337342
## Lag 500                                                   -0.1618186
## Lag 1000                                                  -0.1329387
## Lag 5000                                                  -0.1239580
##          at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.units
## Lag 0                                                          -0.6583252
## Lag 100                                                        -0.4881849
## Lag 500                                                        -0.2287167
## Lag 1000                                                       -0.1381960
## Lag 5000                                                       -0.1179873
##          at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.units
## Lag 0                                                          -0.6583252
## Lag 100                                                        -0.4881849
## Lag 500                                                        -0.2287167
## Lag 1000                                                       -0.1381960
## Lag 5000                                                       -0.1179873
##          at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.units
## Lag 0                                                             -0.76001059
## Lag 100                                                           -0.57358014
## Lag 500                                                           -0.25179771
## Lag 1000                                                          -0.12123408
## Lag 5000                                                          -0.07986147
##          at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.units
## Lag 0                                                     0.02870904
## Lag 100                                                   0.03399695
## Lag 500                                                   0.05485675
## Lag 1000                                                  0.01651664
## Lag 5000                                                  0.01516504
##          at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.units
## Lag 0                                                         0.039633904
## Lag 100                                                       0.041502118
## Lag 500                                                       0.059018043
## Lag 1000                                                      0.052958967
## Lag 5000                                                     -0.002274568
##          at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.units
## Lag 0                                                         0.039633904
## Lag 100                                                       0.041502118
## Lag 500                                                       0.059018043
## Lag 1000                                                      0.052958967
## Lag 5000                                                     -0.002274568
##          at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.units
## Lag 0                                                              0.04584246
## Lag 100                                                            0.04763329
## Lag 500                                                            0.06852725
## Lag 1000                                                           0.08362165
## Lag 5000                                                          -0.03430204
##
```

```
## , , at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.animal
##
##          at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.animal
## Lag 0                                                        -0.07132000
## Lag 100                                                      -0.06108550
## Lag 500                                                      -0.06344456
## Lag 1000                                                     -0.02628413
## Lag 5000                                                      0.10351490
##          at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.animal
## Lag 0                                                           -0.0696441487
## Lag 100                                                         -0.0685711479
## Lag 500                                                         -0.0543839240
## Lag 1000                                                         0.0004950661
## Lag 5000                                                         0.1221823016
##          at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.animal
## Lag 0                                                           -0.0696441487
## Lag 100                                                         -0.0685711479
## Lag 500                                                         -0.0543839240
## Lag 1000                                                         0.0004950661
## Lag 5000                                                         0.1221823016
##          at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.animal
## Lag 0                                                              -0.0178520882
## Lag 100                                                            -0.0173974776
## Lag 500                                                            -0.0002494694
## Lag 1000                                                            0.0551913450
## Lag 5000                                                            0.1333840825
##          at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.animal
## Lag 0                                                          1.0000000
## Lag 100                                                        0.8242352
## Lag 500                                                        0.5296802
## Lag 1000                                                       0.3040607
## Lag 5000                                                      -0.1276161
##          at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.animal
## Lag 0                                                             0.9099634
## Lag 100                                                           0.8047694
## Lag 500                                                           0.5857973
## Lag 1000                                                          0.3552775
## Lag 5000                                                         -0.1485103
##          at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.animal
## Lag 0                                                             0.9099634
## Lag 100                                                           0.8047694
## Lag 500                                                           0.5857973
## Lag 1000                                                          0.3552775
## Lag 5000                                                         -0.1485103
##          at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.animal
## Lag 0                                                                0.7704756
## Lag 100                                                              0.7082472
```

```
## Lag 500                                                              0.5569812
## Lag 1000                                                             0.3517296
## Lag 5000                                                            -0.1453072
##          traitbwt.byear traittarsus.byear traitbwt.mother traittarsus.mother
## Lag 0       -0.03784246        0.04916122    -0.025145260        -0.13999847
## Lag 100     -0.01888261        0.04551933    -0.009748633        -0.14616483
## Lag 500     -0.01864811        0.07395050     0.029035276        -0.12958636
## Lag 1000    -0.02117775        0.06164183     0.068666314        -0.09577992
## Lag 5000     0.01769136        0.04869291     0.037573009         0.01686724
##          at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.units
## Lag 0                                                      0.048426202
## Lag 100                                                    0.039795097
## Lag 500                                                    0.046311373
## Lag 1000                                                   0.005469282
## Lag 5000                                                  -0.104125437
##          at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.units
## Lag 0                                                         0.043207572
## Lag 100                                                       0.043210916
## Lag 500                                                       0.033044478
## Lag 1000                                                     -0.004411742
## Lag 5000                                                     -0.110707718
##          at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.units
## Lag 0                                                         0.043207572
## Lag 100                                                       0.043210916
## Lag 500                                                       0.033044478
## Lag 1000                                                     -0.004411742
## Lag 5000                                                     -0.110707718
##          at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.units
## Lag 0                                                               0.01554818
## Lag 100                                                             0.02352457
## Lag 500                                                             0.01217491
## Lag 1000                                                           -0.02394172
## Lag 5000                                                           -0.13812594
##          at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.units
## Lag 0                                                       -0.9369474
## Lag 100                                                     -0.8092241
## Lag 500                                                     -0.5186132
## Lag 1000                                                    -0.2947735
## Lag 5000                                                     0.1226249
##          at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.units
## Lag 0                                                          -0.8725969
## Lag 100                                                        -0.7954903
## Lag 500                                                        -0.5688119
## Lag 1000                                                       -0.3390939
## Lag 5000                                                        0.1455303
##          at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.units
## Lag 0                                                          -0.8725969
```

```
## Lag 100                                                    -0.7954903
## Lag 500                                                    -0.5688119
## Lag 1000                                                   -0.3390939
## Lag 5000                                                    0.1455303
##          at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.units
## Lag 0                                                         -0.7525481
## Lag 100                                                       -0.7086874
## Lag 500                                                       -0.5421136
## Lag 1000                                                      -0.3389906
## Lag 5000                                                       0.1485387
##
## , , at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.animal
##
##          at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.animal
## Lag 0                                                    -0.074042865
## Lag 100                                                  -0.072737049
## Lag 500                                                  -0.064855516
## Lag 1000                                                 -0.004245299
## Lag 5000                                                  0.126495395
##          at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.animal
## Lag 0                                                       -0.092665568
## Lag 100                                                     -0.096939661
## Lag 500                                                     -0.070837135
## Lag 1000                                                     0.006501962
## Lag 5000                                                     0.148898005
##          at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.animal
## Lag 0                                                       -0.092665568
## Lag 100                                                     -0.096939661
## Lag 500                                                     -0.070837135
## Lag 1000                                                     0.006501962
## Lag 5000                                                     0.148898005
##          at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.animal
## Lag 0                                                          -0.038020441
## Lag 100                                                        -0.039681669
## Lag 500                                                        -0.006820427
## Lag 1000                                                        0.063529955
## Lag 5000                                                        0.163665055
##          at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.animal
## Lag 0                                                       0.9099634
## Lag 100                                                     0.7863387
## Lag 500                                                     0.5413307
## Lag 1000                                                    0.3118422
## Lag 5000                                                   -0.1191809
##          at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.animal
## Lag 0                                                          1.0000000
## Lag 100                                                        0.8933098
## Lag 500                                                        0.6382613
```

```
## Lag 1000                                                         0.3875538
## Lag 5000                                                        -0.1480316
##          at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.animal
## Lag 0                                                            1.0000000
## Lag 100                                                          0.8933098
## Lag 500                                                          0.6382613
## Lag 1000                                                         0.3875538
## Lag 5000                                                        -0.1480316
##          at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.animal
## Lag 0                                                               0.9445430
## Lag 100                                                             0.8642926
## Lag 500                                                             0.6377101
## Lag 1000                                                            0.3971583
## Lag 5000                                                           -0.1545401
##          traitbwt.byear traittarsus.byear traitbwt.mother traittarsus.mother
## Lag 0       -0.04691870        0.05505699      0.03372293        -0.18311492
## Lag 100     -0.03261563        0.04790144      0.03175029        -0.18180192
## Lag 500     -0.02904559        0.05050843      0.04377317        -0.16642684
## Lag 1000    -0.03811545        0.05361475      0.07019878        -0.12467546
## Lag 5000     0.04062218        0.04654678      0.03310770         0.01019974
##          at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.units
## Lag 0                                                       0.04443896
## Lag 100                                                     0.04551916
## Lag 500                                                     0.04357037
## Lag 1000                                                   -0.01792034
## Lag 5000                                                   -0.12752563
##          at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.units
## Lag 0                                                          0.04900783
## Lag 100                                                        0.06050152
## Lag 500                                                        0.04114675
## Lag 1000                                                      -0.01839006
## Lag 5000                                                      -0.13689966
##          at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.units
## Lag 0                                                          0.04900783
## Lag 100                                                        0.06050152
## Lag 500                                                        0.04114675
## Lag 1000                                                      -0.01839006
## Lag 5000                                                      -0.13689966
##          at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.units
## Lag 0                                                             0.02477085
## Lag 100                                                           0.03939172
## Lag 500                                                           0.02069295
## Lag 1000                                                         -0.04020316
## Lag 5000                                                         -0.16427556
##          at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.units
## Lag 0                                                        -0.8748666
## Lag 100                                                      -0.7865075
```

```
## Lag 500                                          -0.5347377
## Lag 1000                                         -0.3099292
## Lag 5000                                          0.1242901
##          at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.units
## Lag 0                                                          -0.9629330
## Lag 100                                                        -0.8851422
## Lag 500                                                        -0.6211970
## Lag 1000                                                       -0.3754777
## Lag 5000                                                        0.1511004
##          at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.units
## Lag 0                                                          -0.9629330
## Lag 100                                                        -0.8851422
## Lag 500                                                        -0.6211970
## Lag 1000                                                       -0.3754777
## Lag 5000                                                        0.1511004
##          at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.units
## Lag 0                                                             -0.9191068
## Lag 100                                                           -0.8609263
## Lag 500                                                           -0.6233180
## Lag 1000                                                          -0.3879589
## Lag 5000                                                           0.1606066
##
## , , at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.animal
##
##          at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.animal
## Lag 0                                                     -0.074042865
## Lag 100                                                   -0.072737049
## Lag 500                                                   -0.064855516
## Lag 1000                                                  -0.004245299
## Lag 5000                                                   0.126495395
##          at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.animal
## Lag 0                                                        -0.092665568
## Lag 100                                                      -0.096939661
## Lag 500                                                      -0.070837135
## Lag 1000                                                      0.006501962
## Lag 5000                                                      0.148898005
##          at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.animal
## Lag 0                                                        -0.092665568
## Lag 100                                                      -0.096939661
## Lag 500                                                      -0.070837135
## Lag 1000                                                      0.006501962
## Lag 5000                                                      0.148898005
##          at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.animal
## Lag 0                                                           -0.038020441
## Lag 100                                                         -0.039681669
## Lag 500                                                         -0.006820427
## Lag 1000                                                         0.063529955
```

```
## Lag 5000                                                    0.163665055
##          at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.animal
## Lag 0                                                    0.9099634
## Lag 100                                                  0.7863387
## Lag 500                                                  0.5413307
## Lag 1000                                                 0.3118422
## Lag 5000                                                -0.1191809
##          at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.animal
## Lag 0                                                       1.0000000
## Lag 100                                                     0.8933098
## Lag 500                                                     0.6382613
## Lag 1000                                                    0.3875538
## Lag 5000                                                   -0.1480316
##          at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.animal
## Lag 0                                                       1.0000000
## Lag 100                                                     0.8933098
## Lag 500                                                     0.6382613
## Lag 1000                                                    0.3875538
## Lag 5000                                                   -0.1480316
##          at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.animal
## Lag 0                                                          0.9445430
## Lag 100                                                        0.8642926
## Lag 500                                                        0.6377101
## Lag 1000                                                       0.3971583
## Lag 5000                                                      -0.1545401
##          traitbwt.byear traittarsus.byear traitbwt.mother traittarsus.mother
## Lag 0       -0.04691870        0.05505699      0.03372293        -0.18311492
## Lag 100     -0.03261563        0.04790144      0.03175029        -0.18180192
## Lag 500     -0.02904559        0.05050843      0.04377317        -0.16642684
## Lag 1000    -0.03811545        0.05361475      0.07019878        -0.12467546
## Lag 5000     0.04062218        0.04654678      0.03310770         0.01019974
##          at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.units
## Lag 0                                                   0.04443896
## Lag 100                                                 0.04551916
## Lag 500                                                 0.04357037
## Lag 1000                                               -0.01792034
## Lag 5000                                               -0.12752563
##          at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.units
## Lag 0                                                      0.04900783
## Lag 100                                                    0.06050152
## Lag 500                                                    0.04114675
## Lag 1000                                                  -0.01839006
## Lag 5000                                                  -0.13689966
##          at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.units
## Lag 0                                                      0.04900783
## Lag 100                                                    0.06050152
## Lag 500                                                    0.04114675
```

```
## Lag 1000                                                   -0.01839006
## Lag 5000                                                   -0.13689966
##          at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.units
## Lag 0                                                          0.02477085
## Lag 100                                                        0.03939172
## Lag 500                                                        0.02069295
## Lag 1000                                                      -0.04020316
## Lag 5000                                                      -0.16427556
##          at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.units
## Lag 0                                                   -0.8748666
## Lag 100                                                 -0.7865075
## Lag 500                                                 -0.5347377
## Lag 1000                                                -0.3099292
## Lag 5000                                                 0.1242901
##          at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.units
## Lag 0                                                       -0.9629330
## Lag 100                                                     -0.8851422
## Lag 500                                                     -0.6211970
## Lag 1000                                                    -0.3754777
## Lag 5000                                                     0.1511004
##          at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.units
## Lag 0                                                       -0.9629330
## Lag 100                                                     -0.8851422
## Lag 500                                                     -0.6211970
## Lag 1000                                                    -0.3754777
## Lag 5000                                                     0.1511004
##          at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.units
## Lag 0                                                           -0.9191068
## Lag 100                                                         -0.8609263
## Lag 500                                                         -0.6233180
## Lag 1000                                                        -0.3879589
## Lag 5000                                                         0.1606066
##
## , , at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.animal
##
##          at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.animal
## Lag 0                                                  -0.066633008
## Lag 100                                                -0.069354252
## Lag 500                                                -0.053416684
## Lag 1000                                                0.001180564
## Lag 5000                                                0.142470162
##          at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.animal
## Lag 0                                                      -0.102195672
## Lag 100                                                    -0.107130141
## Lag 500                                                    -0.073576929
## Lag 1000                                                   -0.004189061
## Lag 5000                                                    0.167339055
```

```
##          at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.animal
## Lag 0                                                         -0.102195672
## Lag 100                                                       -0.107130141
## Lag 500                                                       -0.073576929
## Lag 1000                                                      -0.004189061
## Lag 5000                                                       0.167339055
##          at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.animal
## Lag 0                                                             -0.05447207
## Lag 100                                                           -0.05707224
## Lag 500                                                           -0.01853426
## Lag 1000                                                           0.04684883
## Lag 5000                                                           0.17837197
##          at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.animal
## Lag 0                                                         0.7704756
## Lag 100                                                       0.6843951
## Lag 500                                                       0.5050605
## Lag 1000                                                      0.2977972
## Lag 5000                                                     -0.1058223
##          at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.animal
## Lag 0                                                            0.9445430
## Lag 100                                                          0.8556548
## Lag 500                                                          0.6303848
## Lag 1000                                                         0.3904095
## Lag 5000                                                        -0.1424423
##          at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.animal
## Lag 0                                                            0.9445430
## Lag 100                                                          0.8556548
## Lag 500                                                          0.6303848
## Lag 1000                                                         0.3904095
## Lag 5000                                                        -0.1424423
##          at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.animal
## Lag 0                                                               1.0000000
## Lag 100                                                             0.9100529
## Lag 500                                                             0.6616827
## Lag 1000                                                            0.4121439
## Lag 5000                                                           -0.1590568
##          traitbwt.byear traittarsus.byear traitbwt.mother traittarsus.mother
## Lag 0       -0.03974818        0.04854354      0.04924110        -0.22289117
## Lag 100     -0.03767078        0.04176415      0.03930577        -0.20950998
## Lag 500     -0.03440434        0.03555315      0.05305906        -0.18185253
## Lag 1000    -0.02822560        0.04567963      0.06510782        -0.12092658
## Lag 5000     0.05272181        0.04246380      0.02211597         0.02036647
##          at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.units
## Lag 0                                                       0.04061110
## Lag 100                                                     0.04206692
## Lag 500                                                     0.03373343
## Lag 1000                                                   -0.01881550
```

```
## Lag 5000                                                     -0.13859641
##          at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.units
## Lag 0                                                            0.05879880
## Lag 100                                                          0.06872711
## Lag 500                                                          0.04634425
## Lag 1000                                                        -0.01579800
## Lag 5000                                                        -0.14960797
##          at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.units
## Lag 0                                                            0.05879880
## Lag 100                                                          0.06872711
## Lag 500                                                          0.04634425
## Lag 1000                                                        -0.01579800
## Lag 5000                                                        -0.14960797
##          at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.units
## Lag 0                                                               0.04254878
## Lag 100                                                             0.05461840
## Lag 500                                                             0.03646094
## Lag 1000                                                           -0.04023461
## Lag 5000                                                           -0.17207003
##          at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.units
## Lag 0                                                         -0.7532567
## Lag 100                                                       -0.6923793
## Lag 500                                                       -0.5032427
## Lag 1000                                                      -0.2991945
## Lag 5000                                                       0.1154818
##          at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.units
## Lag 0                                                            -0.9140715
## Lag 100                                                          -0.8493221
## Lag 500                                                          -0.6164356
## Lag 1000                                                         -0.3808768
## Lag 5000                                                          0.1473936
##          at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.units
## Lag 0                                                            -0.9140715
## Lag 100                                                          -0.8493221
## Lag 500                                                          -0.6164356
## Lag 1000                                                         -0.3808768
## Lag 5000                                                          0.1473936
##          at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.units
## Lag 0                                                               -0.9650519
## Lag 100                                                             -0.9008410
## Lag 500                                                             -0.6496396
## Lag 1000                                                            -0.4073019
## Lag 5000                                                             0.1644354
##
## , , traitbwt.byear
##
##          at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.animal
```

```
## Lag 0                                                   -0.002044905
## Lag 100                                                  0.018082206
## Lag 500                                                 -0.019694583
## Lag 1000                                                -0.033624772
## Lag 5000                                                -0.025949000
##          at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.animal
## Lag 0                                                       -0.03731153
## Lag 100                                                     -0.01355344
## Lag 500                                                     -0.01864081
## Lag 1000                                                    -0.05745850
## Lag 5000                                                    -0.01235998
##          at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.animal
## Lag 0                                                       -0.03731153
## Lag 100                                                     -0.01355344
## Lag 500                                                     -0.01864081
## Lag 1000                                                    -0.05745850
## Lag 5000                                                    -0.01235998
##          at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.animal
## Lag 0                                                          -0.06015994
## Lag 100                                                        -0.03212487
## Lag 500                                                        -0.02412236
## Lag 1000                                                       -0.05846861
## Lag 5000                                                       -0.02882580
##          at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.animal
## Lag 0                                                    -0.03784246
## Lag 100                                                  -0.04180932
## Lag 500                                                  -0.04438042
## Lag 1000                                                 -0.01257459
## Lag 5000                                                  0.00630995
##          at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.animal
## Lag 0                                                       -0.04691870
## Lag 100                                                     -0.04133222
## Lag 500                                                     -0.05230682
## Lag 1000                                                    -0.02870414
## Lag 5000                                                    -0.00469889
##          at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.animal
## Lag 0                                                       -0.04691870
## Lag 100                                                     -0.04133222
## Lag 500                                                     -0.05230682
## Lag 1000                                                    -0.02870414
## Lag 5000                                                    -0.00469889
##          at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.animal
## Lag 0                                                         -0.039748177
## Lag 100                                                       -0.032934501
## Lag 500                                                       -0.055295362
## Lag 1000                                                      -0.027884156
## Lag 5000                                                      -0.007044631
```

```
##          traitbwt.byear traittarsus.byear traitbwt.mother traittarsus.mother
## Lag 0       1.00000000     -0.0251146296      0.03365469         0.03928862
## Lag 100     0.03109454      0.0004436899     -0.05764761        -0.01264335
## Lag 500     0.03937305      0.0006604187     -0.00457655         0.02746272
## Lag 1000    0.01680424     -0.0194711518      0.03737600        -0.04627035
## Lag 5000    0.03318792      0.0155533971     -0.02558374         0.05305580
##          at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.units
## Lag 0                                                      0.005983125
## Lag 100                                                   -0.001889062
## Lag 500                                                   -0.018793288
## Lag 1000                                                   0.027363658
## Lag 5000                                                   0.010334637
##          at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.units
## Lag 0                                                         0.052806759
## Lag 100                                                       0.014657374
## Lag 500                                                      -0.020921457
## Lag 1000                                                      0.041519184
## Lag 5000                                                     -0.000172048
##          at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.units
## Lag 0                                                         0.052806759
## Lag 100                                                       0.014657374
## Lag 500                                                      -0.020921457
## Lag 1000                                                      0.041519184
## Lag 5000                                                     -0.000172048
##          at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.units
## Lag 0                                                            0.072105699
## Lag 100                                                          0.023891187
## Lag 500                                                         -0.022626087
## Lag 1000                                                         0.038071084
## Lag 5000                                                         0.008022532
##          at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.units
## Lag 0                                                        0.02472261
## Lag 100                                                      0.04922524
## Lag 500                                                      0.05684465
## Lag 1000                                                     0.02213746
## Lag 5000                                                    -0.02587314
##          at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.units
## Lag 0                                                         0.035150019
## Lag 100                                                       0.039823504
## Lag 500                                                       0.058615425
## Lag 1000                                                      0.039863168
## Lag 5000                                                     -0.002768445
##          at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.units
## Lag 0                                                         0.035150019
## Lag 100                                                       0.039823504
## Lag 500                                                       0.058615425
## Lag 1000                                                      0.039863168
```

```
## Lag 5000                                                      -0.002768445
##          at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.units
## Lag 0                                                              0.032332494
## Lag 100                                                            0.036826480
## Lag 500                                                            0.056371336
## Lag 1000                                                           0.037506421
## Lag 5000                                                          -0.002071877
##
## , , traittarsus.byear
##
##          at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.animal
## Lag 0                                                      0.06061428
## Lag 100                                                    0.06276970
## Lag 500                                                   -0.02842127
## Lag 1000                                                   0.01799228
## Lag 5000                                                   0.02740499
##          at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.animal
## Lag 0                                                         0.05572330
## Lag 100                                                       0.06655805
## Lag 500                                                      -0.02673025
## Lag 1000                                                      0.04345968
## Lag 5000                                                      0.05112113
##          at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.animal
## Lag 0                                                         0.05572330
## Lag 100                                                       0.06655805
## Lag 500                                                      -0.02673025
## Lag 1000                                                      0.04345968
## Lag 5000                                                      0.05112113
##          at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.animal
## Lag 0                                                            0.064507548
## Lag 100                                                          0.074840509
## Lag 500                                                         -0.003777881
## Lag 1000                                                         0.058609933
## Lag 5000                                                         0.063485567
##          at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.animal
## Lag 0                                                     0.049161224
## Lag 100                                                   0.009105861
## Lag 500                                                   0.005065210
## Lag 1000                                                  0.016389664
## Lag 5000                                                 -0.029590445
##          at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.animal
## Lag 0                                                        0.055056994
## Lag 100                                                      0.035711495
## Lag 500                                                      0.012368434
## Lag 1000                                                     0.004770290
## Lag 5000                                                    -0.009144398
##          at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.animal
```

```
## Lag 0                                                                  0.055056994
## Lag 100                                                                0.035711495
## Lag 500                                                                0.012368434
## Lag 1000                                                               0.004770290
## Lag 5000                                                              -0.009144398
##         at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.animal
## Lag 0                                                                    0.048543542
## Lag 100                                                                  0.034488675
## Lag 500                                                                  0.009703880
## Lag 1000                                                                -0.001685047
## Lag 5000                                                                 0.005011858
##         traitbwt.byear traittarsus.byear traitbwt.mother traittarsus.mother
## Lag 0     -0.025114630       1.000000000      0.03708995         0.07084541
## Lag 100   -0.033801997       0.041927040     -0.06653239         0.04503853
## Lag 500    0.009533405      -0.020053055      0.01042960        -0.03755216
## Lag 1000  -0.003946143       0.011455578     -0.01588844         0.01986940
## Lag 5000   0.027020776       0.002689451     -0.02585871         0.02687208
##         at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.units
## Lag 0                                                          -0.10335662
## Lag 100                                                        -0.05376108
## Lag 500                                                         0.01626001
## Lag 1000                                                       -0.01344940
## Lag 5000                                                       -0.02833156
##         at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.units
## Lag 0                                                             -0.09746412
## Lag 100                                                           -0.05607997
## Lag 500                                                            0.01829969
## Lag 1000                                                          -0.04558284
## Lag 5000                                                          -0.04241014
##         at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.units
## Lag 0                                                             -0.09746412
## Lag 100                                                           -0.05607997
## Lag 500                                                            0.01829969
## Lag 1000                                                          -0.04558284
## Lag 5000                                                          -0.04241014
##         at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.units
## Lag 0                                                               -0.108393481
## Lag 100                                                             -0.049448255
## Lag 500                                                              0.002404817
## Lag 1000                                                            -0.086421792
## Lag 5000                                                            -0.055605953
##         at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.units
## Lag 0                                                         -0.025767223
## Lag 100                                                       -0.006184423
## Lag 500                                                       -0.002201914
## Lag 1000                                                      -0.011174601
## Lag 5000                                                       0.029950491
```

```
##          at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.units
## Lag 0                                                         -0.049170830
## Lag 100                                                       -0.040276502
## Lag 500                                                        0.003528012
## Lag 1000                                                      -0.010662330
## Lag 5000                                                       0.002523808
##          at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.units
## Lag 0                                                         -0.049170830
## Lag 100                                                       -0.040276502
## Lag 500                                                        0.003528012
## Lag 1000                                                      -0.010662330
## Lag 5000                                                       0.002523808
##          at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.units
## Lag 0                                                            -0.053929470
## Lag 100                                                          -0.043281273
## Lag 500                                                           0.009317392
## Lag 1000                                                         -0.010594624
## Lag 5000                                                         -0.013754908
##
## , , traitbwt.mother
##
##          at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.animal
## Lag 0                                                        -0.13681757
## Lag 100                                                      -0.09694549
## Lag 500                                                      -0.06857367
## Lag 1000                                                     -0.04540954
## Lag 5000                                                     -0.01652050
##          at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.animal
## Lag 0                                                           -0.12626725
## Lag 100                                                         -0.12449687
## Lag 500                                                         -0.05181080
## Lag 1000                                                        -0.03932960
## Lag 5000                                                        -0.01141931
##          at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.animal
## Lag 0                                                           -0.12626725
## Lag 100                                                         -0.12449687
## Lag 500                                                         -0.05181080
## Lag 1000                                                        -0.03932960
## Lag 5000                                                        -0.01141931
##          at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.animal
## Lag 0                                                              -0.09733219
## Lag 100                                                            -0.10049386
## Lag 500                                                            -0.04634235
## Lag 1000                                                           -0.01749975
## Lag 5000                                                           -0.03285757
##          at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.animal
## Lag 0                                                        -0.02514526
```

```
## Lag 100                                                    0.01494004
## Lag 500                                                   -0.05400749
## Lag 1000                                                  -0.02644804
## Lag 5000                                                  -0.02759428
##          at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.animal
## Lag 0                                                       0.0337229276
## Lag 100                                                     0.0355284011
## Lag 500                                                    -0.0008562576
## Lag 1000                                                   -0.0192570169
## Lag 5000                                                   -0.0314028551
##          at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.animal
## Lag 0                                                       0.0337229276
## Lag 100                                                     0.0355284011
## Lag 500                                                    -0.0008562576
## Lag 1000                                                   -0.0192570169
## Lag 5000                                                   -0.0314028551
##          at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.animal
## Lag 0                                                            0.04924110
## Lag 100                                                          0.04492689
## Lag 500                                                          0.02422838
## Lag 1000                                                        -0.04034312
## Lag 5000                                                        -0.03784851
##          traitbwt.byear traittarsus.byear traitbwt.mother traittarsus.mother
## Lag 0       0.033654686       0.037089946     1.000000000       -0.267715213
## Lag 100     0.020365368       0.031597781     0.039464037        0.006711605
## Lag 500     0.007110008       0.046188516     0.095615498       -0.023010721
## Lag 1000   -0.019597442       0.001266059     0.065362608        0.041196297
## Lag 5000    0.019704700      -0.034265234    -0.005121853        0.041919494
##          at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.units
## Lag 0                                                   0.093898173
## Lag 100                                                 0.109444195
## Lag 500                                                 0.055322096
## Lag 1000                                                0.036648121
## Lag 5000                                                0.003492676
##          at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.units
## Lag 0                                                        0.11659923
## Lag 100                                                      0.12608289
## Lag 500                                                      0.03369955
## Lag 1000                                                     0.04312267
## Lag 5000                                                    -0.01418292
##          at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.units
## Lag 0                                                        0.11659923
## Lag 100                                                      0.12608289
## Lag 500                                                      0.03369955
## Lag 1000                                                     0.04312267
## Lag 5000                                                    -0.01418292
##          at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.units
```

```
## Lag 0                                                        0.1007331132
## Lag 100                                                      0.0846271381
## Lag 500                                                      0.0314559531
## Lag 1000                                                     0.0313378649
## Lag 5000                                                     0.0006030047
##          at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.units
## Lag 0                                                    -0.02385685
## Lag 100                                                  -0.01929710
## Lag 500                                                   0.05442789
## Lag 1000                                                  0.02999688
## Lag 5000                                                  0.02354946
##          at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.units
## Lag 0                                                       -0.037784916
## Lag 100                                                     -0.040619404
## Lag 500                                                      0.009246757
## Lag 1000                                                     0.021585046
## Lag 5000                                                     0.029657103
##          at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.units
## Lag 0                                                       -0.037784916
## Lag 100                                                     -0.040619404
## Lag 500                                                      0.009246757
## Lag 1000                                                     0.021585046
## Lag 5000                                                     0.029657103
##          at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.units
## Lag 0                                                            -0.04048151
## Lag 100                                                          -0.04664306
## Lag 500                                                          -0.02420607
## Lag 1000                                                          0.03414246
## Lag 5000                                                          0.04075949
##
## , , traittarsus.mother
##
##          at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.animal
## Lag 0                                                       0.06303474
## Lag 100                                                     0.09137304
## Lag 500                                                     0.05137407
## Lag 1000                                                    0.02569160
## Lag 5000                                                   -0.08057411
##          at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.animal
## Lag 0                                                          0.06865980
## Lag 100                                                        0.10336350
## Lag 500                                                        0.01711371
## Lag 1000                                                       0.03032742
## Lag 5000                                                      -0.08530728
##          at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.animal
## Lag 0                                                          0.06865980
## Lag 100                                                        0.10336350
```

```
## Lag 500                                                                   0.01711371
## Lag 1000                                                                  0.03032742
## Lag 5000                                                                 -0.08530728
##           at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.animal
## Lag 0                                                                  -0.009350685
## Lag 100                                                                 0.024288467
## Lag 500                                                                -0.016438414
## Lag 1000                                                               -0.005767054
## Lag 5000                                                               -0.063956859
##           at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.animal
## Lag 0                                                             -0.13999847
## Lag 100                                                           -0.14330129
## Lag 500                                                           -0.12944310
## Lag 1000                                                          -0.08446537
## Lag 5000                                                           0.04104776
##           at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.animal
## Lag 0                                                                -0.18311492
## Lag 100                                                              -0.16614099
## Lag 500                                                              -0.14634974
## Lag 1000                                                             -0.09164415
## Lag 5000                                                              0.05689178
##           at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.animal
## Lag 0                                                                -0.18311492
## Lag 100                                                              -0.16614099
## Lag 500                                                              -0.14634974
## Lag 1000                                                             -0.09164415
## Lag 5000                                                              0.05689178
##           at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.animal
## Lag 0                                                                   -0.22289117
## Lag 100                                                                 -0.19084285
## Lag 500                                                                 -0.14966648
## Lag 1000                                                                -0.07718413
## Lag 5000                                                                 0.07429663
##           traitbwt.byear traittarsus.byear traitbwt.mother traittarsus.mother
## Lag 0        0.039288617        0.07084541    -0.267715213        1.000000000
## Lag 100      0.047364166       -0.01932534    -0.036245609        0.088363955
## Lag 500      0.005475011       -0.04374386    -0.028017777        0.043041568
## Lag 1000    -0.022031785        0.01752292     0.005084865       -0.003286219
## Lag 5000    -0.004605383       -0.01801176    -0.022372822       -0.055614496
##           at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.units
## Lag 0                                                            -0.04283736
## Lag 100                                                          -0.05247358
## Lag 500                                                          -0.03520027
## Lag 1000                                                         -0.02685262
## Lag 5000                                                          0.08204082
##           at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.units
## Lag 0                                                              -0.080407800
```

```
## Lag 100                                                        -0.079283374
## Lag 500                                                         0.007896803
## Lag 1000                                                       -0.024892006
## Lag 5000                                                        0.090297411
##          at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.units
## Lag 0                                                          -0.080407800
## Lag 100                                                        -0.079283374
## Lag 500                                                         0.007896803
## Lag 1000                                                       -0.024892006
## Lag 5000                                                        0.090297411
##          at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.units
## Lag 0                                                              -0.09075088
## Lag 100                                                            -0.04605175
## Lag 500                                                             0.02816248
## Lag 1000                                                            0.01663048
## Lag 5000                                                            0.08246697
##          at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.units
## Lag 0                                                       0.14299876
## Lag 100                                                     0.14159603
## Lag 500                                                     0.13583757
## Lag 1000                                                    0.06878998
## Lag 5000                                                   -0.03559959
##          at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.units
## Lag 0                                                          0.16291072
## Lag 100                                                        0.16523003
## Lag 500                                                        0.14972084
## Lag 1000                                                       0.08594345
## Lag 5000                                                      -0.05664141
##          at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.units
## Lag 0                                                          0.16291072
## Lag 100                                                        0.16523003
## Lag 500                                                        0.14972084
## Lag 1000                                                       0.08594345
## Lag 5000                                                      -0.05664141
##          at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.units
## Lag 0                                                             0.17073426
## Lag 100                                                           0.18983154
## Lag 500                                                           0.15067362
## Lag 1000                                                          0.07940280
## Lag 5000                                                         -0.07670042
##
## , , at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.units
##
##          at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.animal
## Lag 0                                                      -0.84231928
## Lag 100                                                    -0.57945611
## Lag 500                                                    -0.19062716
```

```
## Lag 1000                                                      -0.08668794
## Lag 5000                                                       0.01749515
##          at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.animal
## Lag 0                                                            -0.73143141
## Lag 100                                                          -0.54471632
## Lag 500                                                          -0.20876950
## Lag 1000                                                         -0.08873424
## Lag 5000                                                          0.01590906
##          at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.animal
## Lag 0                                                            -0.73143141
## Lag 100                                                          -0.54471632
## Lag 500                                                          -0.20876950
## Lag 1000                                                         -0.08873424
## Lag 5000                                                          0.01590906
##          at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.animal
## Lag 0                                                               -0.463783799
## Lag 100                                                             -0.353636210
## Lag 500                                                             -0.169902631
## Lag 1000                                                            -0.092155921
## Lag 5000                                                            -0.009813848
##          at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.animal
## Lag 0                                                         0.048426202
## Lag 100                                                       0.082944312
## Lag 500                                                       0.033604930
## Lag 1000                                                      0.005353498
## Lag 5000                                                      0.014843101
##          at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.animal
## Lag 0                                                             0.04443896
## Lag 100                                                           0.05903744
## Lag 500                                                           0.02909782
## Lag 1000                                                          0.01112292
## Lag 5000                                                         -0.02822596
##          at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.animal
## Lag 0                                                             0.04443896
## Lag 100                                                           0.05903744
## Lag 500                                                           0.02909782
## Lag 1000                                                          0.01112292
## Lag 5000                                                         -0.02822596
##          at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.animal
## Lag 0                                                                0.04061110
## Lag 100                                                              0.04147746
## Lag 500                                                              0.01338370
## Lag 1000                                                             0.01709317
## Lag 5000                                                            -0.05401662
##          traitbwt.byear traittarsus.byear traitbwt.mother traittarsus.mother
## Lag 0       0.005983125      -0.103356615    0.0938981727      -0.0428373611
## Lag 100     0.042918382      -0.047853012    0.0762514968      -0.0699317580
```

```
## Lag 500    -0.002564868      -0.017832691    0.0157985450       0.0235550018
## Lag 1000    0.014867426      -0.027311021    0.0003829822      -0.0006460503
## Lag 5000    0.009101393       0.004430949   -0.0233572527       0.0174497074
##          at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.units
## Lag 0                                                        1.000000000
## Lag 100                                                      0.503164974
## Lag 500                                                      0.176766919
## Lag 1000                                                     0.100125592
## Lag 5000                                                     0.003858174
##          at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.units
## Lag 0                                                           0.862131977
## Lag 100                                                         0.467009268
## Lag 500                                                         0.173071923
## Lag 1000                                                        0.091405415
## Lag 5000                                                        0.001214249
##          at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.units
## Lag 0                                                           0.862131977
## Lag 100                                                         0.467009268
## Lag 500                                                         0.173071923
## Lag 1000                                                        0.091405415
## Lag 5000                                                        0.001214249
##          at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.units
## Lag 0                                                              0.556754885
## Lag 100                                                            0.300025056
## Lag 500                                                            0.130914950
## Lag 1000                                                           0.084742808
## Lag 5000                                                           0.008877657
##          at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.units
## Lag 0                                                       -0.066893803
## Lag 100                                                     -0.088991169
## Lag 500                                                     -0.041740101
## Lag 1000                                                    -0.013627370
## Lag 5000                                                    -0.004864431
##          at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.units
## Lag 0                                                          -0.041695516
## Lag 100                                                        -0.058375215
## Lag 500                                                        -0.038590340
## Lag 1000                                                       -0.008465406
## Lag 5000                                                        0.033653455
##          at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.units
## Lag 0                                                          -0.041695516
## Lag 100                                                        -0.058375215
## Lag 500                                                        -0.038590340
## Lag 1000                                                       -0.008465406
## Lag 5000                                                        0.033653455
##          at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.units
## Lag 0                                                             -0.020866307
```

```
## Lag 100                                                    -0.024784750
## Lag 500                                                    -0.024026474
## Lag 1000                                                   -0.008875445
## Lag 5000                                                    0.060413047
##
## , , at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.units
##
##         at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.animal
## Lag 0                                                   -0.70890155
## Lag 100                                                 -0.51875562
## Lag 500                                                 -0.20600428
## Lag 1000                                                -0.10994315
## Lag 5000                                                -0.01039121
##         at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.animal
## Lag 0                                                      -0.82495927
## Lag 100                                                    -0.61316330
## Lag 500                                                    -0.24079957
## Lag 1000                                                   -0.11403500
## Lag 5000                                                   -0.01904085
##         at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.animal
## Lag 0                                                      -0.82495927
## Lag 100                                                    -0.61316330
## Lag 500                                                    -0.24079957
## Lag 1000                                                   -0.11403500
## Lag 5000                                                   -0.01904085
##         at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.animal
## Lag 0                                                         -0.65832516
## Lag 100                                                       -0.49644020
## Lag 500                                                       -0.22156354
## Lag 1000                                                      -0.11606788
## Lag 5000                                                      -0.03431864
##         at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.animal
## Lag 0                                                  0.0432075717
## Lag 100                                                0.0731729081
## Lag 500                                                0.0351321242
## Lag 1000                                               0.0008078044
## Lag 5000                                               0.0060255376
##         at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.animal
## Lag 0                                                       0.04900783
## Lag 100                                                     0.06034422
## Lag 500                                                     0.03147880
## Lag 1000                                                    0.01663910
## Lag 5000                                                   -0.02708842
##         at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.animal
## Lag 0                                                       0.04900783
## Lag 100                                                     0.06034422
## Lag 500                                                     0.03147880
```

```
## Lag 1000                                                 0.01663910
## Lag 5000                                                -0.02708842
##          at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.animal
## Lag 0                                                       0.05879880
## Lag 100                                                     0.06066830
## Lag 500                                                     0.02143188
## Lag 1000                                                    0.02664768
## Lag 5000                                                   -0.05794619
##          traitbwt.byear traittarsus.byear traitbwt.mother traittarsus.mother
## Lag 0        0.05280676      -0.097464115      0.11659923       -0.080407800
## Lag 100      0.06749027      -0.048884392      0.05889480       -0.042771302
## Lag 500      0.01581190      -0.013402510      0.01353140        0.023637489
## Lag 1000     0.02427770      -0.012851631      0.01997733        0.008272035
## Lag 5000    -0.00118757       0.004909443     -0.02042686        0.001970307
##          at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.units
## Lag 0                                                 0.8621320
## Lag 100                                               0.4520274
## Lag 500                                               0.1932988
## Lag 1000                                              0.1091092
## Lag 5000                                              0.0303842
##          at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.units
## Lag 0                                                    1.00000000
## Lag 100                                                  0.52253994
## Lag 500                                                  0.19894517
## Lag 1000                                                 0.10703411
## Lag 5000                                                 0.03011013
##          at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.units
## Lag 0                                                    1.00000000
## Lag 100                                                  0.52253994
## Lag 500                                                  0.19894517
## Lag 1000                                                 0.10703411
## Lag 5000                                                 0.03011013
##          at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.units
## Lag 0                                                       0.83204286
## Lag 100                                                     0.40931694
## Lag 500                                                     0.16394862
## Lag 1000                                                    0.09392225
## Lag 5000                                                    0.02432038
##          at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.units
## Lag 0                                              -0.066443086
## Lag 100                                            -0.077647262
## Lag 500                                            -0.036441782
## Lag 1000                                           -0.007304102
## Lag 5000                                           -0.002379788
##          at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.units
## Lag 0                                                   -0.05557720
## Lag 100                                                 -0.05970375
```

```
## Lag 500                                                        -0.03617882
## Lag 1000                                                       -0.01614682
## Lag 5000                                                        0.03234714
##          at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.units
## Lag 0                                                          -0.05557720
## Lag 100                                                        -0.05970375
## Lag 500                                                        -0.03617882
## Lag 1000                                                       -0.01614682
## Lag 5000                                                        0.03234714
##          at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.units
## Lag 0                                                             -0.04717349
## Lag 100                                                           -0.04356349
## Lag 500                                                           -0.02677549
## Lag 1000                                                          -0.02460366
## Lag 5000                                                           0.06745537
##
## , , at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.units
##
##          at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.animal
## Lag 0                                                        -0.70890155
## Lag 100                                                      -0.51875562
## Lag 500                                                      -0.20600428
## Lag 1000                                                     -0.10994315
## Lag 5000                                                     -0.01039121
##          at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.animal
## Lag 0                                                           -0.82495927
## Lag 100                                                         -0.61316330
## Lag 500                                                         -0.24079957
## Lag 1000                                                        -0.11403500
## Lag 5000                                                        -0.01904085
##          at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.animal
## Lag 0                                                           -0.82495927
## Lag 100                                                         -0.61316330
## Lag 500                                                         -0.24079957
## Lag 1000                                                        -0.11403500
## Lag 5000                                                        -0.01904085
##          at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.animal
## Lag 0                                                              -0.65832516
## Lag 100                                                            -0.49644020
## Lag 500                                                            -0.22156354
## Lag 1000                                                           -0.11606788
## Lag 5000                                                           -0.03431864
##          at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.animal
## Lag 0                                                       0.0432075717
## Lag 100                                                     0.0731729081
## Lag 500                                                     0.0351321242
## Lag 1000                                                    0.0008078044
```

```
## Lag 5000                                                   0.0060255376
##          at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.animal
## Lag 0                                                          0.04900783
## Lag 100                                                        0.06034422
## Lag 500                                                        0.03147880
## Lag 1000                                                       0.01663910
## Lag 5000                                                      -0.02708842
##          at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.animal
## Lag 0                                                          0.04900783
## Lag 100                                                        0.06034422
## Lag 500                                                        0.03147880
## Lag 1000                                                       0.01663910
## Lag 5000                                                      -0.02708842
##          at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.animal
## Lag 0                                                             0.05879880
## Lag 100                                                           0.06066830
## Lag 500                                                           0.02143188
## Lag 1000                                                          0.02664768
## Lag 5000                                                         -0.05794619
##          traitbwt.byear traittarsus.byear traitbwt.mother traittarsus.mother
## Lag 0        0.05280676      -0.097464115      0.11659923       -0.080407800
## Lag 100      0.06749027      -0.048884392      0.05889480       -0.042771302
## Lag 500      0.01581190      -0.013402510      0.01353140        0.023637489
## Lag 1000     0.02427770      -0.012851631      0.01997733        0.008272035
## Lag 5000    -0.00118757       0.004909443     -0.02042686        0.001970307
##          at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.units
## Lag 0                                                        0.8621320
## Lag 100                                                      0.4520274
## Lag 500                                                      0.1932988
## Lag 1000                                                     0.1091092
## Lag 5000                                                     0.0303842
##          at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.units
## Lag 0                                                           1.00000000
## Lag 100                                                         0.52253994
## Lag 500                                                         0.19894517
## Lag 1000                                                        0.10703411
## Lag 5000                                                        0.03011013
##          at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.units
## Lag 0                                                           1.00000000
## Lag 100                                                         0.52253994
## Lag 500                                                         0.19894517
## Lag 1000                                                        0.10703411
## Lag 5000                                                        0.03011013
##          at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.units
## Lag 0                                                              0.83204286
## Lag 100                                                            0.40931694
## Lag 500                                                            0.16394862
```

```
## Lag 1000                                                   0.09392225
## Lag 5000                                                   0.02432038
##         at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.units
## Lag 0                                                 -0.066443086
## Lag 100                                               -0.077647262
## Lag 500                                               -0.036441782
## Lag 1000                                              -0.007304102
## Lag 5000                                              -0.002379788
##         at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.units
## Lag 0                                                    -0.05557720
## Lag 100                                                  -0.05970375
## Lag 500                                                  -0.03617882
## Lag 1000                                                 -0.01614682
## Lag 5000                                                  0.03234714
##         at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.units
## Lag 0                                                    -0.05557720
## Lag 100                                                  -0.05970375
## Lag 500                                                  -0.03617882
## Lag 1000                                                 -0.01614682
## Lag 5000                                                  0.03234714
##         at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.units
## Lag 0                                                       -0.04717349
## Lag 100                                                     -0.04356349
## Lag 500                                                     -0.02677549
## Lag 1000                                                    -0.02460366
## Lag 5000                                                     0.06745537
##
## , , at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.units
##
##         at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.animal
## Lag 0                                                   -0.43812320
## Lag 100                                                 -0.32924526
## Lag 500                                                 -0.13020212
## Lag 1000                                                -0.13254862
## Lag 5000                                                -0.07309476
##         at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.animal
## Lag 0                                                      -0.64394327
## Lag 100                                                    -0.46780888
## Lag 500                                                    -0.20079012
## Lag 1000                                                   -0.14480996
## Lag 5000                                                   -0.09575862
##         at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.animal
## Lag 0                                                      -0.64394327
## Lag 100                                                    -0.46780888
## Lag 500                                                    -0.20079012
## Lag 1000                                                   -0.14480996
## Lag 5000                                                   -0.09575862
```

```
##          at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.animal
## Lag 0                                                              -0.76001059
## Lag 100                                                            -0.54663983
## Lag 500                                                            -0.24713058
## Lag 1000                                                           -0.16089016
## Lag 5000                                                           -0.08907569
##          at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.animal
## Lag 0                                                         0.01554818
## Lag 100                                                       0.03347226
## Lag 500                                                       0.03054674
## Lag 1000                                                      0.01335762
## Lag 5000                                                      0.01644186
##          at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.animal
## Lag 0                                                          0.0247708510
## Lag 100                                                        0.0298811053
## Lag 500                                                        0.0393319911
## Lag 1000                                                       0.0410794684
## Lag 5000                                                       0.0003106287
##          at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.animal
## Lag 0                                                          0.0247708510
## Lag 100                                                        0.0298811053
## Lag 500                                                        0.0393319911
## Lag 1000                                                       0.0410794684
## Lag 5000                                                       0.0003106287
##          at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.animal
## Lag 0                                                               0.04254878
## Lag 100                                                             0.04748420
## Lag 500                                                             0.04789053
## Lag 1000                                                            0.06796255
## Lag 5000                                                           -0.01851941
##          traitbwt.byear traittarsus.byear traitbwt.mother traittarsus.mother
## Lag 0       0.072105699     -0.1083934806    0.1007331132       -0.090750879
## Lag 100     0.069867202     -0.0486077910    0.0545104394       -0.013859645
## Lag 500     0.026575267     -0.0133212485    0.0286661585        0.008613454
## Lag 1000    0.015663649     -0.0195256514    0.0413886079        0.020780006
## Lag 5000   -0.002018726     -0.0001505633    0.0007733641       -0.036366883
##          at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.units
## Lag 0                                                       0.55675488
## Lag 100                                                     0.28216537
## Lag 500                                                     0.12989226
## Lag 1000                                                    0.12353001
## Lag 5000                                                    0.07787577
##          at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.units
## Lag 0                                                           0.83204286
## Lag 100                                                         0.39760050
## Lag 500                                                         0.17265831
## Lag 1000                                                        0.12489795
```

```
## Lag 5000                                                  0.08926567
##          at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.units
## Lag 0                                                     0.83204286
## Lag 100                                                   0.39760050
## Lag 500                                                   0.17265831
## Lag 1000                                                  0.12489795
## Lag 5000                                                  0.08926567
##          at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.units
## Lag 0                                                        1.00000000
## Lag 100                                                      0.43985525
## Lag 500                                                      0.18705457
## Lag 1000                                                     0.11273003
## Lag 5000                                                     0.07297707
##          at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.units
## Lag 0                                                  -0.03083664
## Lag 100                                                -0.03304267
## Lag 500                                                -0.03123886
## Lag 1000                                               -0.02337670
## Lag 5000                                               -0.02222725
##          at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.units
## Lag 0                                                   -0.0304234955
## Lag 100                                                 -0.0241051816
## Lag 500                                                 -0.0412351901
## Lag 1000                                                -0.0471997761
## Lag 5000                                                 0.0005985541
##          at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.units
## Lag 0                                                   -0.0304234955
## Lag 100                                                 -0.0241051816
## Lag 500                                                 -0.0412351901
## Lag 1000                                                -0.0471997761
## Lag 5000                                                 0.0005985541
##          at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.units
## Lag 0                                                       -0.03748483
## Lag 100                                                     -0.02874080
## Lag 500                                                     -0.04666191
## Lag 1000                                                    -0.07162962
## Lag 5000                                                     0.02693394
##
## , , at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.units
##
##          at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.animal
## Lag 0                                                   0.07807105
## Lag 100                                                 0.04809322
## Lag 500                                                 0.07342298
## Lag 1000                                                0.02747559
## Lag 5000                                               -0.08865706
##          at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.animal
```

```
## Lag 0                                                      0.082481767
## Lag 100                                                    0.069884466
## Lag 500                                                    0.053669242
## Lag 1000                                                  -0.003247808
## Lag 5000                                                  -0.105675290
##          at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.animal
## Lag 0                                                      0.082481767
## Lag 100                                                    0.069884466
## Lag 500                                                    0.053669242
## Lag 1000                                                  -0.003247808
## Lag 5000                                                  -0.105675290
##          at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.animal
## Lag 0                                                         0.0287090438
## Lag 100                                                       0.0207457037
## Lag 500                                                       0.0006081912
## Lag 1000                                                     -0.0572950737
## Lag 5000                                                     -0.1156100914
##          at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.animal
## Lag 0                                                 -0.9369474
## Lag 100                                               -0.8074872
## Lag 500                                               -0.5046449
## Lag 1000                                              -0.2917207
## Lag 5000                                               0.1083680
##          at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.animal
## Lag 0                                                    -0.8748666
## Lag 100                                                  -0.8019088
## Lag 500                                                  -0.5689707
## Lag 1000                                                 -0.3490005
## Lag 5000                                                  0.1337402
##          at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.animal
## Lag 0                                                    -0.8748666
## Lag 100                                                  -0.8019088
## Lag 500                                                  -0.5689707
## Lag 1000                                                 -0.3490005
## Lag 5000                                                  0.1337402
##          at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.animal
## Lag 0                                                       -0.7532567
## Lag 100                                                     -0.7106727
## Lag 500                                                     -0.5497772
## Lag 1000                                                    -0.3502307
## Lag 5000                                                     0.1338020
##          traitbwt.byear traittarsus.byear traitbwt.mother traittarsus.mother
## Lag 0       0.024722609       -0.02576722     -0.02385685         0.14299876
## Lag 100     0.017186912       -0.04974888     -0.00291607         0.12584167
## Lag 500     0.027788923       -0.07216401     -0.03437633         0.12502432
## Lag 1000    0.030599400       -0.05970350     -0.07019603         0.09866987
## Lag 5000    0.003688852       -0.03623879     -0.01956357        -0.02929408
```

```
##          at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.units
## Lag 0                                                      -0.066893803
## Lag 100                                                    -0.023868973
## Lag 500                                                    -0.055699109
## Lag 1000                                                   -0.006728342
## Lag 5000                                                    0.089063097
##          at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.units
## Lag 0                                                          -0.06644309
## Lag 100                                                        -0.03252225
## Lag 500                                                        -0.03013542
## Lag 1000                                                        0.00413424
## Lag 5000                                                        0.09523719
##          at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.units
## Lag 0                                                          -0.06644309
## Lag 100                                                        -0.03252225
## Lag 500                                                        -0.03013542
## Lag 1000                                                        0.00413424
## Lag 5000                                                        0.09523719
##          at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.units
## Lag 0                                                            -0.030836644
## Lag 100                                                          -0.012261003
## Lag 500                                                          -0.009828189
## Lag 1000                                                          0.015985541
## Lag 5000                                                          0.120961240
##          at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.units
## Lag 0                                                         1.0000000
## Lag 100                                                       0.7895424
## Lag 500                                                       0.4966907
## Lag 1000                                                      0.2824837
## Lag 5000                                                     -0.1086586
##          at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.units
## Lag 0                                                             0.9162648
## Lag 100                                                           0.7897342
## Lag 500                                                           0.5546655
## Lag 1000                                                          0.3340592
## Lag 5000                                                         -0.1357395
##          at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.units
## Lag 0                                                             0.9162648
## Lag 100                                                           0.7897342
## Lag 500                                                           0.5546655
## Lag 1000                                                          0.3340592
## Lag 5000                                                         -0.1357395
##          at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.units
## Lag 0                                                                0.7818908
## Lag 100                                                              0.7088815
## Lag 500                                                              0.5356249
## Lag 1000                                                             0.3410568
```

```
## Lag 5000                                                       -0.1407239
##
## , , at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.units
##
##          at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.animal
## Lag 0                                                        0.066793402
## Lag 100                                                      0.050378446
## Lag 500                                                      0.077515159
## Lag 1000                                                     0.008812794
## Lag 5000                                                    -0.121465553
##          at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.animal
## Lag 0                                                           0.093083697
## Lag 100                                                         0.084384646
## Lag 500                                                         0.074812950
## Lag 1000                                                       -0.007598499
## Lag 5000                                                       -0.145198558
##          at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.animal
## Lag 0                                                           0.093083697
## Lag 100                                                         0.084384646
## Lag 500                                                         0.074812950
## Lag 1000                                                       -0.007598499
## Lag 5000                                                       -0.145198558
##          at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.animal
## Lag 0                                                              0.039633904
## Lag 100                                                            0.030631751
## Lag 500                                                            0.008216661
## Lag 1000                                                          -0.067574178
## Lag 5000                                                          -0.158681853
##          at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.animal
## Lag 0                                                         -0.8725969
## Lag 100                                                       -0.7772224
## Lag 500                                                       -0.5293889
## Lag 1000                                                      -0.3047292
## Lag 5000                                                       0.1032909
##          at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.animal
## Lag 0                                                            -0.9629330
## Lag 100                                                          -0.8857980
## Lag 500                                                          -0.6314814
## Lag 1000                                                         -0.3830396
## Lag 5000                                                          0.1372333
##          at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.animal
## Lag 0                                                            -0.9629330
## Lag 100                                                          -0.8857980
## Lag 500                                                          -0.6314814
## Lag 1000                                                         -0.3830396
## Lag 5000                                                          0.1372333
##          at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.animal
```

```
## Lag 0                                                           -0.9140715
## Lag 100                                                         -0.8566927
## Lag 500                                                         -0.6364708
## Lag 1000                                                        -0.3975119
## Lag 5000                                                         0.1452190
##           traitbwt.byear traittarsus.byear traitbwt.mother traittarsus.mother
## Lag 0         0.03515002       -0.04917083     -0.03778492         0.16291072
## Lag 100       0.03091121       -0.05304287     -0.03754739         0.16477625
## Lag 500       0.02594763       -0.04411058     -0.04091176         0.15960207
## Lag 1000      0.03943697       -0.05730659     -0.07505811         0.12634662
## Lag 5000     -0.02494957       -0.03580137     -0.02083442        -0.01955372
##           at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.units
## Lag 0                                                       -0.04169552
## Lag 100                                                     -0.02400995
## Lag 500                                                     -0.05483846
## Lag 1000                                                     0.01413904
## Lag 5000                                                     0.12137475
##           at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.units
## Lag 0                                                          -0.05557720
## Lag 100                                                        -0.04292481
## Lag 500                                                        -0.04373833
## Lag 1000                                                        0.01820822
## Lag 5000                                                        0.13061028
##           at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.units
## Lag 0                                                          -0.05557720
## Lag 100                                                        -0.04292481
## Lag 500                                                        -0.04373833
## Lag 1000                                                        0.01820822
## Lag 5000                                                        0.13061028
##           at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.units
## Lag 0                                                             -0.03042350
## Lag 100                                                           -0.02364770
## Lag 500                                                           -0.02090983
## Lag 1000                                                           0.03823823
## Lag 5000                                                           0.15598999
##           at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.units
## Lag 0                                                         0.9162648
## Lag 100                                                       0.7742948
## Lag 500                                                       0.5235576
## Lag 1000                                                      0.3032634
## Lag 5000                                                     -0.1115658
##           at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.units
## Lag 0                                                             1.0000000
## Lag 100                                                           0.8752177
## Lag 500                                                           0.6156893
## Lag 1000                                                          0.3715418
## Lag 5000                                                         -0.1435973
```

```
##          at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.units
## Lag 0                                                           1.0000000
## Lag 100                                                         0.8752177
## Lag 500                                                         0.6156893
## Lag 1000                                                        0.3715418
## Lag 5000                                                       -0.1435973
##          at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.units
## Lag 0                                                              0.9475981
## Lag 100                                                            0.8522663
## Lag 500                                                            0.6217954
## Lag 1000                                                           0.3896947
## Lag 5000                                                          -0.1540929
##
## , , at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.units
##
##          at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.animal
## Lag 0                                                       0.066793402
## Lag 100                                                     0.050378446
## Lag 500                                                     0.077515159
## Lag 1000                                                    0.008812794
## Lag 5000                                                   -0.121465553
##          at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.animal
## Lag 0                                                          0.093083697
## Lag 100                                                        0.084384646
## Lag 500                                                        0.074812950
## Lag 1000                                                      -0.007598499
## Lag 5000                                                      -0.145198558
##          at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.animal
## Lag 0                                                          0.093083697
## Lag 100                                                        0.084384646
## Lag 500                                                        0.074812950
## Lag 1000                                                      -0.007598499
## Lag 5000                                                      -0.145198558
##          at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.animal
## Lag 0                                                             0.039633904
## Lag 100                                                           0.030631751
## Lag 500                                                           0.008216661
## Lag 1000                                                         -0.067574178
## Lag 5000                                                         -0.158681853
##          at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.animal
## Lag 0                                                        -0.8725969
## Lag 100                                                      -0.7772224
## Lag 500                                                      -0.5293889
## Lag 1000                                                     -0.3047292
## Lag 5000                                                      0.1032909
##          at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.animal
## Lag 0                                                           -0.9629330
```

```
## Lag 100                                                          -0.8857980
## Lag 500                                                          -0.6314814
## Lag 1000                                                         -0.3830396
## Lag 5000                                                          0.1372333
##          at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.animal
## Lag 0                                                            -0.9629330
## Lag 100                                                          -0.8857980
## Lag 500                                                          -0.6314814
## Lag 1000                                                         -0.3830396
## Lag 5000                                                          0.1372333
##          at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.animal
## Lag 0                                                               -0.9140715
## Lag 100                                                             -0.8566927
## Lag 500                                                             -0.6364708
## Lag 1000                                                            -0.3975119
## Lag 5000                                                             0.1452190
##          traitbwt.byear traittarsus.byear traitbwt.mother traittarsus.mother
## Lag 0        0.03515002       -0.04917083     -0.03778492         0.16291072
## Lag 100      0.03091121       -0.05304287     -0.03754739         0.16477625
## Lag 500      0.02594763       -0.04411058     -0.04091176         0.15960207
## Lag 1000     0.03943697       -0.05730659     -0.07505811         0.12634662
## Lag 5000    -0.02494957       -0.03580137     -0.02083442        -0.01955372
##          at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.units
## Lag 0                                                      -0.04169552
## Lag 100                                                    -0.02400995
## Lag 500                                                    -0.05483846
## Lag 1000                                                    0.01413904
## Lag 5000                                                    0.12137475
##          at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.units
## Lag 0                                                         -0.05557720
## Lag 100                                                       -0.04292481
## Lag 500                                                       -0.04373833
## Lag 1000                                                       0.01820822
## Lag 5000                                                       0.13061028
##          at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.units
## Lag 0                                                         -0.05557720
## Lag 100                                                       -0.04292481
## Lag 500                                                       -0.04373833
## Lag 1000                                                       0.01820822
## Lag 5000                                                       0.13061028
##          at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.units
## Lag 0                                                            -0.03042350
## Lag 100                                                          -0.02364770
## Lag 500                                                          -0.02090983
## Lag 1000                                                          0.03823823
## Lag 5000                                                          0.15598999
##          at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.units
```

```
## Lag 0                                                           0.9162648
## Lag 100                                                         0.7742948
## Lag 500                                                         0.5235576
## Lag 1000                                                        0.3032634
## Lag 5000                                                       -0.1115658
##          at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.units
## Lag 0                                                              1.0000000
## Lag 100                                                            0.8752177
## Lag 500                                                            0.6156893
## Lag 1000                                                           0.3715418
## Lag 5000                                                          -0.1435973
##          at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.units
## Lag 0                                                              1.0000000
## Lag 100                                                            0.8752177
## Lag 500                                                            0.6156893
## Lag 1000                                                           0.3715418
## Lag 5000                                                          -0.1435973
##          at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.units
## Lag 0                                                                 0.9475981
## Lag 100                                                               0.8522663
## Lag 500                                                               0.6217954
## Lag 1000                                                              0.3896947
## Lag 5000                                                             -0.1540929
##
## , , at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.units
##
##          at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.animal
## Lag 0                                                        0.047978981
## Lag 100                                                      0.045079451
## Lag 500                                                      0.067970538
## Lag 1000                                                    -0.006909171
## Lag 5000                                                    -0.132371879
##          at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.animal
## Lag 0                                                               0.08843633
## Lag 100                                                             0.08879180
## Lag 500                                                             0.08319912
## Lag 1000                                                           -0.00586568
## Lag 5000                                                           -0.15675135
##          at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.animal
## Lag 0                                                               0.08843633
## Lag 100                                                             0.08879180
## Lag 500                                                             0.08319912
## Lag 1000                                                           -0.00586568
## Lag 5000                                                           -0.15675135
##          at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.animal
## Lag 0                                                                  0.04584246
## Lag 100                                                                0.04189200
```

```
## Lag 500                                                          0.02195919
## Lag 1000                                                        -0.05747491
## Lag 5000                                                        -0.16717974
##          at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.animal
## Lag 0                                                    -0.75254810
## Lag 100                                                  -0.68626575
## Lag 500                                                  -0.50089775
## Lag 1000                                                 -0.29031256
## Lag 5000                                                  0.09258748
##          at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.animal
## Lag 0                                                       -0.9191068
## Lag 100                                                     -0.8549977
## Lag 500                                                     -0.6281177
## Lag 1000                                                    -0.3837276
## Lag 5000                                                     0.1299735
##          at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.animal
## Lag 0                                                       -0.9191068
## Lag 100                                                     -0.8549977
## Lag 500                                                     -0.6281177
## Lag 1000                                                    -0.3837276
## Lag 5000                                                     0.1299735
##          at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.animal
## Lag 0                                                          -0.9650519
## Lag 100                                                        -0.9020388
## Lag 500                                                        -0.6603730
## Lag 1000                                                       -0.4085407
## Lag 5000                                                        0.1451290
##          traitbwt.byear traittarsus.byear traitbwt.mother traittarsus.mother
## Lag 0        0.03233249       -0.05392947     -0.04048151         0.17073426
## Lag 100      0.03971497       -0.04863212     -0.04603016         0.19100707
## Lag 500      0.02833531       -0.02831174     -0.04356222         0.17180604
## Lag 1000     0.03018475       -0.05344380     -0.07230573         0.12082866
## Lag 5000    -0.04000580       -0.02623878     -0.01322038        -0.01980137
##          at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.units
## Lag 0                                                   -0.02086631
## Lag 100                                                 -0.02091564
## Lag 500                                                 -0.04738890
## Lag 1000                                                 0.02308918
## Lag 5000                                                 0.12589958
##          at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.units
## Lag 0                                                      -0.04717349
## Lag 100                                                    -0.04819145
## Lag 500                                                    -0.05369332
## Lag 1000                                                    0.02184183
## Lag 5000                                                    0.13760532
##          at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.units
## Lag 0                                                      -0.04717349
```

```
## Lag 100                                                     -0.04819145
## Lag 500                                                     -0.05369332
## Lag 1000                                                     0.02184183
## Lag 5000                                                     0.13760532
##          at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.units
## Lag 0                                                          -0.03748483
## Lag 100                                                        -0.03257654
## Lag 500                                                        -0.03463265
## Lag 1000                                                        0.04295442
## Lag 5000                                                        0.15951258
##          at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.units
## Lag 0                                                     0.7818908
## Lag 100                                                   0.6906357
## Lag 500                                                   0.4994770
## Lag 1000                                                  0.2932880
## Lag 5000                                                 -0.1017144
##          at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.units
## Lag 0                                                        0.9475981
## Lag 100                                                      0.8462154
## Lag 500                                                      0.6150082
## Lag 1000                                                     0.3748486
## Lag 5000                                                    -0.1355925
##          at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.units
## Lag 0                                                        0.9475981
## Lag 100                                                      0.8462154
## Lag 500                                                      0.6150082
## Lag 1000                                                     0.3748486
## Lag 5000                                                    -0.1355925
##          at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.units
## Lag 0                                                           1.0000000
## Lag 100                                                         0.8919817
## Lag 500                                                         0.6480975
## Lag 1000                                                        0.4037684
## Lag 5000                                                       -0.1516651
```

As before we can obtain the raw variance component estimates and genetic correlations for the random effects:

```
posterior.mode(model2.4$VCV)
```

```
##       at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.animal
##                                                            0.9669729
##    at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.animal
##                                                            0.1859324
##    at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.animal
##                                                            0.1859324
## at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.animal
```

```
##                                                            1.9958915
##       at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.animal
##                                                            0.8390295
##    at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.animal
##                                                           -0.1015747
##    at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.animal
##                                                           -0.1015747
## at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.animal
##                                                            0.6444978
##                                                        traitbwt.byear
##                                                            0.8339224
##                                                     traittarsus.byear
##                                                            2.9032045
##                                                       traitbwt.mother
##                                                            1.8371233
##                                                    traittarsus.mother
##                                                            6.4835733
##        at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.units
##                                                            2.1384066
##     at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.units
##                                                            4.8421570
##     at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.units
##                                                            4.8421570
##  at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.units
##                                                           13.0119702
##        at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.units
##                                                            2.1428481
##     at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.units
##                                                            6.0868703
##     at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.units
##                                                            6.0868703
##  at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.units
##                                                           18.3836767
```

```
#
genetic.correlation2.4.F <- model2.4$VCV[, "at.level(sex, \"1\"):traittarsus:at.level(sex,
residual.correlation2.4.F <- model2.4$VCV[, "at.level(sex, \"1\"):traittarsus:at.level(sex
genetic.correlation2.4.M <- model2.4$VCV[, "at.level(sex, \"2\"):traittarsus:at.level(sex,
residual.correlation2.4.M <- model2.4$VCV[, "at.level(sex, \"2\"):traittarsus:at.level(sex
#
posterior.mode(genetic.correlation2.4.F)
```

```
##      var1
## 0.7852385
```

```r
posterior.mode(residual.correlation2.4.F)
```

```
##      var1
## 0.8738073
```

```r
posterior.mode(genetic.correlation2.4.M)
```

```
##      var1
## 0.9166822
```

```r
posterior.mode(residual.correlation2.4.M)
```

```
##      var1
## 0.8658358
```

Evaluation of the statistical support for these sex-specific correlations is straightforward. Because we imposed no constraint on their estimation, we can evaluate the extent to which the posterior distributions overlap zero or overlap each other:

```r
HPDinterval(genetic.correlation2.4.F, 0.95)
```

```
##           lower    upper
## var1 -0.3742433 0.963575
## attr(,"Probability")
## [1] 0.95
```

```r
HPDinterval(genetic.correlation2.4.M, 0.95)
```

```
##           lower     upper
## var1 -0.3275444 0.9801895
## attr(,"Probability")
## [1] 0.95
```

```r
HPDinterval(residual.correlation2.4.F, 0.95)
```

```
##         lower    upper
## var1 0.698292 0.962472
## attr(,"Probability")
## [1] 0.95
```

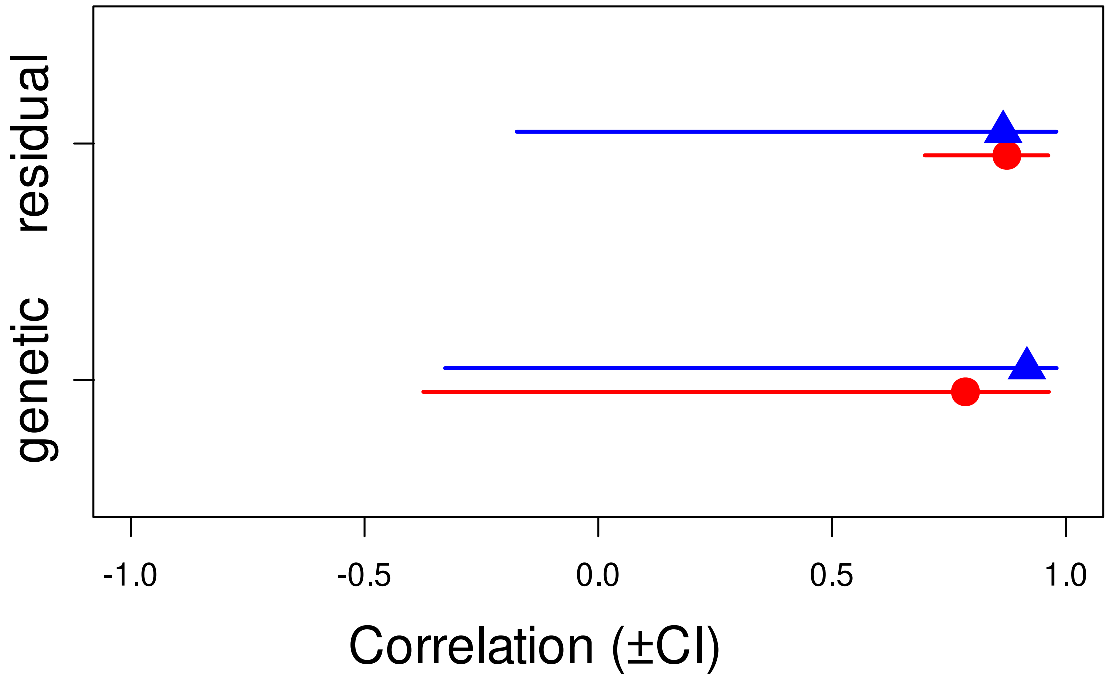
```r
HPDinterval(residual.correlation2.4.M, 0.95)
```

```
##           lower     upper
```

```
## var1 -0.1744922 0.9796736
## attr(,"Probability")
## [1] 0.95
```

Here a plot to visualize the overlaps of covariances.

```
cor.est <- rbind(
  cbind(posterior.mode(genetic.correlation2.4.F, ), HPDinterval(genetic.correlation2.4.F,
  cbind(posterior.mode(genetic.correlation2.4.M), HPDinterval(genetic.correlation2.4.M, 0.
  cbind(posterior.mode(residual.correlation2.4.F, ), HPDinterval(residual.correlation2.4.F
  cbind(posterior.mode(residual.correlation2.4.M), HPDinterval(residual.correlation2.4.M,
)


plot(c(0.95, 1.05, 1.95, 2.05) ~ cor.est[, 1], xlim = c(-1, 1), ylim = c(0.5, 2.5), xlab =
arrows(y0 = 0.95, x0 = cor.est[1, 2], y1 = 0.95, x1 = cor.est[1, 3], code = 3, angle = 90,
arrows(y0 = 1.05, x0 = cor.est[2, 2], y1 = 1.05, x1 = cor.est[2, 3], code = 3, angle = 90,
arrows(y0 = 1.95, x0 = cor.est[3, 2], y1 = 1.95, x1 = cor.est[3, 3], code = 3, angle = 90,
arrows(y0 = 2.05, x0 = cor.est[4, 2], y1 = 2.05, x1 = cor.est[4, 3], code = 3, angle = 90,
mtext("Correlation (±CI)", side = 1, las = 1, adj = 0.4, line = 3, cex = 1.6)
axis(2, at = 1, labels = c("genetic"), las = 3, cex.axis = 1.6)
axis(2, at = 2, labels = c("residual"), las = 3, cex.axis = 1.6)
```



These posterior distributions overlap between each other, which suggested the correlation were not significantly different between sexes.

By using `corgh`instead of `us`, we can extract the BLUPs and plot the sex-specific correlation.

```
gryphon2$T1 <- gryphon2$bwt
gryphon2$T2 <- gryphon2$tarsus
#
model2.5 <- MCMCglmm(cbind(T1, T2) ~ trait - 1 + trait:sex,
  random = ~ corgh(at.level(sex, "1"):trait):animal + corgh(at.level(sex, "2"):trait):anim
  rcov = ~ us(at.level(sex, "1"):trait):units + us(at.level(sex, "2"):trait):units,
  family = c("gaussian", "gaussian"),
  ginv = list(animal = Ainv), data = gryphon2,
  nitt = 130000, thin = 100, burnin = 30000,
  prior = prior2.3, verbose = FALSE, pr = TRUE,
)

save(model2.5, file = "data/MCMCglmm_model2_5_LongRun.rda")
```

Again we have provided the data from one such run. It can be accessed using the code:

```
load(file = "data/MCMCglmm_model2_5_LongRun.rda")
summary(model2.5)
```

```
##
##  Iterations = 30001:129901
##  Thinning interval  = 100
##  Sample size  = 1000
##
##  DIC: 6271.158
##
##  G-structure:  ~corgh(at.level(sex, "1"):trait):animal
##
##                                                              post.mean l-95% CI
## at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT1.animal         1        1
## at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT1.animal         1        1
## at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT2.animal         1        1
## at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT2.animal         1        1
##                                                              u-95% CI eff.samp
## at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT1.animal        1      0.0
## at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT1.animal        1    139.2
## at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT2.animal        1    139.2
## at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT2.animal        1      0.0
##
##                ~corgh(at.level(sex, "2"):trait):animal
##
##                                                              post.mean l-95% CI
```

```
## at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT1.animal        1        1
## at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT1.animal        1        1
## at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT2.animal        1        1
## at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT2.animal        1        1
##                                                               u-95% CI eff.samp
## at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT1.animal        1      0.0
## at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT1.animal        1    117.2
## at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT2.animal        1    117.2
## at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT2.animal        1      0.0
##
##                ~idh(trait):byear
##
##               post.mean l-95% CI u-95% CI eff.samp
## traitT1.byear    0.9381   0.4298    1.542     1309
## traitT2.byear    3.9257   1.7247    6.792     1000
##
##                ~idh(trait):mother
##
##                post.mean l-95% CI u-95% CI eff.samp
## traitT1.mother     1.906    1.405    2.353     1000
## traitT2.mother     7.756    5.064   10.104     1000
##
##  R-structure:  ~us(at.level(sex, "1"):trait):units
##
##                                                              post.mean l-95% CI
## at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT1.units     2.138    1.538
## at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT1.units     4.599    3.264
## at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT2.units     4.599    3.264
## at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT2.units    15.897   12.695
##                                                              u-95% CI eff.samp
## at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT1.units    2.724     1010
## at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT1.units    5.762     1000
## at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT2.units    5.762     1000
## at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT2.units   19.557     1000
##
##                ~us(at.level(sex, "2"):trait):units
##
##                                                              post.mean l-95% CI
## at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT1.units     2.304    1.705
## at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT1.units     5.578    4.305
## at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT2.units     5.578    4.305
## at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT2.units    20.399   16.622
##                                                              u-95% CI eff.samp
## at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT1.units    2.860     1000
## at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT1.units    6.909     1099
## at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT2.units    6.909     1099
## at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT2.units   24.475     1000
```

```
##
##  Location effects: cbind(T1, T2) ~ trait - 1 + trait:sex
##
##              post.mean l-95% CI u-95% CI eff.samp  pMCMC
## traitT1        6.31127  5.82475  6.73755     1138 <0.001 ***
## traitT2       20.51915 19.62675 21.52179     1000 <0.001 ***
## traitT1:sex2   2.01404  1.61651  2.40538     1000 <0.001 ***
## traitT2:sex2   0.07302 -0.73542  0.84480      825  0.862
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

```r
autocorr(model2.5$VCV)
```

```
## , , at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT1.animal
##
##          at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT1.animal
## Lag 0                                                     1.000000000
## Lag 100                                                  -0.001391944
## Lag 500                                                  -0.001397506
## Lag 1000                                                 -0.001404458
## Lag 5000                                                 -0.001983576
##          at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT1.animal
## Lag 0                                                    -0.004648432
## Lag 100                                                  -0.004565467
## Lag 500                                                  -0.005210530
## Lag 1000                                                 -0.011578289
## Lag 5000                                                 -0.005168617
##          at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT2.animal
## Lag 0                                                    -0.004648432
## Lag 100                                                  -0.004565467
## Lag 500                                                  -0.005210530
## Lag 1000                                                 -0.011578289
## Lag 5000                                                 -0.005168617
##          at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT2.animal
## Lag 0                                                     1.000000000
## Lag 100                                                  -0.001391944
## Lag 500                                                  -0.001397506
## Lag 1000                                                 -0.001404458
## Lag 5000                                                 -0.001983576
##          at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT1.animal
## Lag 0                                                   -0.0006350552
## Lag 100                                                 -0.0006356902
## Lag 500                                                 -0.0006382304
## Lag 1000                                                -0.0010042903
## Lag 5000                                                -0.0010296922
##          at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT1.animal
```

```
## Lag 0                                                    -0.001456198
## Lag 100                                                  -0.001077247
## Lag 500                                                  -0.002490439
## Lag 1000                                                 -0.005282054
## Lag 5000                                                 -0.006612499
##          at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT2.animal
## Lag 0                                                    -0.001456198
## Lag 100                                                  -0.001077247
## Lag 500                                                  -0.002490439
## Lag 1000                                                 -0.005282054
## Lag 5000                                                 -0.006612499
##          at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT2.animal
## Lag 0                                                   -0.0006350554
## Lag 100                                                 -0.0006356904
## Lag 500                                                 -0.0006382306
## Lag 1000                                                -0.0010042906
## Lag 5000                                                -0.0010296924
##          traitT1.byear traitT2.byear traitT1.mother traitT2.mother
## Lag 0       0.01795130   0.009525697     0.01165057   -0.022459989
## Lag 100    -0.02230357   0.018537495     0.01908830   -0.004395967
## Lag 500     0.01133334   0.034563646     0.02966327   -0.024803073
## Lag 1000    0.02568159  -0.072909756     0.01174105    0.008341327
## Lag 5000   -0.00165152  -0.040694308    -0.01713262   -0.022155338
##          at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT1.units
## Lag 0                                                    0.022762565
## Lag 100                                                  0.013550715
## Lag 500                                                  0.023394975
## Lag 1000                                                 0.003721016
## Lag 5000                                                -0.019698113
##          at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT1.units
## Lag 0                                                    0.022365674
## Lag 100                                                  0.041651846
## Lag 500                                                  0.012710980
## Lag 1000                                                -0.011480840
## Lag 5000                                                -0.001466941
##          at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT2.units
## Lag 0                                                    0.022365674
## Lag 100                                                  0.041651846
## Lag 500                                                  0.012710980
## Lag 1000                                                -0.011480840
## Lag 5000                                                -0.001466941
##          at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT2.units
## Lag 0                                                   -0.010314628
## Lag 100                                                  0.055525653
## Lag 500                                                 -0.003105893
## Lag 1000                                                -0.025454553
## Lag 5000                                                 0.008550330
```

```
##           at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT1.units
## Lag 0                                                     0.041893462
## Lag 100                                                  -0.005652676
## Lag 500                                                   0.062306138
## Lag 1000                                                  0.021660306
## Lag 5000                                                 -0.009682721
##           at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT1.units
## Lag 0                                                    0.0674542988
## Lag 100                                                 -0.0276604979
## Lag 500                                                  0.0278254174
## Lag 1000                                                 0.0335689393
## Lag 5000                                                 0.0008595584
##           at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT2.units
## Lag 0                                                    0.0674542988
## Lag 100                                                 -0.0276604979
## Lag 500                                                  0.0278254174
## Lag 1000                                                 0.0335689393
## Lag 5000                                                 0.0008595584
##           at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT2.units
## Lag 0                                                     0.081823186
## Lag 100                                                  -0.039860699
## Lag 500                                                   0.008092171
## Lag 1000                                                  0.008412668
## Lag 5000                                                  0.021467565
##
## , , at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT1.animal
##
##           at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT1.animal
## Lag 0                                                      -0.004648432
## Lag 100                                                    -0.004625049
## Lag 500                                                    -0.003531126
## Lag 1000                                                   -0.004439099
## Lag 5000                                                   -0.006278871
##           at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT1.animal
## Lag 0                                                       1.000000000
## Lag 100                                                     0.723181023
## Lag 500                                                     0.292398811
## Lag 1000                                                    0.092837234
## Lag 5000                                                   -0.009749071
##           at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT2.animal
## Lag 0                                                       1.000000000
## Lag 100                                                     0.723181023
## Lag 500                                                     0.292398811
## Lag 1000                                                    0.092837234
## Lag 5000                                                   -0.009749071
##           at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT2.animal
## Lag 0                                                      -0.004648437
```

```
## Lag 100                                                  -0.004625085
## Lag 500                                                  -0.003531141
## Lag 1000                                                 -0.004439104
## Lag 5000                                                 -0.006278871
##          at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT1.animal
## Lag 0                                                    -0.002312162
## Lag 100                                                  -0.002217551
## Lag 500                                                  -0.001837789
## Lag 1000                                                 -0.002977420
## Lag 5000                                                 -0.004726772
##          at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT1.animal
## Lag 0                                                    -0.010685598
## Lag 100                                                  -0.008503067
## Lag 500                                                  -0.007387620
## Lag 1000                                                 -0.012150586
## Lag 5000                                                 -0.019200093
##          at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT2.animal
## Lag 0                                                    -0.010685598
## Lag 100                                                  -0.008503067
## Lag 500                                                  -0.007387620
## Lag 1000                                                 -0.012150586
## Lag 5000                                                 -0.019200093
##          at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT2.animal
## Lag 0                                                    -0.002312162
## Lag 100                                                  -0.002217551
## Lag 500                                                  -0.001837789
## Lag 1000                                                 -0.002977420
## Lag 5000                                                 -0.004726772
##          traitT1.byear traitT2.byear traitT1.mother traitT2.mother
## Lag 0       0.03206603   0.001388092    -0.01597305   -0.012121778
## Lag 100     0.02062954  -0.034683825     0.01430611   -0.050389774
## Lag 500     0.01419036   0.020814008     0.03068981   -0.018472864
## Lag 1000    0.02272278  -0.003124614    -0.03666507    0.008391569
## Lag 5000   -0.01889532  -0.003299003    -0.03161363    0.042393770
##          at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT1.units
## Lag 0                                                   -0.022308219
## Lag 100                                                 -0.004067301
## Lag 500                                                 -0.004473470
## Lag 1000                                                 0.048582961
## Lag 5000                                                 0.001202075
##          at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT1.units
## Lag 0                                                   -0.015759766
## Lag 100                                                  0.017032779
## Lag 500                                                 -0.003108186
## Lag 1000                                                 0.042126244
## Lag 5000                                                -0.016955230
##          at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT2.units
```

```
## Lag 0                                                  -0.015759766
## Lag 100                                                 0.017032779
## Lag 500                                                -0.003108186
## Lag 1000                                                0.042126244
## Lag 5000                                               -0.016955230
##          at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT2.units
## Lag 0                                                  -0.008530358
## Lag 100                                                 0.019755361
## Lag 500                                                -0.013140805
## Lag 1000                                                0.013898534
## Lag 5000                                               -0.033469898
##          at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT1.units
## Lag 0                                                   0.005815507
## Lag 100                                                 0.001279903
## Lag 500                                                -0.004227436
## Lag 1000                                               -0.037409946
## Lag 5000                                                0.027223985
##          at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT1.units
## Lag 0                                                  -0.028111911
## Lag 100                                                -0.015823870
## Lag 500                                                -0.002146573
## Lag 1000                                               -0.016376141
## Lag 5000                                                0.038876537
##          at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT2.units
## Lag 0                                                  -0.028111911
## Lag 100                                                -0.015823870
## Lag 500                                                -0.002146573
## Lag 1000                                               -0.016376141
## Lag 5000                                                0.038876537
##          at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT2.units
## Lag 0                                                  -0.042456056
## Lag 100                                                -0.010621969
## Lag 500                                                 0.009797485
## Lag 1000                                               -0.019305202
## Lag 5000                                                0.033404201
##
## , , at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT2.animal
##
##          at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT1.animal
## Lag 0                                                   -0.004648432
## Lag 100                                                 -0.004625049
## Lag 500                                                 -0.003531126
## Lag 1000                                                -0.004439099
## Lag 5000                                                -0.006278871
##          at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT1.animal
## Lag 0                                                    1.000000000
## Lag 100                                                  0.723181023
```

```
## Lag 500                                                       0.292398811
## Lag 1000                                                      0.092837234
## Lag 5000                                                     -0.009749071
##          at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT2.animal
## Lag 0                                                         1.000000000
## Lag 100                                                       0.723181023
## Lag 500                                                       0.292398811
## Lag 1000                                                      0.092837234
## Lag 5000                                                     -0.009749071
##          at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT2.animal
## Lag 0                                                        -0.004648437
## Lag 100                                                      -0.004625085
## Lag 500                                                      -0.003531141
## Lag 1000                                                     -0.004439104
## Lag 5000                                                     -0.006278871
##          at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT1.animal
## Lag 0                                                        -0.002312162
## Lag 100                                                      -0.002217551
## Lag 500                                                      -0.001837789
## Lag 1000                                                     -0.002977420
## Lag 5000                                                     -0.004726772
##          at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT1.animal
## Lag 0                                                        -0.010685598
## Lag 100                                                      -0.008503067
## Lag 500                                                      -0.007387620
## Lag 1000                                                     -0.012150586
## Lag 5000                                                     -0.019200093
##          at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT2.animal
## Lag 0                                                        -0.010685598
## Lag 100                                                      -0.008503067
## Lag 500                                                      -0.007387620
## Lag 1000                                                     -0.012150586
## Lag 5000                                                     -0.019200093
##          at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT2.animal
## Lag 0                                                        -0.002312162
## Lag 100                                                      -0.002217551
## Lag 500                                                      -0.001837789
## Lag 1000                                                     -0.002977420
## Lag 5000                                                     -0.004726772
##          traitT1.byear traitT2.byear traitT1.mother traitT2.mother
## Lag 0       0.03206603   0.001388092    -0.01597305   -0.012121778
## Lag 100     0.02062954  -0.034683825     0.01430611   -0.050389774
## Lag 500     0.01419036   0.020814008     0.03068981   -0.018472864
## Lag 1000    0.02272278  -0.003124614    -0.03666507    0.008391569
## Lag 5000   -0.01889532  -0.003299003    -0.03161363    0.042393770
##          at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT1.units
## Lag 0                                                       -0.022308219
```

```
## Lag 100                                                     -0.004067301
## Lag 500                                                     -0.004473470
## Lag 1000                                                     0.048582961
## Lag 5000                                                     0.001202075
##          at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT1.units
## Lag 0                                                       -0.015759766
## Lag 100                                                      0.017032779
## Lag 500                                                     -0.003108186
## Lag 1000                                                     0.042126244
## Lag 5000                                                    -0.016955230
##          at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT2.units
## Lag 0                                                       -0.015759766
## Lag 100                                                      0.017032779
## Lag 500                                                     -0.003108186
## Lag 1000                                                     0.042126244
## Lag 5000                                                    -0.016955230
##          at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT2.units
## Lag 0                                                       -0.008530358
## Lag 100                                                      0.019755361
## Lag 500                                                     -0.013140805
## Lag 1000                                                     0.013898534
## Lag 5000                                                    -0.033469898
##          at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT1.units
## Lag 0                                                        0.005815507
## Lag 100                                                      0.001279903
## Lag 500                                                     -0.004227436
## Lag 1000                                                    -0.037409946
## Lag 5000                                                     0.027223985
##          at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT1.units
## Lag 0                                                       -0.028111911
## Lag 100                                                     -0.015823870
## Lag 500                                                     -0.002146573
## Lag 1000                                                    -0.016376141
## Lag 5000                                                     0.038876537
##          at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT2.units
## Lag 0                                                       -0.028111911
## Lag 100                                                     -0.015823870
## Lag 500                                                     -0.002146573
## Lag 1000                                                    -0.016376141
## Lag 5000                                                     0.038876537
##          at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT2.units
## Lag 0                                                       -0.042456056
## Lag 100                                                     -0.010621969
## Lag 500                                                      0.009797485
## Lag 1000                                                    -0.019305202
## Lag 5000                                                     0.033404201
##
```

```
## , , at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT2.animal
##
##          at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT1.animal
## Lag 0                                                     1.000000000
## Lag 100                                                  -0.001391944
## Lag 500                                                  -0.001397506
## Lag 1000                                                 -0.001404458
## Lag 5000                                                 -0.001983576
##          at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT1.animal
## Lag 0                                                    -0.004648437
## Lag 100                                                  -0.004565469
## Lag 500                                                  -0.005210530
## Lag 1000                                                 -0.011578289
## Lag 5000                                                 -0.005168617
##          at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT2.animal
## Lag 0                                                    -0.004648437
## Lag 100                                                  -0.004565469
## Lag 500                                                  -0.005210530
## Lag 1000                                                 -0.011578289
## Lag 5000                                                 -0.005168617
##          at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT2.animal
## Lag 0                                                     1.000000000
## Lag 100                                                  -0.001391944
## Lag 500                                                  -0.001397506
## Lag 1000                                                 -0.001404458
## Lag 5000                                                 -0.001983576
##          at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT1.animal
## Lag 0                                                   -0.0006350551
## Lag 100                                                 -0.0006356902
## Lag 500                                                 -0.0006382304
## Lag 1000                                                -0.0010042903
## Lag 5000                                                -0.0010296921
##          at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT1.animal
## Lag 0                                                    -0.001456198
## Lag 100                                                  -0.001077247
## Lag 500                                                  -0.002490439
## Lag 1000                                                 -0.005282054
## Lag 5000                                                 -0.006612499
##          at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT2.animal
## Lag 0                                                    -0.001456198
## Lag 100                                                  -0.001077247
## Lag 500                                                  -0.002490439
## Lag 1000                                                 -0.005282054
## Lag 5000                                                 -0.006612499
##          at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT2.animal
## Lag 0                                                   -0.0006350554
## Lag 100                                                 -0.0006356904
```

```
## Lag 500                                                 -0.0006382306
## Lag 1000                                                -0.0010042906
## Lag 5000                                                -0.0010296924
##          traitT1.byear traitT2.byear traitT1.mother traitT2.mother
## Lag 0      0.017951297   0.009525703     0.01165057   -0.022459984
## Lag 100   -0.022303567   0.018537496     0.01908830   -0.004395967
## Lag 500    0.011333343   0.034563646     0.02966327   -0.024803074
## Lag 1000   0.025681592  -0.072909754     0.01174105    0.008341327
## Lag 5000  -0.001651524  -0.040694308    -0.01713262   -0.022155336
##          at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT1.units
## Lag 0                                                0.022762562
## Lag 100                                              0.013550715
## Lag 500                                              0.023394973
## Lag 1000                                             0.003721019
## Lag 5000                                            -0.019698116
##          at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT1.units
## Lag 0                                                0.022365669
## Lag 100                                              0.041651846
## Lag 500                                              0.012710977
## Lag 1000                                            -0.011480840
## Lag 5000                                            -0.001466943
##          at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT2.units
## Lag 0                                                0.022365669
## Lag 100                                              0.041651846
## Lag 500                                              0.012710977
## Lag 1000                                            -0.011480840
## Lag 5000                                            -0.001466943
##          at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT2.units
## Lag 0                                               -0.010314633
## Lag 100                                              0.055525653
## Lag 500                                             -0.003105895
## Lag 1000                                            -0.025454554
## Lag 5000                                             0.008550329
##          at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT1.units
## Lag 0                                                0.041893463
## Lag 100                                             -0.005652675
## Lag 500                                              0.062306141
## Lag 1000                                             0.021660305
## Lag 5000                                            -0.009682725
##          at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT1.units
## Lag 0                                               0.0674542971
## Lag 100                                            -0.0276604962
## Lag 500                                             0.0278254213
## Lag 1000                                            0.0335689362
## Lag 5000                                            0.0008595534
##          at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT2.units
## Lag 0                                               0.0674542971
```

```
## Lag 100                                                  -0.0276604962
## Lag 500                                                   0.0278254213
## Lag 1000                                                  0.0335689362
## Lag 5000                                                  0.0008595534
##         at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT2.units
## Lag 0                                                       0.081823182
## Lag 100                                                    -0.039860695
## Lag 500                                                     0.008092176
## Lag 1000                                                    0.008412663
## Lag 5000                                                    0.021467560
##
## , , at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT1.animal
##
##         at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT1.animal
## Lag 0                                                     -0.0006350552
## Lag 100                                                   -0.0002728055
## Lag 500                                                   -0.0002753457
## Lag 1000                                                  -0.0002785209
## Lag 5000                                                  -0.0005430012
##         at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT1.animal
## Lag 0                                                     -0.0023121624
## Lag 100                                                   -0.0018131603
## Lag 500                                                   -0.0021171712
## Lag 1000                                                  -0.0002636656
## Lag 5000                                                  -0.0007281379
##         at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT2.animal
## Lag 0                                                     -0.0023121624
## Lag 100                                                   -0.0018131603
## Lag 500                                                   -0.0021171712
## Lag 1000                                                  -0.0002636656
## Lag 5000                                                  -0.0007281379
##         at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT2.animal
## Lag 0                                                     -0.0006350551
## Lag 100                                                   -0.0002728055
## Lag 500                                                   -0.0002753457
## Lag 1000                                                  -0.0002785209
## Lag 5000                                                  -0.0005430012
##         at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT1.animal
## Lag 0                                                      1.0000000000
## Lag 100                                                   -0.0001245872
## Lag 500                                                    0.0472252652
## Lag 1000                                                  -0.0002929252
## Lag 5000                                                  -0.0003045261
##         at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT1.animal
## Lag 0                                                     -0.0030464876
## Lag 100                                                   -0.0012272569
## Lag 500                                                   -0.0012428417
```

```
## Lag 1000                                                 -0.0009101059
## Lag 5000                                                 -0.0098179074
##          at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT2.animal
## Lag 0                                                    -0.0030464876
## Lag 100                                                  -0.0012272569
## Lag 500                                                  -0.0012428417
## Lag 1000                                                 -0.0009101059
## Lag 5000                                                 -0.0098179074
##          at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT2.animal
## Lag 0                                                     1.0000000000
## Lag 100                                                  -0.0001245873
## Lag 500                                                   0.0472252675
## Lag 1000                                                 -0.0002929253
## Lag 5000                                                 -0.0003045262
##          traitT1.byear traitT2.byear traitT1.mother traitT2.mother
## Lag 0      0.007859897  -0.048647022    0.014169960    -0.01277587
## Lag 100   -0.031686328   0.044252052    0.001418991    -0.00470343
## Lag 500   -0.006041444  -0.003672647    0.026635103    -0.05216309
## Lag 1000   0.040389650   0.001576320   -0.008599945    -0.03098371
## Lag 5000  -0.014128580  -0.030023647    0.016865943    -0.08562409
##          at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT1.units
## Lag 0                                                     0.019317584
## Lag 100                                                  -0.006883423
## Lag 500                                                   0.005456272
## Lag 1000                                                 -0.040428229
## Lag 5000                                                 -0.019377516
##          at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT1.units
## Lag 0                                                     0.002652222
## Lag 100                                                  -0.016499071
## Lag 500                                                  -0.004463759
## Lag 1000                                                 -0.044909299
## Lag 5000                                                 -0.009389202
##          at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT2.units
## Lag 0                                                     0.002652222
## Lag 100                                                  -0.016499071
## Lag 500                                                  -0.004463759
## Lag 1000                                                 -0.044909299
## Lag 5000                                                 -0.009389202
##          at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT2.units
## Lag 0                                                    -0.002054456
## Lag 100                                                   0.002237526
## Lag 500                                                   0.013746887
## Lag 1000                                                 -0.048289160
## Lag 5000                                                  0.014216318
##          at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT1.units
## Lag 0                                                     -0.01258769
## Lag 100                                                    0.01872011
```

```
## Lag 500                                                   0.01882522
## Lag 1000                                                  0.03756773
## Lag 5000                                                 -0.02411450
##          at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT1.units
## Lag 0                                                   -0.005906983
## Lag 100                                                  0.013146223
## Lag 500                                                  0.043916861
## Lag 1000                                                 0.033507898
## Lag 5000                                                -0.008078930
##          at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT2.units
## Lag 0                                                   -0.005906983
## Lag 100                                                  0.013146223
## Lag 500                                                  0.043916861
## Lag 1000                                                 0.033507898
## Lag 5000                                                -0.008078930
##          at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT2.units
## Lag 0                                                   0.0006335032
## Lag 100                                                 0.0037825580
## Lag 500                                                 0.0543707513
## Lag 1000                                                0.0360053763
## Lag 5000                                               -0.0061125594
##
## , , at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT1.animal
##
##          at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT1.animal
## Lag 0                                                     -0.001456198
## Lag 100                                                    0.001715826
## Lag 500                                                   -0.003740235
## Lag 1000                                                  -0.005014592
## Lag 5000                                                  -0.010487126
##          at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT1.animal
## Lag 0                                                      -0.01068560
## Lag 100                                                    -0.01235479
## Lag 500                                                    -0.01399016
## Lag 1000                                                   -0.01676244
## Lag 5000                                                   -0.01431417
##          at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT2.animal
## Lag 0                                                      -0.01068560
## Lag 100                                                    -0.01235479
## Lag 500                                                    -0.01399016
## Lag 1000                                                   -0.01676244
## Lag 5000                                                   -0.01431417
##          at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT2.animal
## Lag 0                                                     -0.001456198
## Lag 100                                                    0.001715826
## Lag 500                                                   -0.003740235
## Lag 1000                                                  -0.005014592
```

```
## Lag 5000                                                 -0.010487126
##          at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT1.animal
## Lag 0                                                    -0.003046488
## Lag 100                                                  -0.003153963
## Lag 500                                                  -0.002352225
## Lag 1000                                                 -0.003782156
## Lag 5000                                                 -0.002857518
##          at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT1.animal
## Lag 0                                                      1.00000000
## Lag 100                                                    0.83058654
## Lag 500                                                    0.23387736
## Lag 1000                                                   0.12487172
## Lag 5000                                                  -0.02765118
##          at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT2.animal
## Lag 0                                                      1.00000000
## Lag 100                                                    0.83058654
## Lag 500                                                    0.23387736
## Lag 1000                                                   0.12487172
## Lag 5000                                                  -0.02765118
##          at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT2.animal
## Lag 0                                                    -0.003046486
## Lag 100                                                  -0.003153962
## Lag 500                                                  -0.002352224
## Lag 1000                                                 -0.003782157
## Lag 5000                                                 -0.002857519
##          traitT1.byear traitT2.byear traitT1.mother traitT2.mother
## Lag 0     -0.013526377   -0.01774985   -0.013841217    0.022701877
## Lag 100    0.004093624   -0.01386591    0.001219680    0.015022006
## Lag 500    0.021634587    0.01429551   -0.019234622    0.022081044
## Lag 1000  -0.020668120    0.05928732   -0.059492408    0.033606722
## Lag 5000  -0.009719164    0.04539140   -0.005427111   -0.008612086
##          at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT1.units
## Lag 0                                                   -0.024077943
## Lag 100                                                 -0.002203887
## Lag 500                                                  0.010909995
## Lag 1000                                                 0.018505117
## Lag 5000                                                -0.065135988
##          at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT1.units
## Lag 0                                                  -0.0072931648
## Lag 100                                                 0.0003911575
## Lag 500                                                 0.0164572902
## Lag 1000                                                0.0161183049
## Lag 5000                                               -0.0518609896
##          at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT2.units
## Lag 0                                                  -0.0072931648
## Lag 100                                                 0.0003911575
## Lag 500                                                 0.0164572902
```

```
## Lag 1000                                                         0.0161183049
## Lag 5000                                                        -0.0518609896
##            at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT2.units
## Lag 0                                                              0.002102035
## Lag 100                                                            0.002516452
## Lag 500                                                            0.016614009
## Lag 1000                                                           0.009102492
## Lag 5000                                                          -0.057713146
##            at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT1.units
## Lag 0                                                              0.003830731
## Lag 100                                                           -0.005606418
## Lag 500                                                            0.005332862
## Lag 1000                                                           0.009183940
## Lag 5000                                                          -0.021145579
##            at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT1.units
## Lag 0                                                              0.001171218
## Lag 100                                                           -0.012536100
## Lag 500                                                            0.002347666
## Lag 1000                                                           0.012765703
## Lag 5000                                                          -0.035720789
##            at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT2.units
## Lag 0                                                              0.001171218
## Lag 100                                                           -0.012536100
## Lag 500                                                            0.002347666
## Lag 1000                                                           0.012765703
## Lag 5000                                                          -0.035720789
##            at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT2.units
## Lag 0                                                              0.011573448
## Lag 100                                                            0.010597731
## Lag 500                                                            0.009234753
## Lag 1000                                                           0.017510534
## Lag 5000                                                          -0.019205136
##
## , , at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT2.animal
##
##            at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT1.animal
## Lag 0                                                               -0.001456198
## Lag 100                                                              0.001715826
## Lag 500                                                             -0.003740235
## Lag 1000                                                            -0.005014592
## Lag 5000                                                            -0.010487126
##            at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT1.animal
## Lag 0                                                                -0.01068560
## Lag 100                                                              -0.01235479
## Lag 500                                                              -0.01399016
## Lag 1000                                                             -0.01676244
## Lag 5000                                                             -0.01431417
```

```
##          at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT2.animal
## Lag 0                                                      -0.01068560
## Lag 100                                                    -0.01235479
## Lag 500                                                    -0.01399016
## Lag 1000                                                   -0.01676244
## Lag 5000                                                   -0.01431417
##          at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT2.animal
## Lag 0                                                     -0.001456198
## Lag 100                                                    0.001715826
## Lag 500                                                   -0.003740235
## Lag 1000                                                  -0.005014592
## Lag 5000                                                  -0.010487126
##          at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT1.animal
## Lag 0                                                     -0.003046488
## Lag 100                                                   -0.003153963
## Lag 500                                                   -0.002352225
## Lag 1000                                                  -0.003782156
## Lag 5000                                                  -0.002857518
##          at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT1.animal
## Lag 0                                                       1.00000000
## Lag 100                                                     0.83058654
## Lag 500                                                     0.23387736
## Lag 1000                                                    0.12487172
## Lag 5000                                                   -0.02765118
##          at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT2.animal
## Lag 0                                                       1.00000000
## Lag 100                                                     0.83058654
## Lag 500                                                     0.23387736
## Lag 1000                                                    0.12487172
## Lag 5000                                                   -0.02765118
##          at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT2.animal
## Lag 0                                                     -0.003046486
## Lag 100                                                   -0.003153962
## Lag 500                                                   -0.002352224
## Lag 1000                                                  -0.003782157
## Lag 5000                                                  -0.002857519
##          traitT1.byear traitT2.byear traitT1.mother traitT2.mother
## Lag 0     -0.013526377   -0.01774985   -0.013841217    0.022701877
## Lag 100    0.004093624   -0.01386591    0.001219680    0.015022006
## Lag 500    0.021634587    0.01429551   -0.019234622    0.022081044
## Lag 1000  -0.020668120    0.05928732   -0.059492408    0.033606722
## Lag 5000  -0.009719164    0.04539140   -0.005427111   -0.008612086
##          at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT1.units
## Lag 0                                                     -0.024077943
## Lag 100                                                   -0.002203887
## Lag 500                                                    0.010909995
## Lag 1000                                                   0.018505117
```

```
## Lag 5000                                                    -0.065135988
##          at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT1.units
## Lag 0                                                      -0.0072931648
## Lag 100                                                     0.0003911575
## Lag 500                                                     0.0164572902
## Lag 1000                                                    0.0161183049
## Lag 5000                                                   -0.0518609896
##          at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT2.units
## Lag 0                                                      -0.0072931648
## Lag 100                                                     0.0003911575
## Lag 500                                                     0.0164572902
## Lag 1000                                                    0.0161183049
## Lag 5000                                                   -0.0518609896
##          at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT2.units
## Lag 0                                                        0.002102035
## Lag 100                                                      0.002516452
## Lag 500                                                      0.016614009
## Lag 1000                                                     0.009102492
## Lag 5000                                                    -0.057713146
##          at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT1.units
## Lag 0                                                        0.003830731
## Lag 100                                                     -0.005606418
## Lag 500                                                      0.005332862
## Lag 1000                                                     0.009183940
## Lag 5000                                                    -0.021145579
##          at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT1.units
## Lag 0                                                        0.001171218
## Lag 100                                                     -0.012536100
## Lag 500                                                      0.002347666
## Lag 1000                                                     0.012765703
## Lag 5000                                                    -0.035720789
##          at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT2.units
## Lag 0                                                        0.001171218
## Lag 100                                                     -0.012536100
## Lag 500                                                      0.002347666
## Lag 1000                                                     0.012765703
## Lag 5000                                                    -0.035720789
##          at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT2.units
## Lag 0                                                        0.011573448
## Lag 100                                                      0.010597731
## Lag 500                                                      0.009234753
## Lag 1000                                                     0.017510534
## Lag 5000                                                    -0.019205136
##
## , , at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT2.animal
##
##          at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT1.animal
```

```
## Lag 0                                                        -0.0006350554
## Lag 100                                                      -0.0002727894
## Lag 500                                                      -0.0002753459
## Lag 1000                                                     -0.0002785211
## Lag 5000                                                     -0.0005430015
##            at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT1.animal
## Lag 0                                                        -0.0023121624
## Lag 100                                                      -0.0018131609
## Lag 500                                                      -0.0021171719
## Lag 1000                                                     -0.0002636663
## Lag 5000                                                     -0.0007281383
##            at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT2.animal
## Lag 0                                                        -0.0023121624
## Lag 100                                                      -0.0018131609
## Lag 500                                                      -0.0021171719
## Lag 1000                                                     -0.0002636663
## Lag 5000                                                     -0.0007281383
##            at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT2.animal
## Lag 0                                                        -0.0006350554
## Lag 100                                                      -0.0002727894
## Lag 500                                                      -0.0002753459
## Lag 1000                                                     -0.0002785211
## Lag 5000                                                     -0.0005430015
##            at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT1.animal
## Lag 0                                                         1.0000000000
## Lag 100                                                      -0.0001245873
## Lag 500                                                       0.0472252591
## Lag 1000                                                     -0.0002929253
## Lag 5000                                                     -0.0003045262
##            at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT1.animal
## Lag 0                                                        -0.0030464862
## Lag 100                                                      -0.0012272567
## Lag 500                                                      -0.0012428427
## Lag 1000                                                     -0.0009101069
## Lag 5000                                                     -0.0098178961
##            at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT2.animal
## Lag 0                                                        -0.0030464862
## Lag 100                                                      -0.0012272567
## Lag 500                                                      -0.0012428427
## Lag 1000                                                     -0.0009101069
## Lag 5000                                                     -0.0098178961
##            at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT2.animal
## Lag 0                                                         1.0000000000
## Lag 100                                                      -0.0001245874
## Lag 500                                                       0.0472252614
## Lag 1000                                                     -0.0002929254
## Lag 5000                                                     -0.0003045263
```

```
##           traitT1.byear traitT2.byear traitT1.mother traitT2.mother
## Lag 0       0.007859899  -0.048647026    0.014169961   -0.012775870
## Lag 100    -0.031686329   0.044252052    0.001418992   -0.004703428
## Lag 500    -0.006041443  -0.003672647    0.026635104   -0.052163087
## Lag 1000    0.040389655   0.001576326   -0.008599948   -0.030983703
## Lag 5000   -0.014128581  -0.030023647    0.016865937   -0.085624096
##           at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT1.units
## Lag 0                                                     0.019317585
## Lag 100                                                  -0.006883421
## Lag 500                                                   0.005456271
## Lag 1000                                                 -0.040428232
## Lag 5000                                                 -0.019377514
##           at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT1.units
## Lag 0                                                     0.002652225
## Lag 100                                                  -0.016499068
## Lag 500                                                  -0.004463759
## Lag 1000                                                 -0.044909300
## Lag 5000                                                 -0.009389200
##           at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT2.units
## Lag 0                                                     0.002652225
## Lag 100                                                  -0.016499068
## Lag 500                                                  -0.004463759
## Lag 1000                                                 -0.044909300
## Lag 5000                                                 -0.009389200
##           at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT2.units
## Lag 0                                                    -0.002054453
## Lag 100                                                   0.002237526
## Lag 500                                                   0.013746888
## Lag 1000                                                 -0.048289160
## Lag 5000                                                  0.014216318
##           at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT1.units
## Lag 0                                                     -0.01258769
## Lag 100                                                    0.01872011
## Lag 500                                                    0.01882522
## Lag 1000                                                   0.03756772
## Lag 5000                                                  -0.02411450
##           at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT1.units
## Lag 0                                                    -0.005906985
## Lag 100                                                   0.013146221
## Lag 500                                                   0.043916862
## Lag 1000                                                  0.033507897
## Lag 5000                                                 -0.008078924
##           at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT2.units
## Lag 0                                                    -0.005906985
## Lag 100                                                   0.013146221
## Lag 500                                                   0.043916862
## Lag 1000                                                  0.033507897
```

```
## Lag 5000                                                  -0.008078924
##          at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT2.units
## Lag 0                                                     0.0006335012
## Lag 100                                                   0.0037825564
## Lag 500                                                   0.0543707522
## Lag 1000                                                  0.0360053770
## Lag 5000                                                 -0.0061125543
##
## , , traitT1.byear
##
##          at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT1.animal
## Lag 0                                                       0.017951297
## Lag 100                                                    -0.015650603
## Lag 500                                                    -0.048310004
## Lag 1000                                                    0.006748945
## Lag 5000                                                   -0.024695487
##          at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT1.animal
## Lag 0                                                        0.03206603
## Lag 100                                                      0.03644816
## Lag 500                                                      0.02462867
## Lag 1000                                                     0.03134031
## Lag 5000                                                    -0.02813186
##          at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT2.animal
## Lag 0                                                        0.03206603
## Lag 100                                                      0.03644816
## Lag 500                                                      0.02462867
## Lag 1000                                                     0.03134031
## Lag 5000                                                    -0.02813186
##          at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT2.animal
## Lag 0                                                       0.017951297
## Lag 100                                                    -0.015650603
## Lag 500                                                    -0.048310005
## Lag 1000                                                    0.006748946
## Lag 5000                                                   -0.024695489
##          at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT1.animal
## Lag 0                                                       0.007859897
## Lag 100                                                     0.008951424
## Lag 500                                                    -0.075193837
## Lag 1000                                                   -0.056006662
## Lag 5000                                                    0.056756820
##          at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT1.animal
## Lag 0                                                      -0.013526377
## Lag 100                                                    -0.008509234
## Lag 500                                                     0.016651269
## Lag 1000                                                   -0.028261999
## Lag 5000                                                    0.036871813
##          at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT2.animal
```

```
## Lag 0                                                    -0.013526377
## Lag 100                                                  -0.008509234
## Lag 500                                                   0.016651269
## Lag 1000                                                 -0.028261999
## Lag 5000                                                  0.036871813
##            at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT2.animal
## Lag 0                                                     0.007859899
## Lag 100                                                   0.008951426
## Lag 500                                                  -0.075193836
## Lag 1000                                                 -0.056006660
## Lag 5000                                                  0.056756821
##            traitT1.byear traitT2.byear traitT1.mother traitT2.mother
## Lag 0         1.00000000  -0.023340160    -0.06849446    0.027498789
## Lag 100      -0.05704935  -0.031640453     0.02105239    0.005021463
## Lag 500      -0.09276121   0.013578861    -0.02647627    0.017938010
## Lag 1000     -0.02013395  -0.042064858     0.03145873   -0.021329142
## Lag 5000     -0.04698339  -0.007786385    -0.04540802   -0.011391335
##            at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT1.units
## Lag 0                                                     0.03137990
## Lag 100                                                   0.03791656
## Lag 500                                                  -0.02619206
## Lag 1000                                                 -0.05409955
## Lag 5000                                                 -0.04538239
##            at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT1.units
## Lag 0                                                   0.0040622738
## Lag 100                                                 0.0677383954
## Lag 500                                                -0.0005605853
## Lag 1000                                               -0.0411199654
## Lag 5000                                               -0.0290154960
##            at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT2.units
## Lag 0                                                   0.0040622738
## Lag 100                                                 0.0677383954
## Lag 500                                                -0.0005605853
## Lag 1000                                               -0.0411199654
## Lag 5000                                               -0.0290154960
##            at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT2.units
## Lag 0                                                   -0.024177752
## Lag 100                                                  0.080268776
## Lag 500                                                  0.017538142
## Lag 1000                                                -0.040908697
## Lag 5000                                                -0.005206272
##            at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT1.units
## Lag 0                                                   -0.024662838
## Lag 100                                                 -0.008402504
## Lag 500                                                  0.095917314
## Lag 1000                                                -0.042564597
## Lag 5000                                                -0.002506247
```

```
##          at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT1.units
## Lag 0                                                   -0.02752719
## Lag 100                                                 -0.01695931
## Lag 500                                                  0.05741234
## Lag 1000                                                -0.04606330
## Lag 5000                                                 0.04134386
##          at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT2.units
## Lag 0                                                   -0.02752719
## Lag 100                                                 -0.01695931
## Lag 500                                                  0.05741234
## Lag 1000                                                -0.04606330
## Lag 5000                                                 0.04134386
##          at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT2.units
## Lag 0                                                  -0.008651050
## Lag 100                                                -0.028966290
## Lag 500                                                -0.004977943
## Lag 1000                                               -0.040848683
## Lag 5000                                                0.085512002
##
## , , traitT2.byear
##
##          at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT1.animal
## Lag 0                                                     0.009525697
## Lag 100                                                  -0.064974801
## Lag 500                                                  -0.028789100
## Lag 1000                                                 -0.043603295
## Lag 5000                                                  0.020618670
##          at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT1.animal
## Lag 0                                                     0.001388092
## Lag 100                                                   0.040474658
## Lag 500                                                  -0.014654139
## Lag 1000                                                  0.021983132
## Lag 5000                                                  0.038125394
##          at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT2.animal
## Lag 0                                                     0.001388092
## Lag 100                                                   0.040474658
## Lag 500                                                  -0.014654139
## Lag 1000                                                  0.021983132
## Lag 5000                                                  0.038125394
##          at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT2.animal
## Lag 0                                                     0.009525703
## Lag 100                                                  -0.064974806
## Lag 500                                                  -0.028789102
## Lag 1000                                                 -0.043603295
## Lag 5000                                                  0.020618669
##          at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT1.animal
## Lag 0                                                    -4.864702e-02
```

```
## Lag 100                                                   5.788328e-02
## Lag 500                                                  -3.017681e-05
## Lag 1000                                                 -5.850992e-03
## Lag 5000                                                  2.420463e-04
##          at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT1.animal
## Lag 0                                                   -0.0177498454
## Lag 100                                                  0.0063808442
## Lag 500                                                 -0.0049424163
## Lag 1000                                                -0.0003719052
## Lag 5000                                                 0.0521589142
##          at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT2.animal
## Lag 0                                                   -0.0177498454
## Lag 100                                                  0.0063808442
## Lag 500                                                 -0.0049424163
## Lag 1000                                                -0.0003719052
## Lag 5000                                                 0.0521589142
##          at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT2.animal
## Lag 0                                                   -4.864703e-02
## Lag 100                                                  5.788328e-02
## Lag 500                                                 -3.016908e-05
## Lag 1000                                                -5.850992e-03
## Lag 5000                                                 2.420437e-04
##          traitT1.byear traitT2.byear traitT1.mother traitT2.mother
## Lag 0     -0.023340160   1.000000000   -0.040047907     0.07501106
## Lag 100   -0.025201131   0.041181362    0.026543851    -0.02763272
## Lag 500   -0.013876500   0.025109718   -0.007886112    -0.01358018
## Lag 1000  -0.001175324   0.050652913   -0.058106033     0.02511307
## Lag 5000  -0.027192208   0.002883567   -0.007135063     0.05428665
##          at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT1.units
## Lag 0                                                     -0.04513833
## Lag 100                                                    0.04234089
## Lag 500                                                   -0.03057247
## Lag 1000                                                  -0.07029298
## Lag 5000                                                   0.00168274
##          at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT1.units
## Lag 0                                                    -0.087126652
## Lag 100                                                   0.019735995
## Lag 500                                                  -0.036577541
## Lag 1000                                                 -0.082722967
## Lag 5000                                                  0.004687441
##          at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT2.units
## Lag 0                                                    -0.087126652
## Lag 100                                                   0.019735995
## Lag 500                                                  -0.036577541
## Lag 1000                                                 -0.082722967
## Lag 5000                                                  0.004687441
##          at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT2.units
```

```
## Lag 0                                                  -0.123422570
## Lag 100                                                -0.036523126
## Lag 500                                                -0.009320346
## Lag 1000                                               -0.058354272
## Lag 5000                                                0.005124232
##            at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT1.units
## Lag 0                                                     0.02756337
## Lag 100                                                   0.03558955
## Lag 500                                                   0.00835486
## Lag 1000                                                 -0.01369138
## Lag 5000                                                 -0.01097255
##            at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT1.units
## Lag 0                                                    -0.02016065
## Lag 100                                                   0.04165810
## Lag 500                                                   0.01434291
## Lag 1000                                                 -0.01828566
## Lag 5000                                                 -0.02257444
##            at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT2.units
## Lag 0                                                    -0.02016065
## Lag 100                                                   0.04165810
## Lag 500                                                   0.01434291
## Lag 1000                                                 -0.01828566
## Lag 5000                                                 -0.02257444
##            at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT2.units
## Lag 0                                                    -0.05004816
## Lag 100                                                   0.05046643
## Lag 500                                                  -0.01284557
## Lag 1000                                                 -0.02219803
## Lag 5000                                                 -0.01385276
##
## , , traitT1.mother
##
##            at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT1.animal
## Lag 0                                                      0.01165057
## Lag 100                                                    0.08905786
## Lag 500                                                    0.02244386
## Lag 1000                                                  -0.03313281
## Lag 5000                                                   0.02806631
##            at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT1.animal
## Lag 0                                                     -0.01597305
## Lag 100                                                   -0.00334208
## Lag 500                                                    0.02847650
## Lag 1000                                                   0.04457421
## Lag 5000                                                   0.02068766
##            at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT2.animal
## Lag 0                                                     -0.01597305
## Lag 100                                                   -0.00334208
```

```
## Lag 500                                                         0.02847650
## Lag 1000                                                        0.04457421
## Lag 5000                                                        0.02068766
##          at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT2.animal
## Lag 0                                                           0.01165057
## Lag 100                                                         0.08905786
## Lag 500                                                         0.02244385
## Lag 1000                                                       -0.03313282
## Lag 5000                                                        0.02806631
##          at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT1.animal
## Lag 0                                                          0.014169960
## Lag 100                                                        0.079761436
## Lag 500                                                        0.048204670
## Lag 1000                                                       0.009553326
## Lag 5000                                                      -0.004370446
##          at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT1.animal
## Lag 0                                                         -0.013841217
## Lag 100                                                        0.001743246
## Lag 500                                                       -0.004551783
## Lag 1000                                                      -0.020295969
## Lag 5000                                                       0.017570665
##          at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT2.animal
## Lag 0                                                         -0.013841217
## Lag 100                                                        0.001743246
## Lag 500                                                       -0.004551783
## Lag 1000                                                      -0.020295969
## Lag 5000                                                       0.017570665
##          at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT2.animal
## Lag 0                                                          0.014169961
## Lag 100                                                        0.079761439
## Lag 500                                                        0.048204674
## Lag 1000                                                       0.009553326
## Lag 5000                                                      -0.004370444
##          traitT1.byear traitT2.byear traitT1.mother traitT2.mother
## Lag 0      -0.06849446 -0.0400479067    1.000000000   -0.297139239
## Lag 100     0.01901561  0.0230734698   -0.009027192   -0.005184777
## Lag 500    -0.03709457 -0.0475231945   -0.006020676   -0.021229786
## Lag 1000    0.03016960 -0.0002406725    0.017633995    0.014194686
## Lag 5000   -0.01390477  0.0350936719   -0.001330014   -0.010498917
##          at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT1.units
## Lag 0                                                       -0.074914843
## Lag 100                                                     -0.011337055
## Lag 500                                                      0.019960354
## Lag 1000                                                     0.019122566
## Lag 5000                                                     0.006225052
##          at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT1.units
## Lag 0                                                       -0.008518268
```

```
## Lag 100                                                  -0.016248199
## Lag 500                                                   0.044751016
## Lag 1000                                                  0.024827801
## Lag 5000                                                 -0.001860750
##          at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT2.units
## Lag 0                                                    -0.008518268
## Lag 100                                                  -0.016248199
## Lag 500                                                   0.044751016
## Lag 1000                                                  0.024827801
## Lag 5000                                                 -0.001860750
##          at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT2.units
## Lag 0                                                      0.02902645
## Lag 100                                                   -0.01253698
## Lag 500                                                    0.05556811
## Lag 1000                                                   0.02173176
## Lag 5000                                                  -0.01956112
##          at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT1.units
## Lag 0                                                     -0.11230235
## Lag 100                                                   -0.02682760
## Lag 500                                                    0.00620533
## Lag 1000                                                  -0.02055078
## Lag 5000                                                   0.03081905
##          at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT1.units
## Lag 0                                                     0.011701233
## Lag 100                                                  -0.010011619
## Lag 500                                                   0.008428736
## Lag 1000                                                 -0.022933341
## Lag 5000                                                  0.023963672
##          at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT2.units
## Lag 0                                                     0.011701233
## Lag 100                                                  -0.010011619
## Lag 500                                                   0.008428736
## Lag 1000                                                 -0.022933341
## Lag 5000                                                  0.023963672
##          at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT2.units
## Lag 0                                                      0.06312437
## Lag 100                                                   -0.01937043
## Lag 500                                                    0.01541354
## Lag 1000                                                  -0.02002003
## Lag 5000                                                   0.02002943
##
## , , traitT2.mother
##
##          at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT1.animal
## Lag 0                                                       -0.02245999
## Lag 100                                                      0.01287933
## Lag 500                                                     -0.06937135
```

```
## Lag 1000                                                    -0.03408051
## Lag 5000                                                    -0.03437527
##          at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT1.animal
## Lag 0                                                       -0.01212178
## Lag 100                                                      0.02432570
## Lag 500                                                      0.03510369
## Lag 1000                                                     0.02757162
## Lag 5000                                                    -0.01614218
##          at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT2.animal
## Lag 0                                                       -0.01212178
## Lag 100                                                      0.02432570
## Lag 500                                                      0.03510369
## Lag 1000                                                     0.02757162
## Lag 5000                                                    -0.01614218
##          at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT2.animal
## Lag 0                                                       -0.02245998
## Lag 100                                                      0.01287933
## Lag 500                                                     -0.06937135
## Lag 1000                                                    -0.03408051
## Lag 5000                                                    -0.03437528
##          at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT1.animal
## Lag 0                                                      -0.012775867
## Lag 100                                                     0.043772797
## Lag 500                                                    -0.011619254
## Lag 1000                                                   -0.047193555
## Lag 5000                                                    0.009181997
##          at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT1.animal
## Lag 0                                                       0.022701877
## Lag 100                                                     0.020020010
## Lag 500                                                    -0.007184152
## Lag 1000                                                    0.027822588
## Lag 5000                                                   -0.010936045
##          at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT2.animal
## Lag 0                                                       0.022701877
## Lag 100                                                     0.020020010
## Lag 500                                                    -0.007184152
## Lag 1000                                                    0.027822588
## Lag 5000                                                   -0.010936045
##          at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT2.animal
## Lag 0                                                      -0.012775870
## Lag 100                                                     0.043772795
## Lag 500                                                    -0.011619258
## Lag 1000                                                   -0.047193553
## Lag 5000                                                    0.009181997
##          traitT1.byear traitT2.byear traitT1.mother traitT2.mother
## Lag 0      0.027498789   0.075011059    -0.29713924     1.00000000
## Lag 100   -0.004330013   0.019387759     0.01135535     0.01111072
```

```
## Lag 500   -0.022534204   0.013976131    -0.03024673     0.03135127
## Lag 1000   0.018105482  -0.004480605    -0.01622036     0.01843071
## Lag 5000  -0.021285124  -0.015352704     0.01171495    -0.03266031
##           at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT1.units
## Lag 0                                                     0.010656057
## Lag 100                                                  -0.014350075
## Lag 500                                                  -0.025329139
## Lag 1000                                                 -0.020213976
## Lag 5000                                                  0.006746823
##           at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT1.units
## Lag 0                                                    -0.052640698
## Lag 100                                                  -0.011683409
## Lag 500                                                  -0.061476681
## Lag 1000                                                 -0.016566750
## Lag 5000                                                 -0.002144703
##           at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT2.units
## Lag 0                                                    -0.052640698
## Lag 100                                                  -0.011683409
## Lag 500                                                  -0.061476681
## Lag 1000                                                 -0.016566750
## Lag 5000                                                 -0.002144703
##           at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT2.units
## Lag 0                                                    -0.150664503
## Lag 100                                                  -0.030124097
## Lag 500                                                  -0.035301755
## Lag 1000                                                  0.006326746
## Lag 5000                                                 -0.034639670
##           at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT1.units
## Lag 0                                                      0.03843077
## Lag 100                                                    0.10864998
## Lag 500                                                   -0.01765222
## Lag 1000                                                  -0.04802417
## Lag 5000                                                  -0.02312820
##           at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT1.units
## Lag 0                                                     -0.07682037
## Lag 100                                                    0.08857155
## Lag 500                                                   -0.03270686
## Lag 1000                                                  -0.04309358
## Lag 5000                                                  -0.03198783
##           at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT2.units
## Lag 0                                                     -0.07682037
## Lag 100                                                    0.08857155
## Lag 500                                                   -0.03270686
## Lag 1000                                                  -0.04309358
## Lag 5000                                                  -0.03198783
##           at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT2.units
## Lag 0                                                    -0.186833159
```

```
## Lag 100                                                 0.068802531
## Lag 500                                                 0.010939808
## Lag 1000                                               -0.046597710
## Lag 5000                                               -0.009495369
##
## , , at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT1.units
##
##         at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT1.animal
## Lag 0                                                    0.022762565
## Lag 100                                                  0.058195840
## Lag 500                                                 -0.006642960
## Lag 1000                                                -0.003238572
## Lag 5000                                                -0.006463485
##         at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT1.animal
## Lag 0                                                   -0.022308219
## Lag 100                                                 -0.042901544
## Lag 500                                                 -0.007774208
## Lag 1000                                                -0.024987119
## Lag 5000                                                 0.022428057
##         at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT2.animal
## Lag 0                                                   -0.022308219
## Lag 100                                                 -0.042901544
## Lag 500                                                 -0.007774208
## Lag 1000                                                -0.024987119
## Lag 5000                                                 0.022428057
##         at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT2.animal
## Lag 0                                                    0.022762562
## Lag 100                                                  0.058195842
## Lag 500                                                 -0.006642962
## Lag 1000                                                -0.003238573
## Lag 5000                                                -0.006463481
##         at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT1.animal
## Lag 0                                                    0.019317584
## Lag 100                                                  0.006631109
## Lag 500                                                 -0.010021686
## Lag 1000                                                -0.028126873
## Lag 5000                                                 0.027531394
##         at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT1.animal
## Lag 0                                                   -0.024077943
## Lag 100                                                 -0.008773569
## Lag 500                                                 -0.036834295
## Lag 1000                                                 0.002484525
## Lag 5000                                                -0.006980967
##         at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT2.animal
## Lag 0                                                   -0.024077943
## Lag 100                                                 -0.008773569
## Lag 500                                                 -0.036834295
```

```
## Lag 1000                                                    0.002484525
## Lag 5000                                                   -0.006980967
##          at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT2.animal
## Lag 0                                                       0.019317585
## Lag 100                                                     0.006631109
## Lag 500                                                    -0.010021687
## Lag 1000                                                   -0.028126868
## Lag 5000                                                    0.027531392
##          traitT1.byear traitT2.byear traitT1.mother traitT2.mother
## Lag 0       0.03137990  -0.045138331   -0.074914843    0.010656057
## Lag 100     0.01846540  -0.057249918    0.023899199    0.064677145
## Lag 500     0.03717666   0.038894481   -0.058146358   -0.003011312
## Lag 1000   -0.02033719  -0.027871935    0.007427151   -0.040316314
## Lag 5000   -0.01443541  -0.006005922   -0.022039264   -0.041817387
##          at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT1.units
## Lag 0                                                     1.00000000
## Lag 100                                                   0.01369121
## Lag 500                                                   0.04194817
## Lag 1000                                                 -0.07246259
## Lag 5000                                                  0.02792893
##          at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT1.units
## Lag 0                                                    0.823958396
## Lag 100                                                 -0.008329624
## Lag 500                                                  0.062460340
## Lag 1000                                                -0.039303741
## Lag 5000                                                 0.054712853
##          at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT2.units
## Lag 0                                                    0.823958396
## Lag 100                                                 -0.008329624
## Lag 500                                                  0.062460340
## Lag 1000                                                -0.039303741
## Lag 5000                                                 0.054712853
##          at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT2.units
## Lag 0                                                     0.50406802
## Lag 100                                                  -0.04934121
## Lag 500                                                   0.04076741
## Lag 1000                                                  0.01261949
## Lag 5000                                                  0.07086807
##          at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT1.units
## Lag 0                                                   -0.033043522
## Lag 100                                                  0.041554101
## Lag 500                                                 -0.009477397
## Lag 1000                                                -0.009847229
## Lag 5000                                                -0.007099129
##          at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT1.units
## Lag 0                                                  -0.0215659725
## Lag 100                                                 0.0520737617
```

```
## Lag 500                                                  -0.0336840982
## Lag 1000                                                 -0.0001323435
## Lag 5000                                                  0.0032024860
##          at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT2.units
## Lag 0                                                    -0.0215659725
## Lag 100                                                   0.0520737617
## Lag 500                                                  -0.0336840982
## Lag 1000                                                 -0.0001323435
## Lag 5000                                                  0.0032024860
##          at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT2.units
## Lag 0                                                      -0.02355430
## Lag 100                                                     0.03658290
## Lag 500                                                    -0.05089403
## Lag 1000                                                    0.01436107
## Lag 5000                                                    0.02999856
##
## , , at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT1.units
##
##          at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT1.animal
## Lag 0                                                        0.02236567
## Lag 100                                                      0.06353895
## Lag 500                                                      0.01792884
## Lag 1000                                                    -0.01728677
## Lag 5000                                                     0.01065908
##          at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT1.animal
## Lag 0                                                       -0.01575977
## Lag 100                                                     -0.04742525
## Lag 500                                                     -0.03550099
## Lag 1000                                                    -0.02954787
## Lag 5000                                                    -0.00496397
##          at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT2.animal
## Lag 0                                                       -0.01575977
## Lag 100                                                     -0.04742525
## Lag 500                                                     -0.03550099
## Lag 1000                                                    -0.02954787
## Lag 5000                                                    -0.00496397
##          at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT2.animal
## Lag 0                                                        0.02236567
## Lag 100                                                      0.06353895
## Lag 500                                                      0.01792884
## Lag 1000                                                    -0.01728677
## Lag 5000                                                     0.01065908
##          at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT1.animal
## Lag 0                                                       0.002652222
## Lag 100                                                    -0.010429352
## Lag 500                                                    -0.021288103
## Lag 1000                                                   -0.007999975
```

```
## Lag 5000                                                     0.019762979
##           at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT1.animal
## Lag 0                                                       -0.007293165
## Lag 100                                                      0.005227658
## Lag 500                                                     -0.033764314
## Lag 1000                                                     0.017945899
## Lag 5000                                                    -0.001672632
##           at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT2.animal
## Lag 0                                                       -0.007293165
## Lag 100                                                      0.005227658
## Lag 500                                                     -0.033764314
## Lag 1000                                                     0.017945899
## Lag 5000                                                    -0.001672632
##           at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT2.animal
## Lag 0                                                        0.002652225
## Lag 100                                                     -0.010429349
## Lag 500                                                     -0.021288102
## Lag 1000                                                    -0.007999970
## Lag 5000                                                     0.019762979
##           traitT1.byear traitT2.byear traitT1.mother traitT2.mother
## Lag 0       0.004062274   -0.08712665   -0.008518268    -0.05264070
## Lag 100     0.010963120   -0.01901086   -0.010654363     0.07192496
## Lag 500     0.020424796    0.02733555   -0.030878714    -0.01768252
## Lag 1000   -0.027055067   -0.02492168   -0.001611622    -0.04952808
## Lag 5000   -0.001142555   -0.01083790   -0.022179343    -0.03555068
##           at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT1.units
## Lag 0                                                      0.823958396
## Lag 100                                                    0.004401269
## Lag 500                                                    0.017203529
## Lag 1000                                                  -0.030453790
## Lag 5000                                                   0.015804862
##           at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT1.units
## Lag 0                                                      1.000000000
## Lag 100                                                   -0.006182391
## Lag 500                                                    0.061955983
## Lag 1000                                                  -0.010693302
## Lag 5000                                                   0.036099351
##           at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT2.units
## Lag 0                                                      1.000000000
## Lag 100                                                   -0.006182391
## Lag 500                                                    0.061955983
## Lag 1000                                                  -0.010693302
## Lag 5000                                                   0.036099351
##           at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT2.units
## Lag 0                                                       0.82256826
## Lag 100                                                    -0.03667399
## Lag 500                                                     0.04993746
```

```
## Lag 1000                                                  0.01636640
## Lag 5000                                                  0.04643465
##          at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT1.units
## Lag 0                                                  -0.024405654
## Lag 100                                                 0.050538857
## Lag 500                                                 0.004825519
## Lag 1000                                                0.006447716
## Lag 5000                                               -0.034705839
##          at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT1.units
## Lag 0                                                   -0.02293030
## Lag 100                                                  0.04705166
## Lag 500                                                 -0.01213092
## Lag 1000                                                 0.01884484
## Lag 5000                                                -0.01173929
##          at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT2.units
## Lag 0                                                   -0.02293030
## Lag 100                                                  0.04705166
## Lag 500                                                 -0.01213092
## Lag 1000                                                 0.01884484
## Lag 5000                                                -0.01173929
##          at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT2.units
## Lag 0                                                   -0.01731642
## Lag 100                                                  0.03837677
## Lag 500                                                 -0.02371802
## Lag 1000                                                 0.04334219
## Lag 5000                                                 0.02973740
##
## , , at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT2.units
##
##          at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT1.animal
## Lag 0                                                     0.02236567
## Lag 100                                                   0.06353895
## Lag 500                                                   0.01792884
## Lag 1000                                                 -0.01728677
## Lag 5000                                                  0.01065908
##          at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT1.animal
## Lag 0                                                    -0.01575977
## Lag 100                                                  -0.04742525
## Lag 500                                                  -0.03550099
## Lag 1000                                                 -0.02954787
## Lag 5000                                                 -0.00496397
##          at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT2.animal
## Lag 0                                                    -0.01575977
## Lag 100                                                  -0.04742525
## Lag 500                                                  -0.03550099
## Lag 1000                                                 -0.02954787
## Lag 5000                                                 -0.00496397
```

```
##          at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT2.animal
## Lag 0                                                       0.02236567
## Lag 100                                                     0.06353895
## Lag 500                                                     0.01792884
## Lag 1000                                                   -0.01728677
## Lag 5000                                                    0.01065908
##          at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT1.animal
## Lag 0                                                      0.002652222
## Lag 100                                                   -0.010429352
## Lag 500                                                   -0.021288103
## Lag 1000                                                  -0.007999975
## Lag 5000                                                   0.019762979
##          at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT1.animal
## Lag 0                                                     -0.007293165
## Lag 100                                                    0.005227658
## Lag 500                                                   -0.033764314
## Lag 1000                                                   0.017945899
## Lag 5000                                                  -0.001672632
##          at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT2.animal
## Lag 0                                                     -0.007293165
## Lag 100                                                    0.005227658
## Lag 500                                                   -0.033764314
## Lag 1000                                                   0.017945899
## Lag 5000                                                  -0.001672632
##          at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT2.animal
## Lag 0                                                      0.002652225
## Lag 100                                                   -0.010429349
## Lag 500                                                   -0.021288102
## Lag 1000                                                  -0.007999970
## Lag 5000                                                   0.019762979
##          traitT1.byear traitT2.byear traitT1.mother traitT2.mother
## Lag 0      0.004062274   -0.08712665   -0.008518268    -0.05264070
## Lag 100    0.010963120   -0.01901086   -0.010654363     0.07192496
## Lag 500    0.020424796    0.02733555   -0.030878714    -0.01768252
## Lag 1000  -0.027055067   -0.02492168   -0.001611622    -0.04952808
## Lag 5000  -0.001142555   -0.01083790   -0.022179343    -0.03555068
##          at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT1.units
## Lag 0                                                     0.823958396
## Lag 100                                                   0.004401269
## Lag 500                                                   0.017203529
## Lag 1000                                                 -0.030453790
## Lag 5000                                                  0.015804862
##          at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT1.units
## Lag 0                                                     1.000000000
## Lag 100                                                  -0.006182391
## Lag 500                                                   0.061955983
## Lag 1000                                                 -0.010693302
```

```
## Lag 5000                                               0.036099351
##         at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT2.units
## Lag 0                                                  1.000000000
## Lag 100                                               -0.006182391
## Lag 500                                                0.061955983
## Lag 1000                                              -0.010693302
## Lag 5000                                               0.036099351
##         at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT2.units
## Lag 0                                                   0.82256826
## Lag 100                                                -0.03667399
## Lag 500                                                 0.04993746
## Lag 1000                                                0.01636640
## Lag 5000                                                0.04643465
##         at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT1.units
## Lag 0                                                 -0.024405654
## Lag 100                                                0.050538857
## Lag 500                                                0.004825519
## Lag 1000                                               0.006447716
## Lag 5000                                              -0.034705839
##         at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT1.units
## Lag 0                                                  -0.02293030
## Lag 100                                                 0.04705166
## Lag 500                                                -0.01213092
## Lag 1000                                                0.01884484
## Lag 5000                                               -0.01173929
##         at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT2.units
## Lag 0                                                  -0.02293030
## Lag 100                                                 0.04705166
## Lag 500                                                -0.01213092
## Lag 1000                                                0.01884484
## Lag 5000                                               -0.01173929
##         at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT2.units
## Lag 0                                                  -0.01731642
## Lag 100                                                 0.03837677
## Lag 500                                                -0.02371802
## Lag 1000                                                0.04334219
## Lag 5000                                                0.02973740
##
## , , at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT2.units
##
##         at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT1.animal
## Lag 0                                                    -0.01031463
## Lag 100                                                   0.04023582
## Lag 500                                                   0.04917285
## Lag 1000                                                 -0.03055049
## Lag 5000                                                  0.02723070
##         at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT1.animal
```

```
## Lag 0                                                    -0.008530358
## Lag 100                                                  -0.035788854
## Lag 500                                                  -0.049379232
## Lag 1000                                                 -0.021325041
## Lag 5000                                                 -0.010162718
##            at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT2.animal
## Lag 0                                                    -0.008530358
## Lag 100                                                  -0.035788854
## Lag 500                                                  -0.049379232
## Lag 1000                                                 -0.021325041
## Lag 5000                                                 -0.010162718
##            at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT2.animal
## Lag 0                                                     -0.01031463
## Lag 100                                                    0.04023582
## Lag 500                                                    0.04917285
## Lag 1000                                                  -0.03055049
## Lag 5000                                                   0.02723070
##            at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT1.animal
## Lag 0                                                   -0.0020544560
## Lag 100                                                 -0.0421619393
## Lag 500                                                 -0.0255939041
## Lag 1000                                                 0.0255731937
## Lag 5000                                                 0.0001228549
##            at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT1.animal
## Lag 0                                                     0.002102035
## Lag 100                                                  -0.001379098
## Lag 500                                                  -0.043434436
## Lag 1000                                                  0.029664521
## Lag 5000                                                  0.008098285
##            at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT2.animal
## Lag 0                                                     0.002102035
## Lag 100                                                  -0.001379098
## Lag 500                                                  -0.043434436
## Lag 1000                                                  0.029664521
## Lag 5000                                                  0.008098285
##            at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT2.animal
## Lag 0                                                   -0.0020544532
## Lag 100                                                 -0.0421619357
## Lag 500                                                 -0.0255939038
## Lag 1000                                                 0.0255731963
## Lag 5000                                                 0.0001228553
##            traitT1.byear traitT2.byear traitT1.mother traitT2.mother
## Lag 0       -0.024177752   -0.12342257    0.029026453   -0.150664503
## Lag 100      0.002722644    0.01828947   -0.026421477    0.057871224
## Lag 500      0.001177915    0.02306467   -0.008302615   -0.001595395
## Lag 1000    -0.024450338   -0.01252743    0.007380387   -0.059682493
## Lag 5000     0.025952792   -0.01290027   -0.016603877   -0.008151565
```

```
##         at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT1.units
## Lag 0                                                    0.50406802
## Lag 100                                                 -0.01684331
## Lag 500                                                 -0.02957066
## Lag 1000                                                -0.01048833
## Lag 5000                                                 0.03126125
##         at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT1.units
## Lag 0                                                   0.822568265
## Lag 100                                                -0.018771091
## Lag 500                                                 0.005255697
## Lag 1000                                               -0.022320801
## Lag 5000                                                0.035047964
##         at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT2.units
## Lag 0                                                   0.822568265
## Lag 100                                                -0.018771091
## Lag 500                                                 0.005255697
## Lag 1000                                               -0.022320801
## Lag 5000                                                0.035047964
##         at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT2.units
## Lag 0                                                   1.000000000
## Lag 100                                                -0.023522308
## Lag 500                                                 0.009564241
## Lag 1000                                               -0.003345884
## Lag 5000                                                0.033520801
##         at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT1.units
## Lag 0                                                  -0.016051070
## Lag 100                                                 0.025579389
## Lag 500                                                 0.032949698
## Lag 1000                                                0.002284379
## Lag 5000                                               -0.052985152
##         at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT1.units
## Lag 0                                                  -0.015097854
## Lag 100                                                 0.015648340
## Lag 500                                                 0.018098141
## Lag 1000                                                0.008134587
## Lag 5000                                               -0.022911727
##         at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT2.units
## Lag 0                                                  -0.015097854
## Lag 100                                                 0.015648340
## Lag 500                                                 0.018098141
## Lag 1000                                                0.008134587
## Lag 5000                                               -0.022911727
##         at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT2.units
## Lag 0                                                   -0.01042859
## Lag 100                                                  0.01241322
## Lag 500                                                 -0.01095842
## Lag 1000                                                 0.04284066
```

```
## Lag 5000                                                 0.01861245
##
## , , at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT1.units
##
##           at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT1.animal
## Lag 0                                                      0.041893462
## Lag 100                                                    0.013012827
## Lag 500                                                    0.018612812
## Lag 1000                                                   0.007230337
## Lag 5000                                                  -0.035189323
##           at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT1.animal
## Lag 0                                                      0.005815507
## Lag 100                                                   -0.013543955
## Lag 500                                                    0.005673448
## Lag 1000                                                   0.036662349
## Lag 5000                                                  -0.015403733
##           at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT2.animal
## Lag 0                                                      0.005815507
## Lag 100                                                   -0.013543955
## Lag 500                                                    0.005673448
## Lag 1000                                                   0.036662349
## Lag 5000                                                  -0.015403733
##           at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT2.animal
## Lag 0                                                      0.041893463
## Lag 100                                                    0.013012825
## Lag 500                                                    0.018612808
## Lag 1000                                                   0.007230335
## Lag 5000                                                  -0.035189323
##           at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT1.animal
## Lag 0                                                     -0.012587692
## Lag 100                                                    0.013086359
## Lag 500                                                   -0.045715917
## Lag 1000                                                  -0.011715657
## Lag 5000                                                   0.005419636
##           at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT1.animal
## Lag 0                                                      0.003830731
## Lag 100                                                    0.018194535
## Lag 500                                                    0.007394958
## Lag 1000                                                   0.037075016
## Lag 5000                                                   0.032991654
##           at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT2.animal
## Lag 0                                                      0.003830731
## Lag 100                                                    0.018194535
## Lag 500                                                    0.007394958
## Lag 1000                                                   0.037075016
## Lag 5000                                                   0.032991654
##           at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT2.animal
```

```
## Lag 0                                                   -0.012587692
## Lag 100                                                  0.013086358
## Lag 500                                                 -0.045715919
## Lag 1000                                                -0.011715659
## Lag 5000                                                 0.005419638
##           traitT1.byear traitT2.byear traitT1.mother traitT2.mother
## Lag 0     -0.0246628378   0.027563373  -0.1123023496    0.038430775
## Lag 100   -0.0006534773   0.023430140   0.0483097879   -0.071115069
## Lag 500   -0.0089061496  -0.023938075   0.0538343828   -0.035653713
## Lag 1000   0.0388264676   0.047908029  -0.0034643972   -0.069348371
## Lag 5000   0.0094923504  -0.007668143   0.0005980899    0.001697667
##           at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT1.units
## Lag 0                                                    -0.03304352
## Lag 100                                                   0.02067113
## Lag 500                                                  -0.01234139
## Lag 1000                                                  0.02649335
## Lag 5000                                                 -0.02026354
##           at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT1.units
## Lag 0                                                   -0.024405654
## Lag 100                                                  0.028902660
## Lag 500                                                  0.002513982
## Lag 1000                                                 0.029707035
## Lag 5000                                                 0.003612644
##           at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT2.units
## Lag 0                                                   -0.024405654
## Lag 100                                                  0.028902660
## Lag 500                                                  0.002513982
## Lag 1000                                                 0.029707035
## Lag 5000                                                 0.003612644
##           at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT2.units
## Lag 0                                                   -0.016051070
## Lag 100                                                  0.023913919
## Lag 500                                                  0.007815152
## Lag 1000                                                 0.007869038
## Lag 5000                                                 0.042763915
##           at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT1.units
## Lag 0                                                    1.000000000
## Lag 100                                                 -0.010070063
## Lag 500                                                  0.008873360
## Lag 1000                                                -0.034546071
## Lag 5000                                                -0.003176807
##           at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT1.units
## Lag 0                                                    0.834736019
## Lag 100                                                 -0.056847293
## Lag 500                                                  0.016590019
## Lag 1000                                                -0.043298737
## Lag 5000                                                 0.004888737
```

```
##          at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT2.units
## Lag 0                                                    0.834736019
## Lag 100                                                 -0.056847293
## Lag 500                                                  0.016590019
## Lag 1000                                                -0.043298737
## Lag 5000                                                 0.004888737
##          at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT2.units
## Lag 0                                                     0.53614652
## Lag 100                                                  -0.05605043
## Lag 500                                                   0.01141045
## Lag 1000                                                 -0.03702388
## Lag 5000                                                  0.01411382
##
## , , at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT1.units
##
##          at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT1.animal
## Lag 0                                                      0.067454299
## Lag 100                                                    0.032113695
## Lag 500                                                    0.004944910
## Lag 1000                                                   0.004241478
## Lag 5000                                                  -0.024462625
##          at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT1.animal
## Lag 0                                                      -0.02811191
## Lag 100                                                    -0.03088823
## Lag 500                                                    -0.02192075
## Lag 1000                                                    0.02858712
## Lag 5000                                                   -0.02228574
##          at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT2.animal
## Lag 0                                                      -0.02811191
## Lag 100                                                    -0.03088823
## Lag 500                                                    -0.02192075
## Lag 1000                                                    0.02858712
## Lag 5000                                                   -0.02228574
##          at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT2.animal
## Lag 0                                                      0.067454297
## Lag 100                                                    0.032113696
## Lag 500                                                    0.004944906
## Lag 1000                                                   0.004241477
## Lag 5000                                                  -0.024462625
##          at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT1.animal
## Lag 0                                                     -0.005906983
## Lag 100                                                    0.025695166
## Lag 500                                                   -0.026539717
## Lag 1000                                                  -0.002673988
## Lag 5000                                                   0.007084844
##          at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT1.animal
## Lag 0                                                      0.001171218
```

```
## Lag 100                                                0.022089501
## Lag 500                                                0.011075437
## Lag 1000                                               0.024246787
## Lag 5000                                               0.009425114
##          at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT2.animal
## Lag 0                                                  0.001171218
## Lag 100                                                0.022089501
## Lag 500                                                0.011075437
## Lag 1000                                               0.024246787
## Lag 5000                                               0.009425114
##          at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT2.animal
## Lag 0                                                 -0.005906985
## Lag 100                                                0.025695166
## Lag 500                                               -0.026539718
## Lag 1000                                              -0.002673987
## Lag 5000                                               0.007084847
##          traitT1.byear traitT2.byear traitT1.mother traitT2.mother
## Lag 0    -0.0275271884  -0.020160651    0.011701233    -0.07682037
## Lag 100   0.0089350042  -0.001230592    0.036811929    -0.08498764
## Lag 500  -0.0171963815  -0.030526948    0.032191211    -0.03111354
## Lag 1000  0.0202456175  -0.006661377    0.011866900    -0.05501113
## Lag 5000 -0.0002988564   0.002999329   -0.006049455     0.01140095
##          at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT1.units
## Lag 0                                                -0.021565973
## Lag 100                                               0.022888235
## Lag 500                                               0.008505413
## Lag 1000                                              0.031209139
## Lag 5000                                             -0.020380719
##          at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT1.units
## Lag 0                                               -0.0229302985
## Lag 100                                              0.0380673613
## Lag 500                                              0.0297742244
## Lag 1000                                             0.0451962823
## Lag 5000                                             0.0008947703
##          at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT2.units
## Lag 0                                               -0.0229302985
## Lag 100                                              0.0380673613
## Lag 500                                              0.0297742244
## Lag 1000                                             0.0451962823
## Lag 5000                                             0.0008947703
##          at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT2.units
## Lag 0                                                  -0.01509785
## Lag 100                                                 0.03378488
## Lag 500                                                 0.01426613
## Lag 1000                                                0.02943689
## Lag 5000                                                0.01788225
##          at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT1.units
```

```
## Lag 0                                                   0.834736019
## Lag 100                                                -0.009799499
## Lag 500                                                 0.013020026
## Lag 1000                                               -0.045786597
## Lag 5000                                               -0.003017397
##          at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT1.units
## Lag 0                                                   1.000000000
## Lag 100                                                -0.047701283
## Lag 500                                                 0.019555344
## Lag 1000                                               -0.056983801
## Lag 5000                                               -0.003963176
##          at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT2.units
## Lag 0                                                   1.000000000
## Lag 100                                                -0.047701283
## Lag 500                                                 0.019555344
## Lag 1000                                               -0.056983801
## Lag 5000                                               -0.003963176
##          at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT2.units
## Lag 0                                                    0.84509620
## Lag 100                                                 -0.04080851
## Lag 500                                                  0.01669182
## Lag 1000                                                -0.04879806
## Lag 5000                                                -0.01025480
##
## , , at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT2.units
##
##          at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT1.animal
## Lag 0                                                     0.067454299
## Lag 100                                                   0.032113695
## Lag 500                                                   0.004944910
## Lag 1000                                                  0.004241478
## Lag 5000                                                 -0.024462625
##          at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT1.animal
## Lag 0                                                     -0.02811191
## Lag 100                                                   -0.03088823
## Lag 500                                                   -0.02192075
## Lag 1000                                                   0.02858712
## Lag 5000                                                  -0.02228574
##          at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT2.animal
## Lag 0                                                     -0.02811191
## Lag 100                                                   -0.03088823
## Lag 500                                                   -0.02192075
## Lag 1000                                                   0.02858712
## Lag 5000                                                  -0.02228574
##          at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT2.animal
## Lag 0                                                     0.067454297
## Lag 100                                                   0.032113696
```

```
## Lag 500                                                    0.004944906
## Lag 1000                                                   0.004241477
## Lag 5000                                                  -0.024462625
##          at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT1.animal
## Lag 0                                                     -0.005906983
## Lag 100                                                    0.025695166
## Lag 500                                                   -0.026539717
## Lag 1000                                                  -0.002673988
## Lag 5000                                                   0.007084844
##          at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT1.animal
## Lag 0                                                      0.001171218
## Lag 100                                                    0.022089501
## Lag 500                                                    0.011075437
## Lag 1000                                                   0.024246787
## Lag 5000                                                   0.009425114
##          at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT2.animal
## Lag 0                                                      0.001171218
## Lag 100                                                    0.022089501
## Lag 500                                                    0.011075437
## Lag 1000                                                   0.024246787
## Lag 5000                                                   0.009425114
##          at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT2.animal
## Lag 0                                                     -0.005906985
## Lag 100                                                    0.025695166
## Lag 500                                                   -0.026539718
## Lag 1000                                                  -0.002673987
## Lag 5000                                                   0.007084847
##          traitT1.byear traitT2.byear traitT1.mother traitT2.mother
## Lag 0    -0.0275271884  -0.020160651    0.011701233    -0.07682037
## Lag 100   0.0089350042  -0.001230592    0.036811929    -0.08498764
## Lag 500  -0.0171963815  -0.030526948    0.032191211    -0.03111354
## Lag 1000  0.0202456175  -0.006661377    0.011866900    -0.05501113
## Lag 5000 -0.0002988564   0.002999329   -0.006049455     0.01140095
##          at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT1.units
## Lag 0                                                   -0.021565973
## Lag 100                                                  0.022888235
## Lag 500                                                  0.008505413
## Lag 1000                                                 0.031209139
## Lag 5000                                                -0.020380719
##          at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT1.units
## Lag 0                                                  -0.0229302985
## Lag 100                                                 0.0380673613
## Lag 500                                                 0.0297742244
## Lag 1000                                                0.0451962823
## Lag 5000                                                0.0008947703
##          at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT2.units
## Lag 0                                                  -0.0229302985
```

```
## Lag 100                                                    0.0380673613
## Lag 500                                                    0.0297742244
## Lag 1000                                                   0.0451962823
## Lag 5000                                                   0.0008947703
##          at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT2.units
## Lag 0                                                       -0.01509785
## Lag 100                                                      0.03378488
## Lag 500                                                      0.01426613
## Lag 1000                                                     0.02943689
## Lag 5000                                                     0.01788225
##          at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT1.units
## Lag 0                                                       0.834736019
## Lag 100                                                    -0.009799499
## Lag 500                                                     0.013020026
## Lag 1000                                                   -0.045786597
## Lag 5000                                                   -0.003017397
##          at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT1.units
## Lag 0                                                       1.000000000
## Lag 100                                                    -0.047701283
## Lag 500                                                     0.019555344
## Lag 1000                                                   -0.056983801
## Lag 5000                                                   -0.003963176
##          at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT2.units
## Lag 0                                                       1.000000000
## Lag 100                                                    -0.047701283
## Lag 500                                                     0.019555344
## Lag 1000                                                   -0.056983801
## Lag 5000                                                   -0.003963176
##          at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT2.units
## Lag 0                                                        0.84509620
## Lag 100                                                     -0.04080851
## Lag 500                                                      0.01669182
## Lag 1000                                                    -0.04879806
## Lag 5000                                                    -0.01025480
##
## , , at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT2.units
##
##          at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT1.animal
## Lag 0                                                        0.081823186
## Lag 100                                                      0.025862129
## Lag 500                                                     -0.001019422
## Lag 1000                                                     0.022038934
## Lag 5000                                                     0.008353223
##          at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT1.animal
## Lag 0                                                       -0.042456056
## Lag 100                                                     -0.036956287
## Lag 500                                                     -0.028788001
```

```
## Lag 1000                                                    0.017511964
## Lag 5000                                                    0.003358484
##          at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT2.animal
## Lag 0                                                      -0.042456056
## Lag 100                                                    -0.036956287
## Lag 500                                                    -0.028788001
## Lag 1000                                                    0.017511964
## Lag 5000                                                    0.003358484
##          at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT2.animal
## Lag 0                                                       0.081823182
## Lag 100                                                     0.025862131
## Lag 500                                                    -0.001019426
## Lag 1000                                                    0.022038934
## Lag 5000                                                    0.008353222
##          at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT1.animal
## Lag 0                                                      0.0006335032
## Lag 100                                                    0.0114320128
## Lag 500                                                   -0.0042014027
## Lag 1000                                                   0.0067096438
## Lag 5000                                                   0.0267444524
##          at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT1.animal
## Lag 0                                                       0.011573448
## Lag 100                                                     0.031257650
## Lag 500                                                     0.029970355
## Lag 1000                                                    0.007774208
## Lag 5000                                                   -0.008009508
##          at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT2.animal
## Lag 0                                                       0.011573448
## Lag 100                                                     0.031257650
## Lag 500                                                     0.029970355
## Lag 1000                                                    0.007774208
## Lag 5000                                                   -0.008009508
##          at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT2.animal
## Lag 0                                                      0.0006335012
## Lag 100                                                    0.0114320134
## Lag 500                                                   -0.0042014032
## Lag 1000                                                   0.0067096460
## Lag 5000                                                   0.0267444553
##          traitT1.byear traitT2.byear traitT1.mother traitT2.mother
## Lag 0     -0.008651050   -0.05004816    0.063124373   -0.186833159
## Lag 100    0.010418974   -0.04495129    0.038216075   -0.079695676
## Lag 500   -0.023819545   -0.01200187   -0.001081368   -0.016737029
## Lag 1000   0.001822076   -0.05243956    0.006894149   -0.049173928
## Lag 5000  -0.003613643    0.01656821   -0.032479008    0.005560052
##          at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT1.units
## Lag 0                                                     -0.023554303
## Lag 100                                                    0.001740856
```

```
## Lag 500                                                    0.012843461
## Lag 1000                                                   0.008680482
## Lag 5000                                                  -0.009920137
##          at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT1.units
## Lag 0                                                     -0.017316421
## Lag 100                                                    0.029916369
## Lag 500                                                    0.033143611
## Lag 1000                                                   0.017296002
## Lag 5000                                                   0.006303038
##          at.level(sex, "1"):traitT1:at.level(sex, "1"):traitT2.units
## Lag 0                                                     -0.017316421
## Lag 100                                                    0.029916369
## Lag 500                                                    0.033143611
## Lag 1000                                                   0.017296002
## Lag 5000                                                   0.006303038
##          at.level(sex, "1"):traitT2:at.level(sex, "1"):traitT2.units
## Lag 0                                                     -0.010428588
## Lag 100                                                    0.029648297
## Lag 500                                                    0.009827887
## Lag 1000                                                   0.014861996
## Lag 5000                                                   0.005418763
##          at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT1.units
## Lag 0                                                      0.536146519
## Lag 100                                                   -0.005826103
## Lag 500                                                    0.037319533
## Lag 1000                                                  -0.030233133
## Lag 5000                                                  -0.008069233
##          at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT1.units
## Lag 0                                                      0.845096201
## Lag 100                                                   -0.021641972
## Lag 500                                                    0.044233606
## Lag 1000                                                  -0.035207990
## Lag 5000                                                  -0.008416608
##          at.level(sex, "2"):traitT1:at.level(sex, "2"):traitT2.units
## Lag 0                                                      0.845096201
## Lag 100                                                   -0.021641972
## Lag 500                                                    0.044233606
## Lag 1000                                                  -0.035207990
## Lag 5000                                                  -0.008416608
##          at.level(sex, "2"):traitT2:at.level(sex, "2"):traitT2.units
## Lag 0                                                      1.000000000
## Lag 100                                                   -0.002381589
## Lag 500                                                    0.036399260
## Lag 1000                                                  -0.027816041
## Lag 5000                                                  -0.019613782
```

Here the simple plot to plot the genetic correlation

```
DvsS <- data.frame(
  Trait = colnames(model2.5$Sol),
  BLUP = posterior.mode(model2.5$Sol),
  CI = HPDinterval((model2.5$Sol))
)
DvsS <- DvsS[5:5240, ] # keep only rows associated with animal
DvsS$ID <- substr(DvsS$Trait, 35, 38)
DvsS$TRAIT <- substr(DvsS$Trait, 25, 26)
DvsS$SEX <- substr(DvsS$Trait, 16, 16)
summary(factor(DvsS$TRAIT))
```

```
##   T1   T2
## 2618 2618
```

```
DvsS$Trait <- NULL
BLUPS <- reshape(DvsS, v.names = c("BLUP", "CI.lower", "CI.upper"), idvar = c("ID", "SEX")
nrow(BLUPS)
```

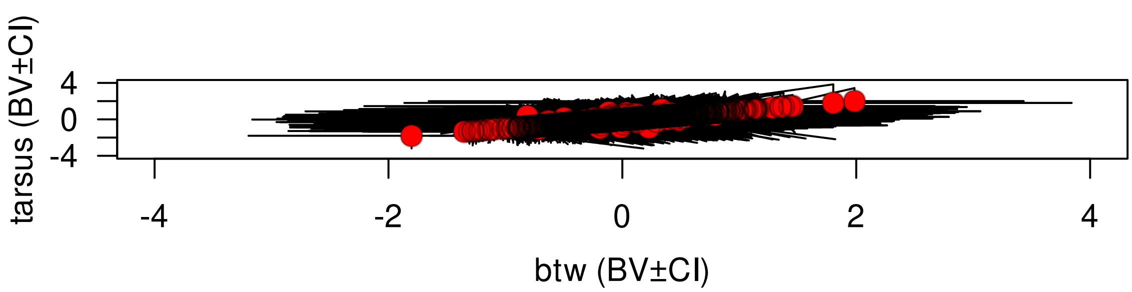
```
## [1] 2618
```

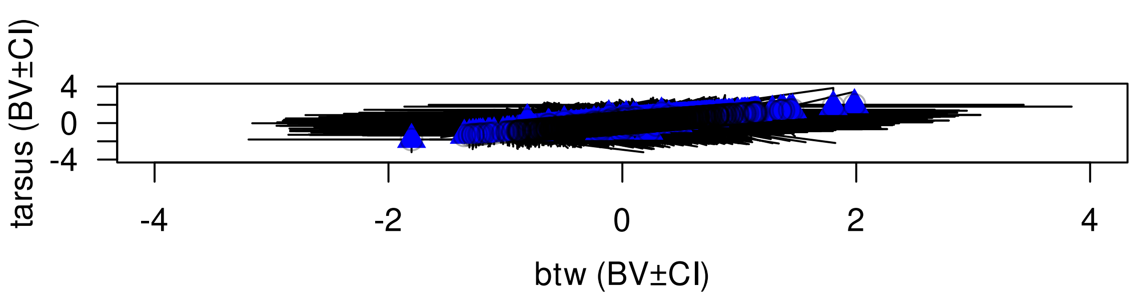
```
rownames(BLUPS) <- c()
colnames(BLUPS) <- c("ID", "SEX", "BLUP.btw", "CI.L.btw", "CI.U.btw", "BLUP.tarsus", "CI.L
summary(BLUPS)
```

```
##       ID                 SEX                BLUP.btw           CI.L.btw
##  Length:2618        Length:2618        Min.   :-1.80272   Min.   :-3.1968
##  Class :character   Class :character   1st Qu.:-0.26298   1st Qu.:-2.0362
##  Mode  :character   Mode  :character   Median : 0.02120   Median :-1.8561
##                                        Mean   : 0.01884   Mean   :-1.8044
##                                        3rd Qu.: 0.29973   3rd Qu.:-1.6116
##                                        Max.   : 1.98486   Max.   : 0.6303
##     CI.U.btw        BLUP.tarsus        CI.L.tarsus      CI.U.tarsus
##  Min.   :-0.1541   Min.   :-1.80246   Min.   :-3.197   Min.   :-0.1557
##  1st Qu.: 1.6313   1st Qu.:-0.26067   1st Qu.:-2.038   1st Qu.: 1.6302
##  Median : 1.8658   Median : 0.02262   Median :-1.854   Median : 1.8671
##  Mean   : 1.8247   Mean   : 0.01982   Mean   :-1.804   Mean   : 1.8249
##  3rd Qu.: 2.0468   3rd Qu.: 0.30215   3rd Qu.:-1.612   3rd Qu.: 2.0483
##  Max.   : 3.8419   Max.   : 1.99604   Max.   : 0.632   Max.   : 3.8431
```

```
#
#
FEM <- subset(BLUPS, SEX == "1")
MAL <- subset(BLUPS, SEX == "1")
par(mfrow = c(2, 1))
```

```
plot(BLUP.tarsus ~ BLUP.btw, FEM, xlab = "", ylab = "", las = 1.2, bty = "o", col = "white
arrows(x0 = BLUPS$BLUP.btw, y0 = FEM$CI.L.tarsus, x1 = FEM$BLUP.btw, y1 = FEM$CI.U.tarsus,
arrows(x0 = BLUPS$CI.L.btw, y0 = FEM$BLUP.tarsus, x1 = FEM$CI.U.btw, y1 = FEM$BLUP.tarsus,
points(BLUP.tarsus ~ BLUP.btw, FEM, pch = 16, col = "red", cex = 1.5)
points(BLUP.tarsus ~ BLUP.btw, FEM, pch = 1, col = rgb(0, 0, 0, 0.3), cex = c(1.5))
mtext("btw (BV±CI)", side = 1, line = 2.4)
mtext("tarsus (BV±CI)", side = 2, line = 2, las = 3)
#
plot(BLUP.tarsus ~ BLUP.btw, MAL, xlab = "", ylab = "", las = 1.2, bty = "o", col = "white
arrows(x0 = BLUPS$BLUP.btw, y0 = MAL$CI.L.tarsus, x1 = MAL$BLUP.btw, y1 = MAL$CI.U.tarsus,
arrows(x0 = BLUPS$CI.L.btw, y0 = MAL$BLUP.tarsus, x1 = MAL$CI.U.btw, y1 = MAL$BLUP.tarsus,
points(BLUP.tarsus ~ BLUP.btw, MAL, pch = 17, col = "blue", cex = 1.5)
points(BLUP.tarsus ~ BLUP.btw, MAL, pch = 1, col = rgb(0, 0, 0, 0.3), cex = c(1.5))
mtext("btw (BV±CI)", side = 1, line = 2.4)
mtext("tarsus (BV±CI)", side = 2, line = 2, las = 3)
```






```
#
```

3.4.5 Between groups (co)variances and the B-matrix

Animal models are amazing model. With different group within a population, it is also possible to estimate how much the different groups shared the same genetic via the cross-group genetic covariance. This covariance is essential to understand ontogenic or sexual conflict, which can constraint or enhanced response to evolution. As an example, we estimate the cross-sex genetic correlation `r_{fm}`

First, we need to dissociate the trait values for females and males into distinct variables. Then, we use a bivariate model (for one trait: `tarsus`) and a multivariate model (for various traits: `tarsus` and `bwt`). With a multivariate model, the cross-sex-cross trait covariance matrix is also named `B matrix`.

The coding is a bit complain but pretty straightforward. It is important to modify the covariance matrix at the residual level to avoid the calculation of a cross-sex residual covariance (no individual switched sex during the experiment).

```
gryphon2$bwt.1 <- NA
gryphon2$tarsus.1 <- NA
animal <- gryphon2[gryphon2$sex == "1", ]$animal
for (i in unique(animal)) {
  gryphon2$bwt.1[which(gryphon2$animal == i)] <- gryphon2$bwt[which(gryphon2$animal == i)]
  gryphon2$tarsus.1[which(gryphon2$animal == i)] <- gryphon2$tarsus[which(gryphon2$animal
}
#
gryphon2$bwt.2 <- NA
gryphon2$tarsus.2 <- NA
animal <- gryphon2[gryphon2$sex == "2", ]$animal
for (i in unique(animal)) {
  gryphon2$bwt.2[which(gryphon2$animal == i)] <- gryphon2$bwt[which(gryphon2$animal == i)]
  gryphon2$tarsus.2[which(gryphon2$animal == i)] <- gryphon2$tarsus[which(gryphon2$animal
}

#
prior2.4 <- list(
  G = list(
    G1 = list(V = diag(2), nu = 1.002),
    G2 = list(V = diag(2), nu = 1.002),
    G3 = list(V = diag(2), nu = 1.002)
  ),
  R = list(
    V1 = list(V = diag(2), nu = 1.002)
  )
)
#
model.BivSex <- MCMCglmm(cbind(tarsus.1, tarsus.2) ~ trait - 1,
  random = ~ us(trait):animal + idh(trait):byear + idh(trait):mother,
```

```
  rcov = ~ us(trait):units,
  family = c("gaussian", "gaussian"),
  ginv = list(animal = Ainv), data = gryphon2,
  nitt = 130000, thin = 100, burnin = 30000,
  prior = prior2.4, verbose = FALSE, pr = TRUE
)

save(model.BivSex, file = "data/MCMCglmm_model_BivSex_LongRun.rda")
```

Again we have provided the data from one such run. It can be accessed using the code:

```
load(file = "data/MCMCglmm_model_BivSex_LongRun.rda")
summary(model.BivSex)
```

```
##
##  Iterations = 30001:129901
##  Thinning interval  = 100
##  Sample size  = 1000
##
##  DIC: 1670.599
##
##  G-structure:  ~us(trait):animal
##
##                                      post.mean l-95% CI u-95% CI eff.samp
## traittarsus.1:traittarsus.1.animal     6.632    2.136    12.69    85.74
## traittarsus.2:traittarsus.1.animal     8.043    2.389    13.54   117.04
## traittarsus.1:traittarsus.2.animal     8.043    2.389    13.54   117.04
## traittarsus.2:traittarsus.2.animal    16.145    3.128    28.93    21.81
##
##                ~idh(trait):byear
##
##                      post.mean l-95% CI u-95% CI eff.samp
## traittarsus.1.byear     3.184    0.505    6.515    357.4
## traittarsus.2.byear     4.576    1.346    8.476    442.5
##
##                ~idh(trait):mother
##
##                       post.mean l-95% CI u-95% CI eff.samp
## traittarsus.1.mother     1.777  0.07858    4.714   299.68
## traittarsus.2.mother     2.980  0.12204    7.328    70.26
##
##  R-structure:  ~us(trait):units
##
##                                     post.mean l-95% CI u-95% CI eff.samp
## traittarsus.1:traittarsus.1.units    15.455    8.998    21.84  104.923
```

```
## traittarsus.2:traittarsus.1.units    -1.497  -15.500    15.53    8.767
## traittarsus.1:traittarsus.2.units    -1.497  -15.500    15.53    8.767
## traittarsus.2:traittarsus.2.units     9.356    0.239    19.10   21.548
##
##  Location effects: cbind(tarsus.1, tarsus.2) ~ trait - 1
##
##              post.mean l-95% CI u-95% CI eff.samp  pMCMC
## traittarsus.1     20.48    19.62    21.48    703.9 <0.001 ***
## traittarsus.2     20.46    19.42    21.40    846.8 <0.001 ***
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

```
autocorr(model.BivSex$VCV)
```

```
## , , traittarsus.1:traittarsus.1.animal
##
##          traittarsus.1:traittarsus.1.animal traittarsus.2:traittarsus.1.animal
## Lag 0                            1.00000000                         0.48422763
## Lag 100                          0.73797990                         0.27701934
## Lag 500                          0.43151596                         0.08460564
## Lag 1000                         0.27709357                         0.03138071
## Lag 5000                         0.09623473                         0.02508175
##          traittarsus.1:traittarsus.2.animal traittarsus.2:traittarsus.2.animal
## Lag 0                            0.48422763                        -0.20835012
## Lag 100                          0.27701934                        -0.26518087
## Lag 500                          0.08460564                        -0.27929151
## Lag 1000                         0.03138071                        -0.23408954
## Lag 5000                         0.02508175                        -0.02431482
##          traittarsus.1.byear traittarsus.2.byear traittarsus.1.mother
## Lag 0             0.05650214        -0.059474225         -0.038396947
## Lag 100           0.03805347        -0.063250151         -0.012779432
## Lag 500           0.03353186        -0.031583736          0.059794328
## Lag 1000          0.02971111         0.032191172         -0.004310584
## Lag 5000          0.04021796        -0.001198619         -0.065221991
##          traittarsus.2.mother traittarsus.1:traittarsus.1.units
## Lag 0               0.1285643                        -0.7394524
## Lag 100             0.1416089                        -0.5874113
## Lag 500             0.1227812                        -0.3892610
## Lag 1000            0.1054744                        -0.2272794
## Lag 5000            0.1046093                        -0.0490914
##          traittarsus.2:traittarsus.1.units traittarsus.1:traittarsus.2.units
## Lag 0                         -0.030661923                      -0.030661923
## Lag 100                       -0.009066847                      -0.009066847
## Lag 500                       -0.014021640                      -0.014021640
## Lag 1000                      -0.038727365                      -0.038727365
## Lag 5000                      -0.053406989                      -0.053406989
```

```
##           traittarsus.2:traittarsus.2.units
## Lag 0                          0.24444681
## Lag 100                        0.28630940
## Lag 500                        0.28676382
## Lag 1000                       0.25016902
## Lag 5000                      -0.01889626
##
## , , traittarsus.2:traittarsus.1.animal
##
##           traittarsus.1:traittarsus.1.animal traittarsus.2:traittarsus.1.animal
## Lag 0                             0.48422763                         1.00000000
## Lag 100                           0.25316393                         0.68722653
## Lag 500                          -0.01525426                         0.30994286
## Lag 1000                         -0.13117432                         0.12750201
## Lag 5000                         -0.03481149                         0.01967858
##           traittarsus.1:traittarsus.2.animal traittarsus.2:traittarsus.2.animal
## Lag 0                             1.00000000                          0.4372811
## Lag 100                           0.68722653                          0.3171927
## Lag 500                           0.30994286                          0.2173200
## Lag 1000                          0.12750201                          0.2034517
## Lag 5000                          0.01967858                          0.1155543
##           traittarsus.1.byear traittarsus.2.byear traittarsus.1.mother
## Lag 0            -0.028123268         -0.10117282          0.068035501
## Lag 100          -0.036441213         -0.06326083          0.058376180
## Lag 500          -0.017206400         -0.06159010         -0.002869166
## Lag 1000         -0.004346341          0.06173108         -0.017320527
## Lag 5000         -0.044798021          0.07734401         -0.083350187
##           traittarsus.2.mother traittarsus.1:traittarsus.1.units
## Lag 0             -0.261520775                       -0.32691256
## Lag 100           -0.219989670                       -0.19037150
## Lag 500           -0.171008994                        0.03568009
## Lag 1000          -0.073253782                        0.15052971
## Lag 5000          -0.002628408                        0.06147675
##           traittarsus.2:traittarsus.1.units traittarsus.1:traittarsus.2.units
## Lag 0                          -0.15561461                       -0.15561461
## Lag 100                        -0.11940169                       -0.11940169
## Lag 500                        -0.10722180                       -0.10722180
## Lag 1000                       -0.11888700                       -0.11888700
## Lag 5000                       -0.07749379                       -0.07749379
##           traittarsus.2:traittarsus.2.units
## Lag 0                           -0.3304177
## Lag 100                         -0.2624116
## Lag 500                         -0.1893048
## Lag 1000                        -0.2045441
## Lag 5000                        -0.1580773
##
## , , traittarsus.1:traittarsus.2.animal
```

```
##
##          traittarsus.1:traittarsus.1.animal traittarsus.2:traittarsus.1.animal
## Lag 0                            0.48422763                         1.00000000
## Lag 100                          0.25316393                         0.68722653
## Lag 500                         -0.01525426                         0.30994286
## Lag 1000                        -0.13117432                         0.12750201
## Lag 5000                        -0.03481149                         0.01967858
##          traittarsus.1:traittarsus.2.animal traittarsus.2:traittarsus.2.animal
## Lag 0                            1.00000000                          0.4372811
## Lag 100                          0.68722653                          0.3171927
## Lag 500                          0.30994286                          0.2173200
## Lag 1000                         0.12750201                          0.2034517
## Lag 5000                         0.01967858                          0.1155543
##          traittarsus.1.byear traittarsus.2.byear traittarsus.1.mother
## Lag 0           -0.028123268         -0.10117282          0.068035501
## Lag 100         -0.036441213         -0.06326083          0.058376180
## Lag 500         -0.017206400         -0.06159010         -0.002869166
## Lag 1000        -0.004346341          0.06173108         -0.017320527
## Lag 5000        -0.044798021          0.07734401         -0.083350187
##          traittarsus.2.mother traittarsus.1:traittarsus.1.units
## Lag 0            -0.261520775                       -0.32691256
## Lag 100          -0.219989670                       -0.19037150
## Lag 500          -0.171008994                        0.03568009
## Lag 1000         -0.073253782                        0.15052971
## Lag 5000         -0.002628408                        0.06147675
##          traittarsus.2:traittarsus.1.units traittarsus.1:traittarsus.2.units
## Lag 0                          -0.15561461                       -0.15561461
## Lag 100                        -0.11940169                       -0.11940169
## Lag 500                        -0.10722180                       -0.10722180
## Lag 1000                       -0.11888700                       -0.11888700
## Lag 5000                       -0.07749379                       -0.07749379
##          traittarsus.2:traittarsus.2.units
## Lag 0                           -0.3304177
## Lag 100                         -0.2624116
## Lag 500                         -0.1893048
## Lag 1000                        -0.2045441
## Lag 5000                        -0.1580773
##
## , , traittarsus.2:traittarsus.2.animal
##
##          traittarsus.1:traittarsus.1.animal traittarsus.2:traittarsus.1.animal
## Lag 0                            -0.2083501                         0.43728107
## Lag 100                          -0.2828015                         0.29272735
## Lag 500                          -0.3313152                         0.14658444
## Lag 1000                         -0.3483078                         0.06012732
## Lag 5000                         -0.1542996                        -0.06471744
##          traittarsus.1:traittarsus.2.animal traittarsus.2:traittarsus.2.animal
```

```
## Lag 0                        0.43728107                           1.00000000
## Lag 100                      0.29272735                           0.87775419
## Lag 500                      0.14658444                           0.72227084
## Lag 1000                     0.06012732                           0.61062886
## Lag 5000                    -0.06471744                           0.08074184
##           traittarsus.1.byear traittarsus.2.byear traittarsus.1.mother
## Lag 0            -0.020084226        -0.013645105          0.007263224
## Lag 100          -0.015303798         0.015235251          0.013922907
## Lag 500          -0.009604004        -0.004276257         -0.022794079
## Lag 1000         -0.036443873         0.045216146          0.038406389
## Lag 5000         -0.046131641         0.012581835         -0.012187074
##           traittarsus.2.mother traittarsus.1:traittarsus.1.units
## Lag 0              -0.50677816                        0.23024103
## Lag 100            -0.46549011                        0.26517948
## Lag 500            -0.35999881                        0.31894466
## Lag 1000           -0.26148886                        0.30787546
## Lag 5000           -0.09601646                        0.09998448
##           traittarsus.2:traittarsus.1.units traittarsus.1:traittarsus.2.units
## Lag 0                            0.03215520                        0.03215520
## Lag 100                          0.04234930                        0.04234930
## Lag 500                          0.01485912                        0.01485912
## Lag 1000                        -0.02777646                       -0.02777646
## Lag 5000                        -0.10000281                       -0.10000281
##           traittarsus.2:traittarsus.2.units
## Lag 0                           -0.90778147
## Lag 100                         -0.84400702
## Lag 500                         -0.70957533
## Lag 1000                        -0.62450980
## Lag 5000                        -0.06262314
##
## , , traittarsus.1.byear
##
##           traittarsus.1:traittarsus.1.animal traittarsus.2:traittarsus.1.animal
## Lag 0                             0.05650214                        -0.02812327
## Lag 100                           0.06068975                        -0.02687949
## Lag 500                           0.02342116                        -0.03285780
## Lag 1000                          0.03532201                        -0.03419221
## Lag 5000                          0.02786557                        -0.01481811
##           traittarsus.1:traittarsus.2.animal traittarsus.2:traittarsus.2.animal
## Lag 0                            -0.02812327                        -0.02008423
## Lag 100                          -0.02687949                        -0.02175035
## Lag 500                          -0.03285780                        -0.01196604
## Lag 1000                         -0.03419221                        -0.03085934
## Lag 5000                         -0.01481811                         0.01496886
##           traittarsus.1.byear traittarsus.2.byear traittarsus.1.mother
## Lag 0              1.00000000        -0.008840935         -0.034026465
## Lag 100            0.23201455        -0.040849216          0.006952432
```

```
## Lag 500          0.10173419        0.018677216         0.021915445
## Lag 1000         0.05656314        0.045347703        -0.069023041
## Lag 5000        -0.02674433        0.003879773        -0.031727649
##           traittarsus.2.mother traittarsus.1:traittarsus.1.units
## Lag 0              0.041524616                      -0.131561587
## Lag 100            0.022654125                      -0.091920671
## Lag 500           -0.003137523                      -0.023174815
## Lag 1000           0.093233105                       0.017723781
## Lag 5000          -0.001576843                       0.003971118
##           traittarsus.2:traittarsus.1.units traittarsus.1:traittarsus.2.units
## Lag 0                            0.06264243                        0.06264243
## Lag 100                          0.06240060                        0.06240060
## Lag 500                          0.03789653                        0.03789653
## Lag 1000                         0.03352306                        0.03352306
## Lag 5000                         0.05768588                        0.05768588
##           traittarsus.2:traittarsus.2.units
## Lag 0                           0.013826338
## Lag 100                         0.015690413
## Lag 500                         0.020546446
## Lag 1000                       -0.006052117
## Lag 5000                       -0.020241900
##
## , , traittarsus.2.byear
##
##           traittarsus.1:traittarsus.1.animal traittarsus.2:traittarsus.1.animal
## Lag 0                           -0.059474225                        -0.10117282
## Lag 100                         -0.029542673                        -0.06571088
## Lag 500                          0.019127206                         0.02553144
## Lag 1000                        -0.006675716                         0.03933732
## Lag 5000                        -0.020363086                        -0.01801919
##           traittarsus.1:traittarsus.2.animal traittarsus.2:traittarsus.2.animal
## Lag 0                            -0.10117282                       -0.013645105
## Lag 100                          -0.06571088                       -0.001743299
## Lag 500                           0.02553144                        0.024080673
## Lag 1000                          0.03933732                        0.020998801
## Lag 5000                         -0.01801919                       -0.036422613
##           traittarsus.1.byear traittarsus.2.byear traittarsus.1.mother
## Lag 0            -0.008840935          1.00000000          0.019871390
## Lag 100           0.003895756          0.15813110          0.000200299
## Lag 500          -0.028206511          0.02861588          0.028238837
## Lag 1000         -0.022327614          0.02577769          0.069995240
## Lag 5000          0.054519302         -0.01863939          0.021348106
##           traittarsus.2.mother traittarsus.1:traittarsus.1.units
## Lag 0               0.02790731                        0.04582166
## Lag 100            -0.02533496                        0.01584625
## Lag 500            -0.04228406                       -0.01965332
## Lag 1000           -0.03776489                       -0.05592538
```

```
## Lag 5000          0.04026220                          0.02293994
##          traittarsus.2:traittarsus.1.units traittarsus.1:traittarsus.2.units
## Lag 0                          -0.01692229                       -0.01692229
## Lag 100                        -0.03014201                       -0.03014201
## Lag 500                        -0.05685394                       -0.05685394
## Lag 1000                       -0.05775898                       -0.05775898
## Lag 5000                       -0.04474406                       -0.04474406
##          traittarsus.2:traittarsus.2.units
## Lag 0                          -0.05647151
## Lag 100                        -0.01120227
## Lag 500                        -0.02826105
## Lag 1000                       -0.01902149
## Lag 5000                        0.04653422
##
## , , traittarsus.1.mother
##
##          traittarsus.1:traittarsus.1.animal traittarsus.2:traittarsus.1.animal
## Lag 0                           -0.03839695                        0.068035501
## Lag 100                         -0.01125448                        0.090872487
## Lag 500                         -0.01822303                        0.074904451
## Lag 1000                        -0.06684368                       -0.009049799
## Lag 5000                         0.01882807                       -0.038704215
##          traittarsus.1:traittarsus.2.animal traittarsus.2:traittarsus.2.animal
## Lag 0                           0.068035501                        0.007263224
## Lag 100                         0.090872487                        0.009427782
## Lag 500                         0.074904451                       -0.008966636
## Lag 1000                       -0.009049799                       -0.062208885
## Lag 5000                       -0.038704215                       -0.090802212
##          traittarsus.1.byear traittarsus.2.byear traittarsus.1.mother
## Lag 0           -0.034026465         0.019871390           1.00000000
## Lag 100         -0.044009625        -0.022642909           0.53848292
## Lag 500          0.033149894        -0.058758981           0.05060514
## Lag 1000        -0.034811076        -0.041691079          -0.01263351
## Lag 5000         0.003520887        -0.007417182          -0.01561154
##          traittarsus.2.mother traittarsus.1:traittarsus.1.units
## Lag 0            -0.053312892                      -0.274551627
## Lag 100          -0.021399368                      -0.183188795
## Lag 500           0.001127949                      -0.004741630
## Lag 1000          0.017008055                       0.049168722
## Lag 5000         -0.013865361                      -0.003898312
##          traittarsus.2:traittarsus.1.units traittarsus.1:traittarsus.2.units
## Lag 0                          0.021389916                       0.021389916
## Lag 100                        0.010504830                       0.010504830
## Lag 500                        0.005067944                       0.005067944
## Lag 1000                       0.024425517                       0.024425517
## Lag 5000                      -0.004626176                      -0.004626176
##          traittarsus.2:traittarsus.2.units
```

```
## Lag 0                         0.02429791
## Lag 100                       0.01285473
## Lag 500                       0.02017728
## Lag 1000                      0.06093906
## Lag 5000                      0.10720949
##
## , , traittarsus.2.mother
##
##          traittarsus.1:traittarsus.1.animal traittarsus.2:traittarsus.1.animal
## Lag 0                            0.12856434                         -0.2615208
## Lag 100                          0.14693139                         -0.2325836
## Lag 500                          0.21342005                         -0.1621874
## Lag 1000                         0.23353394                         -0.1119149
## Lag 5000                         0.02771044                          0.0396288
##          traittarsus.1:traittarsus.2.animal traittarsus.2:traittarsus.2.animal
## Lag 0                            -0.2615208                        -0.50677816
## Lag 100                          -0.2325836                        -0.48725853
## Lag 500                          -0.1621874                        -0.40888208
## Lag 1000                         -0.1119149                        -0.34699264
## Lag 5000                          0.0396288                         0.02549716
##          traittarsus.1.byear traittarsus.2.byear traittarsus.1.mother
## Lag 0             0.04152462         0.027907314          -0.05331289
## Lag 100           0.02194445         0.054336046          -0.04284508
## Lag 500          -0.03327513        -0.020857444          -0.02968159
## Lag 1000          0.02573536        -0.040238713          -0.03336616
## Lag 5000          0.01374507         0.005808512           0.07687084
##          traittarsus.2.mother traittarsus.1:traittarsus.1.units
## Lag 0              1.00000000                       -0.13910701
## Lag 100            0.70222369                       -0.13691118
## Lag 500            0.35625516                       -0.18735521
## Lag 1000           0.19638031                       -0.21082439
## Lag 5000          -0.04114072                       -0.04387536
##          traittarsus.2:traittarsus.1.units traittarsus.1:traittarsus.2.units
## Lag 0                           0.04614450                        0.04614450
## Lag 100                         0.04486226                        0.04486226
## Lag 500                         0.04022585                        0.04022585
## Lag 1000                        0.05277963                        0.05277963
## Lag 5000                        0.04252673                        0.04252673
##          traittarsus.2:traittarsus.2.units
## Lag 0                          0.268960307
## Lag 100                        0.289158808
## Lag 500                        0.345252707
## Lag 1000                       0.323960441
## Lag 5000                      -0.002082367
##
## , , traittarsus.1:traittarsus.1.units
##
```

```
##          traittarsus.1:traittarsus.1.animal traittarsus.2:traittarsus.1.animal
## Lag 0                            -0.7394524                        -0.32691256
## Lag 100                          -0.5906993                        -0.20009588
## Lag 500                          -0.3828210                        -0.08127245
## Lag 1000                         -0.2031251                         0.02298348
## Lag 5000                         -0.0979703                        -0.01920779
##          traittarsus.1:traittarsus.2.animal traittarsus.2:traittarsus.2.animal
## Lag 0                           -0.32691256                         0.23024103
## Lag 100                         -0.20009588                         0.28084172
## Lag 500                         -0.08127245                         0.28272296
## Lag 1000                         0.02298348                         0.28283381
## Lag 5000                        -0.01920779                         0.05177093
##          traittarsus.1.byear traittarsus.2.byear traittarsus.1.mother
## Lag 0            -0.13156159          0.04582166          -0.27455163
## Lag 100          -0.05719958          0.04337991          -0.16825519
## Lag 500          -0.06997182          0.07140946          -0.07087194
## Lag 1000         -0.02088140          0.01426241           0.03955072
## Lag 5000         -0.01887279          0.04431921           0.06767122
##          traittarsus.2.mother traittarsus.1:traittarsus.1.units
## Lag 0              -0.1391070                        1.00000000
## Lag 100            -0.1379410                        0.56579808
## Lag 500            -0.1301093                        0.35250381
## Lag 1000           -0.1253506                        0.15585076
## Lag 5000           -0.0735286                        0.05909602
##          traittarsus.2:traittarsus.1.units traittarsus.1:traittarsus.2.units
## Lag 0                           0.04896537                        0.04896537
## Lag 100                         0.02746645                        0.02746645
## Lag 500                         0.03218528                        0.03218528
## Lag 1000                        0.05596211                        0.05596211
## Lag 5000                        0.05413531                        0.05413531
##          traittarsus.2:traittarsus.2.units
## Lag 0                           -0.2610614
## Lag 100                         -0.3079509
## Lag 500                         -0.2969894
## Lag 1000                        -0.2847495
## Lag 5000                        -0.0427216
##
## , , traittarsus.2:traittarsus.1.units
##
##          traittarsus.1:traittarsus.1.animal traittarsus.2:traittarsus.1.animal
## Lag 0                          -0.030661923                        -0.15561461
## Lag 100                         0.003884354                        -0.11920858
## Lag 500                         0.042099074                        -0.08915914
## Lag 1000                        0.042025296                        -0.07981143
## Lag 5000                       -0.018911064                        -0.09774452
##          traittarsus.1:traittarsus.2.animal traittarsus.2:traittarsus.2.animal
## Lag 0                           -0.15561461                         0.03215520
```

```
## Lag 100                    -0.11920858                         0.04834806
## Lag 500                    -0.08915914                         0.05802195
## Lag 1000                   -0.07981143                         0.02656239
## Lag 5000                   -0.09774452                        -0.04245498
##          traittarsus.1.byear traittarsus.2.byear traittarsus.1.mother
## Lag 0             0.06264243        -0.016922288           0.02138992
## Lag 100           0.06751797        -0.004991909           0.02085557
## Lag 500           0.06731777        -0.030284706           0.05500122
## Lag 1000          0.06629827        -0.044495833           0.10333723
## Lag 5000          0.08927471        -0.038637660           0.06016204
##          traittarsus.2.mother traittarsus.1:traittarsus.1.units
## Lag 0              0.04614450                       0.048965370
## Lag 100            0.04880037                       0.017340477
## Lag 500            0.04329157                      -0.013844496
## Lag 1000           0.06724925                      -0.039591736
## Lag 5000           0.04795409                      -0.003568665
##          traittarsus.2:traittarsus.1.units traittarsus.1:traittarsus.2.units
## Lag 0                            1.0000000                         1.0000000
## Lag 100                          0.9675526                         0.9675526
## Lag 500                          0.9029928                         0.9029928
## Lag 1000                         0.8401123                         0.8401123
## Lag 5000                         0.4663345                         0.4663345
##          traittarsus.2:traittarsus.2.units
## Lag 0                          -0.04275237
## Lag 100                        -0.06227874
## Lag 500                        -0.06672641
## Lag 1000                       -0.04382724
## Lag 5000                        0.03699475
##
## , , traittarsus.1:traittarsus.2.units
##
##          traittarsus.1:traittarsus.1.animal traittarsus.2:traittarsus.1.animal
## Lag 0                          -0.030661923                        -0.15561461
## Lag 100                         0.003884354                        -0.11920858
## Lag 500                         0.042099074                        -0.08915914
## Lag 1000                        0.042025296                        -0.07981143
## Lag 5000                       -0.018911064                        -0.09774452
##          traittarsus.1:traittarsus.2.animal traittarsus.2:traittarsus.2.animal
## Lag 0                           -0.15561461                         0.03215520
## Lag 100                         -0.11920858                         0.04834806
## Lag 500                         -0.08915914                         0.05802195
## Lag 1000                        -0.07981143                         0.02656239
## Lag 5000                        -0.09774452                        -0.04245498
##          traittarsus.1.byear traittarsus.2.byear traittarsus.1.mother
## Lag 0             0.06264243        -0.016922288           0.02138992
## Lag 100           0.06751797        -0.004991909           0.02085557
## Lag 500           0.06731777        -0.030284706           0.05500122
```

```
## Lag 1000          0.06629827       -0.044495833           0.10333723
## Lag 5000          0.08927471       -0.038637660           0.06016204
##          traittarsus.2.mother traittarsus.1:traittarsus.1.units
## Lag 0              0.04614450                       0.048965370
## Lag 100            0.04880037                       0.017340477
## Lag 500            0.04329157                      -0.013844496
## Lag 1000           0.06724925                      -0.039591736
## Lag 5000           0.04795409                      -0.003568665
##          traittarsus.2:traittarsus.1.units traittarsus.1:traittarsus.2.units
## Lag 0                            1.0000000                         1.0000000
## Lag 100                          0.9675526                         0.9675526
## Lag 500                          0.9029928                         0.9029928
## Lag 1000                         0.8401123                         0.8401123
## Lag 5000                         0.4663345                         0.4663345
##          traittarsus.2:traittarsus.2.units
## Lag 0                          -0.04275237
## Lag 100                        -0.06227874
## Lag 500                        -0.06672641
## Lag 1000                       -0.04382724
## Lag 5000                        0.03699475
##
## , , traittarsus.2:traittarsus.2.units
##
##          traittarsus.1:traittarsus.1.animal traittarsus.2:traittarsus.1.animal
## Lag 0                             0.2444468                        -0.33041768
## Lag 100                           0.2953169                        -0.24524259
## Lag 500                           0.3257997                        -0.12021844
## Lag 1000                          0.3204576                        -0.05040170
## Lag 5000                          0.1966910                         0.07386444
##          traittarsus.1:traittarsus.2.animal traittarsus.2:traittarsus.2.animal
## Lag 0                           -0.33041768                         -0.9077815
## Lag 100                         -0.24524259                         -0.8410651
## Lag 500                         -0.12021844                         -0.6969304
## Lag 1000                        -0.05040170                         -0.5893775
## Lag 5000                         0.07386444                         -0.1004775
##          traittarsus.1.byear traittarsus.2.byear traittarsus.1.mother
## Lag 0             0.01382634        -0.056471508          0.024297909
## Lag 100           0.01730830        -0.030701856          0.017739447
## Lag 500           0.03968933         0.004065694          0.010636299
## Lag 1000          0.03341332        -0.048898719         -0.028816725
## Lag 5000          0.05219060        -0.013503372         -0.005167407
##          traittarsus.2.mother traittarsus.1:traittarsus.1.units
## Lag 0               0.2689603                        -0.2610614
## Lag 100             0.3013532                        -0.3031510
## Lag 500             0.3094825                        -0.3179085
## Lag 1000            0.2400190                        -0.2838200
## Lag 5000            0.1233946                        -0.1252443
```

```
##          traittarsus.2:traittarsus.1.units traittarsus.1:traittarsus.2.units
## Lag 0                          -0.04275237                       -0.04275237
## Lag 100                        -0.05037125                       -0.05037125
## Lag 500                        -0.01879502                       -0.01879502
## Lag 1000                        0.02100080                        0.02100080
## Lag 5000                        0.10654662                        0.10654662
##          traittarsus.2:traittarsus.2.units
## Lag 0                           1.00000000
## Lag 100                         0.87986649
## Lag 500                         0.70214749
## Lag 1000                        0.61035106
## Lag 5000                        0.07522425
```

The cross-sex genetic correlation can estimate form the output of the model. For tarsus length at fledging, sexes shared a lot of genetic variance which is commun for a trait with low sexual dimorphism. If the selection is antagonistic between males and females, sexes can not evolve freely form the other sexes and a sexual conflict appears.

```
rfm <- model.BivSex$VCV[, "traittarsus.1:traittarsus.2.animal"] / sqrt(model.BivSex$VCV[,
posterior.mode(rfm)
```

```
##      var1
## 0.9664439
```

```
HPDinterval(rfm, 0.95)
```

```
##          lower    upper
## var1 0.4630817 0.992376
## attr(,"Probability")
## [1] 0.95
```

We can estimate directly the correlation and plot the cross-sex genetic correlation

```
DvsS <- data.frame(
  Trait = colnames(model.BivSex$Sol),
  BLUP = posterior.mode(model.BivSex$Sol),
  CI = HPDinterval((model.BivSex$Sol))
)
DvsS <- DvsS[3:2619, ] # keep only rows associated with animal
DvsS$ID <- substr(DvsS$Trait, 22, 26)
DvsS$TRAIT <- substr(DvsS$Trait, 6, 13)
summary(factor(DvsS$TRAIT))
```

```
## tarsus.1 tarsus.2
##     1309     1308
```

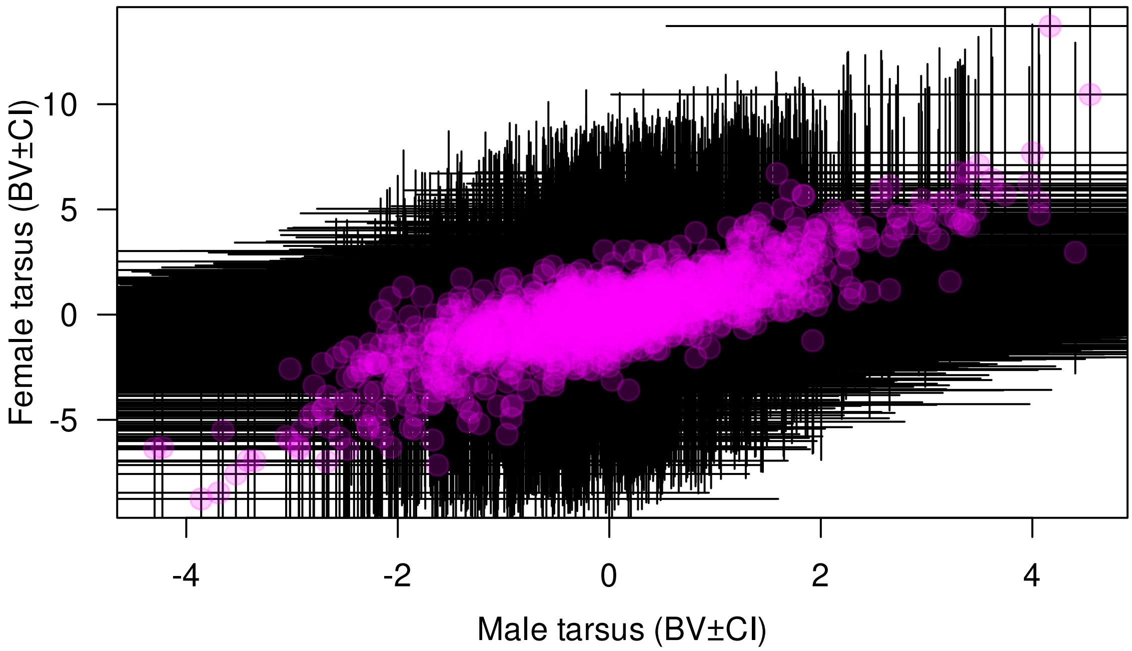
```
DvsS$Trait <- NULL
BLUPS <- reshape(DvsS, v.names = c("BLUP", "CI.lower", "CI.upper"), idvar = "ID", timevar
nrow(BLUPS)
```

```
## [1] 1309
```

```
rownames(BLUPS) <- c()
colnames(BLUPS) <- c("ID", "BLUP.btw", "CI.L.btw", "CI.U.btw", "BLUP.tarsus", "CI.L.tarsus
summary(BLUPS)
```

```
##       ID               BLUP.btw           CI.L.btw          CI.U.btw
##  Length:1309        Min.   :-4.299559   Min.   :-9.4393   Min.   : 0.5871
##  Class :character   1st Qu.:-0.743429   1st Qu.:-5.2018   1st Qu.: 3.5625
##  Mode  :character   Median :-0.000879   Median :-4.3976   Median : 4.5287
##                     Mean   : 0.024573   Mean   :-4.3251   Mean   : 4.4753
##                     3rd Qu.: 0.762532   3rd Qu.:-3.4818   3rd Qu.: 5.3499
##                     Max.   : 4.546380   Max.   : 0.5408   Max.   :10.9441
##
##   BLUP.tarsus        CI.L.tarsus       CI.U.tarsus
##  Min.   :-8.75836   Min.   :-14.320   Min.   :-0.3279
##  1st Qu.:-1.05894   1st Qu.: -8.157   1st Qu.: 4.9941
##  Median : 0.06830   Median : -6.720   Median : 6.8745
##  Mean   : 0.07182   Mean   : -6.467   Mean   : 6.6117
##  3rd Qu.: 1.16904   3rd Qu.: -4.869   3rd Qu.: 8.3023
##  Max.   :13.71503   Max.   :  1.264   Max.   :16.7611
##  NA's   :1          NA's   :1         NA's   :1
```

```
plot(BLUP.tarsus ~ BLUP.btw, BLUPS, xlab = "", ylab = "", las = 1.2, bty = "o", col = "whi
arrows(x0 = BLUPS$BLUP.btw, y0 = BLUPS$CI.L.tarsus, x1 = BLUPS$BLUP.btw, y1 = BLUPS$CI.U.t
arrows(x0 = BLUPS$CI.L.btw, y0 = BLUPS$BLUP.tarsus, x1 = BLUPS$CI.U.btw, y1 = BLUPS$BLUP.t
points(BLUP.tarsus ~ BLUP.btw, BLUPS, pch = 16, col = rgb(1, 0, 1, 0.2), cex = 1.5)
points(BLUP.tarsus ~ BLUP.btw, BLUPS, pch = 1, col = rgb(1, 0, 1, 0.2), cex = c(1.5))
mtext("Male tarsus (BV±CI)", side = 1, line = 2.4)
mtext("Female tarsus (BV±CI)", side = 2, line = 2, las = 3)
```




```
#
```

The B matrix used the same code but in a multivariate animal model framework. Here some example code, however due to the nature of the dataset, the cross-sex genetic covariance for birth weight is hard to estimate making difficulty to fit this multivariate animal model.

```
prior2.5 <- list(
  G = list(
    G1 = list(V = diag(4), nu = 1.002),
    G2 = list(V = diag(4), nu = 1.002),
    G3 = list(V = diag(4), nu = 1.002)
  ),
  R = list(
    V1 = list(V = diag(4), nu = 1.002)
  )
)
#
model.MultivSex <- MCMCglmm(cbind(tarsus.1, bwt.1, tarsus.2, bwt.2) ~ trait - 1,
  random = ~ us(trait):animal + idh(trait):byear + idh(trait):mother,
  rcov = ~ us(trait):units,
  family = c("gaussian", "gaussian", "gaussian", "gaussian"),
  ginv = list(animal = Ainv), data = gryphon2,
```

```r
  nitt = 130000, thin = 100, burnin = 30000,
  prior = prior2.5, verbose = FALSE, pr = TRUE
)
save(model.MultivSex, file = "data/MCMCglmm_model_MultivSex_LongRun.rda")
```

Again we have provided the data from one such run. It can be accessed using the code:

```r
load(file = "data/MCMCglmm_model_MultivSex_LongRun.rda")
summary(model.MultivSex)
```

```
##
##  Iterations = 30001:129901
##  Thinning interval  = 100
##  Sample size  = 1000
##
##  DIC: 2590.513
##
##  G-structure:  ~us(trait):animal
##
##                                       post.mean   l-95% CI u-95% CI eff.samp
## traittarsus.1:traittarsus.1.animal    5.2542  0.6145315   11.414    28.46
## traitbwt.1:traittarsus.1.animal       1.2682 -0.7026690    3.298    63.97
## traittarsus.2:traittarsus.1.animal    5.9945  0.3482679   13.405    21.59
## traitbwt.2:traittarsus.1.animal       1.4467 -0.3853824    4.110    35.84
## traittarsus.1:traitbwt.1.animal       1.2682 -0.7026690    3.298    63.97
## traitbwt.1:traitbwt.1.animal          1.7891  0.5620761    3.005    97.87
## traittarsus.2:traitbwt.1.animal       0.7719 -1.8038433    4.190    22.64
## traitbwt.2:traitbwt.1.animal          0.9939  0.0009052    2.069    50.24
## traittarsus.1:traittarsus.2.animal    5.9945  0.3482679   13.405    21.59
## traitbwt.1:traittarsus.2.animal       0.7719 -1.8038433    4.190    22.64
## traittarsus.2:traittarsus.2.animal   12.7341  1.4093961   23.690    28.81
## traitbwt.2:traittarsus.2.animal       2.7675 -0.5938976    6.927    20.64
## traittarsus.1:traitbwt.2.animal       1.4467 -0.3853824    4.110    35.84
## traitbwt.1:traitbwt.2.animal          0.9939  0.0009052    2.069    50.24
## traittarsus.2:traitbwt.2.animal       2.7675 -0.5938976    6.927    20.64
## traitbwt.2:traitbwt.2.animal          1.5560  0.2002403    3.046    27.21
##
##                ~idh(trait):byear
##
##                       post.mean l-95% CI u-95% CI eff.samp
## traittarsus.1.byear    3.3123   0.9318    6.450    391.3
## traitbwt.1.byear       0.6822   0.2403    1.253    522.1
## traittarsus.2.byear    4.2198   1.3966    7.713    245.2
## traitbwt.2.byear       1.1743   0.5405    1.992    669.6
##
```

```
##                ~idh(trait):mother
##
##                      post.mean l-95% CI u-95% CI eff.samp
## traittarsus.1.mother     4.858   0.5149    8.841    122.5
## traitbwt.1.mother        1.307   0.5752    2.041    369.0
## traittarsus.2.mother     5.389   0.7457    9.557    140.4
## traitbwt.2.mother        2.003   1.2844    2.770    409.1
##
##  R-structure:  ~us(trait):units
##
##                                   post.mean l-95% CI u-95% CI eff.samp
## traittarsus.1:traittarsus.1.units   14.0783   8.6213   20.698   76.808
## traitbwt.1:traittarsus.1.units       4.0764   2.2358    6.357   47.762
## traittarsus.2:traittarsus.1.units   -3.6471 -16.9514   14.938    4.746
## traitbwt.2:traittarsus.1.units      -1.3655  -6.7308    4.970    7.185
## traittarsus.1:traitbwt.1.units       4.0764   2.2358    6.357   47.762
## traitbwt.1:traitbwt.1.units          1.7295   0.7344    2.785   57.968
## traittarsus.2:traitbwt.1.units      -1.1455  -5.8008    4.672    6.837
## traitbwt.2:traitbwt.1.units         -0.4245  -2.3300    1.630    7.646
## traittarsus.1:traittarsus.2.units   -3.6471 -16.9514   14.938    4.746
## traitbwt.1:traittarsus.2.units      -1.1455  -5.8008    4.672    6.837
## traittarsus.2:traittarsus.2.units   10.8365   0.5947   19.576   26.795
## traitbwt.2:traittarsus.2.units       3.7358  -0.1168    6.848   25.426
## traittarsus.1:traitbwt.2.units      -1.3655  -6.7308    4.970    7.185
## traitbwt.1:traitbwt.2.units         -0.4245  -2.3300    1.630    7.646
## traittarsus.2:traitbwt.2.units       3.7358  -0.1168    6.848   25.426
## traitbwt.2:traitbwt.2.units          1.7825   0.2691    2.916   28.817
##
##  Location effects: cbind(tarsus.1, bwt.1, tarsus.2, bwt.2) ~ trait - 1
##
##               post.mean l-95% CI u-95% CI eff.samp  pMCMC
## traittarsus.1    20.424   19.488   21.324    484.6 <0.001 ***
## traitbwt.1        6.143    5.686    6.550    596.7 <0.001 ***
## traittarsus.2    20.487   19.421   21.461    587.3 <0.001 ***
## traitbwt.2        8.247    7.744    8.741    876.7 <0.001 ***
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

```r
autocorr(model.MultivSex$VCV)
```

```
## , , traittarsus.1:traittarsus.1.animal
##
##         traittarsus.1:traittarsus.1.animal traitbwt.1:traittarsus.1.animal
## Lag 0                            1.0000000                       0.6872795
## Lag 100                          0.8646238                       0.6023267
## Lag 500                          0.6217623                       0.4701016
```

```
## Lag 1000                      0.4759845                      0.3306117
## Lag 5000                      0.1189988                      0.1665003
##          traittarsus.2:traittarsus.1.animal traitbwt.2:traittarsus.1.animal
## Lag 0                            0.6821642                      0.5157628
## Lag 100                          0.5837197                      0.4557449
## Lag 500                          0.4393984                      0.3819538
## Lag 1000                         0.3626317                      0.3277211
## Lag 5000                         0.1659171                      0.2490413
##          traittarsus.1:traitbwt.1.animal traitbwt.1:traitbwt.1.animal
## Lag 0                         0.6872795                    0.2316436
## Lag 100                       0.6023267                    0.1917562
## Lag 500                       0.4701016                    0.1506507
## Lag 1000                      0.3306117                    0.1026122
## Lag 5000                      0.1665003                    0.1840457
##          traittarsus.2:traitbwt.1.animal traitbwt.2:traitbwt.1.animal
## Lag 0                         0.4371184                    0.2363148
## Lag 100                       0.3790517                    0.1969987
## Lag 500                       0.3316844                    0.1943316
## Lag 1000                      0.2706112                    0.1653149
## Lag 5000                      0.2226417                    0.2722600
##          traittarsus.1:traittarsus.2.animal traitbwt.1:traittarsus.2.animal
## Lag 0                            0.6821642                      0.4371184
## Lag 100                          0.5837197                      0.3790517
## Lag 500                          0.4393984                      0.3316844
## Lag 1000                         0.3626317                      0.2706112
## Lag 5000                         0.1659171                      0.2226417
##          traittarsus.2:traittarsus.2.animal traitbwt.2:traittarsus.2.animal
## Lag 0                           0.10780644                     0.12397199
## Lag 100                         0.07023035                     0.10315317
## Lag 500                         0.03867618                     0.09153994
## Lag 1000                        0.03903023                     0.09577409
## Lag 5000                        0.21464371                     0.32154133
##          traittarsus.1:traitbwt.2.animal traitbwt.1:traitbwt.2.animal
## Lag 0                         0.5157628                    0.2363148
## Lag 100                       0.4557449                    0.1969987
## Lag 500                       0.3819538                    0.1943316
## Lag 1000                      0.3277211                    0.1653149
## Lag 5000                      0.2490413                    0.2722600
##          traittarsus.2:traitbwt.2.animal traitbwt.2:traitbwt.2.animal
## Lag 0                        0.12397199                   0.07790198
## Lag 100                      0.10315317                   0.07045248
## Lag 500                      0.09153994                   0.07781235
## Lag 1000                     0.09577409                   0.07872349
## Lag 5000                     0.32154133                   0.36408510
##          traittarsus.1.byear traitbwt.1.byear traittarsus.2.byear
## Lag 0          -0.0001991343       0.02533600         0.027261984
## Lag 100         0.0100119397       0.03699313         0.023145145
```

```
## Lag 500        0.0417069693      0.01039048         0.001545709
## Lag 1000       0.0504304342      0.06238542        -0.035646379
## Lag 5000       0.0318527577      0.07041675         0.069731639
##           traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother
## Lag 0          -0.01231264         -0.150788349         0.10750858
## Lag 100        -0.02806645         -0.118379074         0.11004526
## Lag 500         0.01040024         -0.006641147         0.07412673
## Lag 1000       -0.02300762          0.007943789         0.04372918
## Lag 5000       -0.01416454          0.056559933        -0.06110098
##           traittarsus.2.mother traitbwt.2.mother
## Lag 0               0.01502226       0.050820670
## Lag 100             0.01411095       0.039228813
## Lag 500             0.05290822       0.008673539
## Lag 1000            0.06760176      -0.017960145
## Lag 5000            0.02399980      -0.029552126
##           traittarsus.1:traittarsus.1.units traitbwt.1:traittarsus.1.units
## Lag 0                            -0.6964793                     -0.5806661
## Lag 100                          -0.6332557                     -0.5256332
## Lag 500                          -0.5006482                     -0.4211229
## Lag 1000                         -0.3965468                     -0.3341455
## Lag 5000                         -0.1551518                     -0.1703888
##           traittarsus.2:traittarsus.1.units traitbwt.2:traittarsus.1.units
## Lag 0                             0.1834123                      0.1843936
## Lag 100                           0.1989318                      0.1972224
## Lag 500                           0.2183849                      0.2244201
## Lag 1000                          0.2393546                      0.2533883
## Lag 5000                          0.1874294                      0.2352808
##           traittarsus.1:traitbwt.1.units traitbwt.1:traitbwt.1.units
## Lag 0                         -0.5806661                  -0.2972330
## Lag 100                       -0.5256332                  -0.2627074
## Lag 500                       -0.4211229                  -0.1975278
## Lag 1000                      -0.3341455                  -0.1864674
## Lag 5000                      -0.1703888                  -0.1779074
##           traittarsus.2:traitbwt.1.units traitbwt.2:traitbwt.1.units
## Lag 0                          0.1148525                   0.1045202
## Lag 100                        0.1322561                   0.1205853
## Lag 500                        0.1661494                   0.1609281
## Lag 1000                       0.2078063                   0.2097516
## Lag 5000                       0.2120391                   0.2411848
##           traittarsus.1:traittarsus.2.units traitbwt.1:traittarsus.2.units
## Lag 0                             0.1834123                      0.1148525
## Lag 100                           0.1989318                      0.1322561
## Lag 500                           0.2183849                      0.1661494
## Lag 1000                          0.2393546                      0.2078063
## Lag 5000                          0.1874294                      0.2120391
##           traittarsus.2:traittarsus.2.units traitbwt.2:traittarsus.2.units
## Lag 0                           -0.09279221                    -0.09066377
```

```
## Lag 100                     -0.06552157                 -0.08137057
## Lag 500                     -0.03120806                 -0.06842888
## Lag 1000                    -0.04688856                 -0.07652447
## Lag 5000                    -0.22692538                 -0.31476665
##          traittarsus.1:traitbwt.2.units traitbwt.1:traitbwt.2.units
## Lag 0                         0.1843936                   0.1045202
## Lag 100                       0.1972224                   0.1205853
## Lag 500                       0.2244201                   0.1609281
## Lag 1000                      0.2533883                   0.2097516
## Lag 5000                      0.2352808                   0.2411848
##          traittarsus.2:traitbwt.2.units traitbwt.2:traitbwt.2.units
## Lag 0                       -0.09066377                 -0.04305989
## Lag 100                     -0.08137057                 -0.04967401
## Lag 500                     -0.06842888                 -0.06533316
## Lag 1000                    -0.07652447                 -0.05918369
## Lag 5000                    -0.31476665                 -0.34290345
##
## , , traitbwt.1:traittarsus.1.animal
##
##          traittarsus.1:traittarsus.1.animal traitbwt.1:traittarsus.1.animal
## Lag 0                             0.6872795                       1.0000000
## Lag 100                           0.5870266                       0.8045048
## Lag 500                           0.4080911                       0.4908098
## Lag 1000                          0.3227808                       0.3613161
## Lag 5000                          0.1778345                       0.1860991
##          traittarsus.2:traittarsus.1.animal traitbwt.2:traittarsus.1.animal
## Lag 0                             0.3863431                       0.5234222
## Lag 100                           0.3311212                       0.4545868
## Lag 500                           0.2390588                       0.3427345
## Lag 1000                          0.2351271                       0.3004179
## Lag 5000                          0.1671396                       0.1589172
##          traittarsus.1:traitbwt.1.animal traitbwt.1:traitbwt.1.animal
## Lag 0                          1.0000000                    0.7001005
## Lag 100                        0.8045048                    0.5457846
## Lag 500                        0.4908098                    0.3331394
## Lag 1000                       0.3613161                    0.2645656
## Lag 5000                       0.1860991                    0.1481314
##          traittarsus.2:traitbwt.1.animal traitbwt.2:traitbwt.1.animal
## Lag 0                          0.4680554                    0.4293517
## Lag 100                        0.3667985                    0.3303034
## Lag 500                        0.2878690                    0.2612182
## Lag 1000                       0.2588194                    0.2248089
## Lag 5000                       0.2468277                    0.2268437
##          traittarsus.1:traittarsus.2.animal traitbwt.1:traittarsus.2.animal
## Lag 0                             0.3863431                       0.4680554
## Lag 100                           0.3311212                       0.3667985
## Lag 500                           0.2390588                       0.2878690
```

```
## Lag 1000                       0.2351271                        0.2588194
## Lag 5000                       0.1671396                        0.2468277
##          traittarsus.2:traittarsus.2.animal traitbwt.2:traittarsus.2.animal
## Lag 0                           0.096601163                       0.14997594
## Lag 100                         0.063514030                       0.11517198
## Lag 500                         0.007343656                       0.08445112
## Lag 1000                        0.062005867                       0.13299248
## Lag 5000                        0.138711493                       0.22091811
##          traittarsus.1:traitbwt.2.animal traitbwt.1:traitbwt.2.animal
## Lag 0                          0.5234222                    0.4293517
## Lag 100                        0.4545868                    0.3303034
## Lag 500                        0.3427345                    0.2612182
## Lag 1000                       0.3004179                    0.2248089
## Lag 5000                       0.1589172                    0.2268437
##          traittarsus.2:traitbwt.2.animal traitbwt.2:traitbwt.2.animal
## Lag 0                         0.14997594                   0.14180302
## Lag 100                       0.11517198                   0.11177118
## Lag 500                       0.08445112                   0.09651159
## Lag 1000                      0.13299248                   0.13501835
## Lag 5000                      0.22091811                   0.25836873
##          traittarsus.1.byear traitbwt.1.byear traittarsus.2.byear
## Lag 0             0.06781216      -0.04857154        -0.001115860
## Lag 100           0.05744185      -0.04365919        -0.003028122
## Lag 500           0.04182580      -0.01683610        -0.013871766
## Lag 1000          0.08409670       0.04075709        -0.088936973
## Lag 5000          0.07211397       0.04755605         0.061879136
##          traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother
## Lag 0        -0.026101857          0.015326642      -0.015001711
## Lag 100      -0.026229006          0.004791955      -0.002553299
## Lag 500      -0.004795139          0.018197593      -0.001734987
## Lag 1000     -0.025567829         -0.014419690      -0.054320480
## Lag 5000     -0.011401634         -0.003782365      -0.012255190
##          traittarsus.2.mother traitbwt.2.mother
## Lag 0              0.05171415       -0.01155255
## Lag 100            0.04549989       -0.01648838
## Lag 500            0.09888411       -0.02579001
## Lag 1000           0.07526847       -0.03519968
## Lag 5000           0.07495551       -0.03929467
##          traittarsus.1:traittarsus.1.units traitbwt.1:traittarsus.1.units
## Lag 0                           -0.5374156                     -0.7822168
## Lag 100                         -0.4631107                     -0.6561709
## Lag 500                         -0.3115622                     -0.4297448
## Lag 1000                        -0.2502951                     -0.3378405
## Lag 5000                        -0.1757000                     -0.1812141
##          traittarsus.2:traittarsus.1.units traitbwt.2:traittarsus.1.units
## Lag 0                            0.1247101                      0.1399193
## Lag 100                          0.1426212                      0.1604774
```

```
## Lag 500                        0.1604094                        0.2063094
## Lag 1000                       0.1703454                        0.2249688
## Lag 5000                       0.1859265                        0.1911673
##          traittarsus.1:traitbwt.1.units traitbwt.1:traitbwt.1.units
## Lag 0                        -0.7822168                  -0.6444049
## Lag 100                      -0.6561709                  -0.5391921
## Lag 500                      -0.4297448                  -0.3429426
## Lag 1000                     -0.3378405                  -0.2744658
## Lag 5000                     -0.1812141                  -0.1591715
##          traittarsus.2:traitbwt.1.units traitbwt.2:traitbwt.1.units
## Lag 0                         0.1003793                   0.1067549
## Lag 100                       0.1314503                   0.1404067
## Lag 500                       0.1658186                   0.1981668
## Lag 1000                      0.1899850                   0.2354607
## Lag 5000                      0.2090708                   0.1964048
##          traittarsus.1:traittarsus.2.units traitbwt.1:traittarsus.2.units
## Lag 0                            0.1247101                      0.1003793
## Lag 100                          0.1426212                      0.1314503
## Lag 500                          0.1604094                      0.1658186
## Lag 1000                         0.1703454                      0.1899850
## Lag 5000                         0.1859265                      0.2090708
##          traittarsus.2:traittarsus.2.units traitbwt.2:traittarsus.2.units
## Lag 0                          -0.09677793                    -0.12847847
## Lag 100                        -0.06212434                    -0.10051402
## Lag 500                        -0.01671120                    -0.07130994
## Lag 1000                       -0.07460059                    -0.11790351
## Lag 5000                       -0.16171357                    -0.21125583
##          traittarsus.1:traitbwt.2.units traitbwt.1:traitbwt.2.units
## Lag 0                         0.1399193                   0.1067549
## Lag 100                       0.1604774                   0.1404067
## Lag 500                       0.2063094                   0.1981668
## Lag 1000                      0.2249688                   0.2354607
## Lag 5000                      0.1911673                   0.1964048
##          traittarsus.2:traitbwt.2.units traitbwt.2:traitbwt.2.units
## Lag 0                       -0.12847847                 -0.10947233
## Lag 100                     -0.10051402                 -0.09309607
## Lag 500                     -0.07130994                 -0.08545450
## Lag 1000                    -0.11790351                 -0.11149356
## Lag 5000                    -0.21125583                 -0.23203853
##
## , , traittarsus.2:traittarsus.1.animal
##
##          traittarsus.1:traittarsus.1.animal traitbwt.1:traittarsus.1.animal
## Lag 0                           0.682164176                      0.38634307
## Lag 100                         0.591700877                      0.34935277
## Lag 500                         0.451559860                      0.32828629
## Lag 1000                        0.378373002                      0.27249926
```

```
## Lag 5000                    0.004289439                   0.08293975
##          traittarsus.2:traittarsus.1.animal traitbwt.2:traittarsus.1.animal
## Lag 0                         1.00000000                   0.78206164
## Lag 100                       0.87865696                   0.70110541
## Lag 500                       0.69161215                   0.56910648
## Lag 1000                      0.56265051                   0.44347532
## Lag 5000                     -0.04003226                   0.01712343
##          traittarsus.1:traitbwt.1.animal traitbwt.1:traitbwt.1.animal
## Lag 0                      0.38634307                 0.09679049
## Lag 100                    0.34935277                 0.10017661
## Lag 500                    0.32828629                 0.12775760
## Lag 1000                   0.27249926                 0.11433423
## Lag 5000                   0.08293975                 0.09000388
##          traittarsus.2:traitbwt.1.animal traitbwt.2:traitbwt.1.animal
## Lag 0                      0.71265304                 0.46511587
## Lag 100                    0.64354820                 0.41849123
## Lag 500                    0.54967619                 0.35510793
## Lag 1000                   0.45077032                 0.27846473
## Lag 5000                   0.02763651                 0.08826768
##          traittarsus.1:traittarsus.2.animal traitbwt.1:traittarsus.2.animal
## Lag 0                         1.00000000                   0.71265304
## Lag 100                       0.87865696                   0.64354820
## Lag 500                       0.69161215                   0.54967619
## Lag 1000                      0.56265051                   0.45077032
## Lag 5000                     -0.04003226                   0.02763651
##          traittarsus.2:traittarsus.2.animal traitbwt.2:traittarsus.2.animal
## Lag 0                          0.5942621                    0.5613010
## Lag 100                        0.5307170                    0.5141865
## Lag 500                        0.4678297                    0.4619296
## Lag 1000                       0.4001045                    0.3816713
## Lag 5000                       0.1478270                    0.1489578
##          traittarsus.1:traitbwt.2.animal traitbwt.1:traitbwt.2.animal
## Lag 0                      0.78206164                 0.46511587
## Lag 100                    0.70110541                 0.41849123
## Lag 500                    0.56910648                 0.35510793
## Lag 1000                   0.44347532                 0.27846473
## Lag 5000                   0.01712343                 0.08826768
##          traittarsus.2:traitbwt.2.animal traitbwt.2:traitbwt.2.animal
## Lag 0                       0.5613010                  0.4107260
## Lag 100                     0.5141865                  0.3793894
## Lag 500                     0.4619296                  0.3449678
## Lag 1000                    0.3816713                  0.2731469
## Lag 5000                    0.1489578                  0.1431489
##          traittarsus.1.byear traitbwt.1.byear traittarsus.2.byear
## Lag 0             0.01620495       0.04295234         0.052223393
## Lag 100           0.02029711       0.05648775         0.034069858
## Lag 500           0.04765917       0.03285861         0.007554307
```

```
## Lag 1000          0.03767470       0.07587887         0.003191847
## Lag 5000         -0.02249363       0.05599353         0.040862718
##          traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother
## Lag 0         -0.04161269         -0.102952660        0.04055573
## Lag 100       -0.05474586         -0.077407539        0.03752540
## Lag 500       -0.01536913         -0.009985327        0.02041393
## Lag 1000      -0.02242552         -0.016880479        0.02095844
## Lag 5000       0.05382429          0.093039192       -0.03853343
##          traittarsus.2.mother traitbwt.2.mother
## Lag 0            -0.15988076        0.11172969
## Lag 100          -0.14920373        0.08235912
## Lag 500          -0.10669450        0.07860308
## Lag 1000         -0.09563279        0.04882603
## Lag 5000         -0.03477033        0.03882608
##          traittarsus.1:traittarsus.1.units traitbwt.1:traittarsus.1.units
## Lag 0                          -0.48510213                    -0.35513667
## Lag 100                        -0.43884380                    -0.32128424
## Lag 500                        -0.37005382                    -0.29419691
## Lag 1000                       -0.29875897                    -0.25541065
## Lag 5000                       -0.06651357                    -0.08518695
##          traittarsus.2:traittarsus.1.units traitbwt.2:traittarsus.1.units
## Lag 0                            0.1906441                      0.2159001
## Lag 100                          0.2109187                      0.2292953
## Lag 500                          0.2433902                      0.2525070
## Lag 1000                         0.2670207                      0.2801991
## Lag 5000                         0.2055428                      0.2202544
##          traittarsus.1:traitbwt.1.units traitbwt.1:traitbwt.1.units
## Lag 0                       -0.35513667                 -0.16353731
## Lag 100                     -0.32128424                 -0.14737332
## Lag 500                     -0.29419691                 -0.14406290
## Lag 1000                    -0.25541065                 -0.15449858
## Lag 5000                    -0.08518695                 -0.09726346
##          traittarsus.2:traitbwt.1.units traitbwt.2:traitbwt.1.units
## Lag 0                         0.1588923                   0.1751169
## Lag 100                       0.1763493                   0.1863279
## Lag 500                       0.2035612                   0.2019259
## Lag 1000                      0.2408050                   0.2434815
## Lag 5000                      0.2188271                   0.2190020
##          traittarsus.1:traittarsus.2.units traitbwt.1:traittarsus.2.units
## Lag 0                            0.1906441                      0.1588923
## Lag 100                          0.2109187                      0.1763493
## Lag 500                          0.2433902                      0.2035612
## Lag 1000                         0.2670207                      0.2408050
## Lag 5000                         0.2055428                      0.2188271
##          traittarsus.2:traittarsus.2.units traitbwt.2:traittarsus.2.units
## Lag 0                           -0.5600992                     -0.5208193
## Lag 100                         -0.5263626                     -0.5010452
```

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## Lag 500                          -0.4620756                     -0.4434018
## Lag 1000                         -0.4037773                     -0.3729971
## Lag 5000                         -0.1493219                     -0.1529356
##          traittarsus.1:traitbwt.2.units traitbwt.1:traitbwt.2.units
## Lag 0                         0.2159001                   0.1751169
## Lag 100                       0.2292953                   0.1863279
## Lag 500                       0.2525070                   0.2019259
## Lag 1000                      0.2801991                   0.2434815
## Lag 5000                      0.2202544                   0.2190020
##          traittarsus.2:traitbwt.2.units traitbwt.2:traitbwt.2.units
## Lag 0                        -0.5208193                  -0.3939711
## Lag 100                      -0.5010452                  -0.3851102
## Lag 500                      -0.4434018                  -0.3487254
## Lag 1000                     -0.3729971                  -0.2846600
## Lag 5000                     -0.1529356                  -0.1449719
##
## , , traitbwt.2:traittarsus.1.animal
##
##          traittarsus.1:traittarsus.1.animal traitbwt.1:traittarsus.1.animal
## Lag 0                            0.51576277                      0.52342220
## Lag 100                          0.44159056                      0.43580048
## Lag 500                          0.30785687                      0.33037079
## Lag 1000                         0.24390874                      0.26926704
## Lag 5000                        -0.05005481                      0.04687804
##          traittarsus.2:traittarsus.1.animal traitbwt.2:traittarsus.1.animal
## Lag 0                           0.782061640                      1.00000000
## Lag 100                         0.696299215                      0.87453824
## Lag 500                         0.538889846                      0.65219311
## Lag 1000                        0.445389577                      0.48957859
## Lag 5000                       -0.006519724                      0.01842864
##          traittarsus.1:traitbwt.1.animal traitbwt.1:traitbwt.1.animal
## Lag 0                         0.52342220                   0.32999449
## Lag 100                       0.43580048                   0.28148773
## Lag 500                       0.33037079                   0.26589289
## Lag 1000                      0.26926704                   0.24323871
## Lag 5000                      0.04687804                   0.09890983
##          traittarsus.2:traitbwt.1.animal traitbwt.2:traitbwt.1.animal
## Lag 0                         0.59763628                    0.6478170
## Lag 100                       0.52643466                    0.5573055
## Lag 500                       0.44551868                    0.4418750
## Lag 1000                      0.37736602                    0.3442054
## Lag 5000                      0.08285167                    0.1125165
##          traittarsus.1:traittarsus.2.animal traitbwt.1:traittarsus.2.animal
## Lag 0                           0.782061640                      0.59763628
## Lag 100                         0.696299215                      0.52643466
## Lag 500                         0.538889846                      0.44551868
## Lag 1000                        0.445389577                      0.37736602
```

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## Lag 5000                     -0.006519724                        0.08285167
##          traittarsus.2:traittarsus.2.animal traitbwt.2:traittarsus.2.animal
## Lag 0                           0.5635407                         0.6729793
## Lag 100                         0.5125673                         0.6052812
## Lag 500                         0.4465910                         0.5277439
## Lag 1000                        0.4070664                         0.4538221
## Lag 5000                        0.1850370                         0.1792542
##          traittarsus.1:traitbwt.2.animal traitbwt.1:traitbwt.2.animal
## Lag 0                         1.00000000                    0.6478170
## Lag 100                       0.87453824                    0.5573055
## Lag 500                       0.65219311                    0.4418750
## Lag 1000                      0.48957859                    0.3442054
## Lag 5000                      0.01842864                    0.1125165
##          traittarsus.2:traitbwt.2.animal traitbwt.2:traitbwt.2.animal
## Lag 0                          0.6729793                    0.6191252
## Lag 100                        0.6052812                    0.5529718
## Lag 500                        0.5277439                    0.4729419
## Lag 1000                       0.4538221                    0.3884032
## Lag 5000                       0.1792542                    0.1542326
##          traittarsus.1.byear traitbwt.1.byear traittarsus.2.byear
## Lag 0            0.063463728       0.02730871         0.051964042
## Lag 100          0.066558472       0.03961464         0.040967359
## Lag 500          0.076728186       0.05374642        -0.012930939
## Lag 1000         0.100842393       0.09752083        -0.062954038
## Lag 5000        -0.006751012       0.04984406         0.002434151
##          traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother
## Lag 0         -0.09337461           0.02006907       -0.06942502
## Lag 100       -0.09001277           0.02763705       -0.07262374
## Lag 500       -0.04869538           0.02000750       -0.09505843
## Lag 1000      -0.05831890           0.02560894       -0.08617648
## Lag 5000       0.04246982           0.06392166       -0.03722137
##          traittarsus.2.mother traitbwt.2.mother
## Lag 0            -0.026436938        0.04826105
## Lag 100          -0.041329867        0.04078039
## Lag 500          -0.028290001        0.03056152
## Lag 1000         -0.036326123        0.04300492
## Lag 5000         -0.008439906        0.00653221
##          traittarsus.1:traittarsus.1.units traitbwt.1:traittarsus.1.units
## Lag 0                        -0.3969629895                    -0.44235441
## Lag 100                      -0.3457725771                    -0.37788435
## Lag 500                      -0.2409128696                    -0.27612777
## Lag 1000                     -0.2064627528                    -0.23939733
## Lag 5000                     -0.0008284304                    -0.05932951
##          traittarsus.2:traittarsus.1.units traitbwt.2:traittarsus.1.units
## Lag 0                            0.1332860                      0.1894193
## Lag 100                          0.1542105                      0.2129929
## Lag 500                          0.1772766                      0.2426247
```

```
## Lag 1000                           0.1956287                              0.2577964
## Lag 5000                           0.1561845                              0.1623293
##            traittarsus.1:traitbwt.1.units traitbwt.1:traitbwt.1.units
## Lag 0                          -0.44235441                  -0.3300209
## Lag 100                        -0.37788435                  -0.2868342
## Lag 500                        -0.27612777                  -0.2200427
## Lag 1000                       -0.23939733                  -0.2196364
## Lag 5000                       -0.05932951                  -0.1105188
##            traittarsus.2:traitbwt.1.units traitbwt.2:traitbwt.1.units
## Lag 0                            0.1392793                   0.1845588
## Lag 100                          0.1618837                   0.2068320
## Lag 500                          0.1824833                   0.2322375
## Lag 1000                         0.2062851                   0.2545405
## Lag 5000                         0.1708879                   0.1679111
##            traittarsus.1:traittarsus.2.units traitbwt.1:traittarsus.2.units
## Lag 0                               0.1332860                      0.1392793
## Lag 100                             0.1542105                      0.1618837
## Lag 500                             0.1772766                      0.1824833
## Lag 1000                            0.1956287                      0.2062851
## Lag 5000                            0.1561845                      0.1708879
##            traittarsus.2:traittarsus.2.units traitbwt.2:traittarsus.2.units
## Lag 0                              -0.5541670                     -0.6200400
## Lag 100                            -0.5163721                     -0.5823652
## Lag 500                            -0.4591717                     -0.5082023
## Lag 1000                           -0.4081394                     -0.4277328
## Lag 5000                           -0.1850899                     -0.1717978
##            traittarsus.1:traitbwt.2.units traitbwt.1:traitbwt.2.units
## Lag 0                            0.1894193                   0.1845588
## Lag 100                          0.2129929                   0.2068320
## Lag 500                          0.2426247                   0.2322375
## Lag 1000                         0.2577964                   0.2545405
## Lag 5000                         0.1623293                   0.1679111
##            traittarsus.2:traitbwt.2.units traitbwt.2:traitbwt.2.units
## Lag 0                           -0.6200400                  -0.5649761
## Lag 100                         -0.5823652                  -0.5353605
## Lag 500                         -0.5082023                  -0.4627844
## Lag 1000                        -0.4277328                  -0.3777429
## Lag 5000                        -0.1717978                  -0.1507443
##
## , , traittarsus.1:traitbwt.1.animal
##
##            traittarsus.1:traittarsus.1.animal traitbwt.1:traittarsus.1.animal
## Lag 0                                0.6872795                       1.0000000
## Lag 100                              0.5870266                       0.8045048
## Lag 500                              0.4080911                       0.4908098
## Lag 1000                             0.3227808                       0.3613161
## Lag 5000                             0.1778345                       0.1860991
```

```
##           traittarsus.2:traittarsus.1.animal traitbwt.2:traittarsus.1.animal
## Lag 0                              0.3863431                       0.5234222
## Lag 100                            0.3311212                       0.4545868
## Lag 500                            0.2390588                       0.3427345
## Lag 1000                           0.2351271                       0.3004179
## Lag 5000                           0.1671396                       0.1589172
##           traittarsus.1:traitbwt.1.animal traitbwt.1:traitbwt.1.animal
## Lag 0                           1.0000000                    0.7001005
## Lag 100                         0.8045048                    0.5457846
## Lag 500                         0.4908098                    0.3331394
## Lag 1000                        0.3613161                    0.2645656
## Lag 5000                        0.1860991                    0.1481314
##           traittarsus.2:traitbwt.1.animal traitbwt.2:traitbwt.1.animal
## Lag 0                           0.4680554                    0.4293517
## Lag 100                         0.3667985                    0.3303034
## Lag 500                         0.2878690                    0.2612182
## Lag 1000                        0.2588194                    0.2248089
## Lag 5000                        0.2468277                    0.2268437
##           traittarsus.1:traittarsus.2.animal traitbwt.1:traittarsus.2.animal
## Lag 0                              0.3863431                       0.4680554
## Lag 100                            0.3311212                       0.3667985
## Lag 500                            0.2390588                       0.2878690
## Lag 1000                           0.2351271                       0.2588194
## Lag 5000                           0.1671396                       0.2468277
##           traittarsus.2:traittarsus.2.animal traitbwt.2:traittarsus.2.animal
## Lag 0                            0.096601163                      0.14997594
## Lag 100                          0.063514030                      0.11517198
## Lag 500                          0.007343656                      0.08445112
## Lag 1000                         0.062005867                      0.13299248
## Lag 5000                         0.138711493                      0.22091811
##           traittarsus.1:traitbwt.2.animal traitbwt.1:traitbwt.2.animal
## Lag 0                           0.5234222                    0.4293517
## Lag 100                         0.4545868                    0.3303034
## Lag 500                         0.3427345                    0.2612182
## Lag 1000                        0.3004179                    0.2248089
## Lag 5000                        0.1589172                    0.2268437
##           traittarsus.2:traitbwt.2.animal traitbwt.2:traitbwt.2.animal
## Lag 0                          0.14997594                   0.14180302
## Lag 100                        0.11517198                   0.11177118
## Lag 500                        0.08445112                   0.09651159
## Lag 1000                       0.13299248                   0.13501835
## Lag 5000                       0.22091811                   0.25836873
##           traittarsus.1.byear traitbwt.1.byear traittarsus.2.byear
## Lag 0              0.06781216      -0.04857154        -0.001115860
## Lag 100            0.05744185      -0.04365919        -0.003028122
## Lag 500            0.04182580      -0.01683610        -0.013871766
## Lag 1000           0.08409670       0.04075709        -0.088936973
```

```
## Lag 5000          0.07211397       0.04755605         0.061879136
##            traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother
## Lag 0        -0.026101857          0.015326642      -0.015001711
## Lag 100      -0.026229006          0.004791955      -0.002553299
## Lag 500      -0.004795139          0.018197593      -0.001734987
## Lag 1000     -0.025567829         -0.014419690      -0.054320480
## Lag 5000     -0.011401634         -0.003782365      -0.012255190
##            traittarsus.2.mother traitbwt.2.mother
## Lag 0                0.05171415       -0.01155255
## Lag 100              0.04549989       -0.01648838
## Lag 500              0.09888411       -0.02579001
## Lag 1000             0.07526847       -0.03519968
## Lag 5000             0.07495551       -0.03929467
##            traittarsus.1:traittarsus.1.units traitbwt.1:traittarsus.1.units
## Lag 0                             -0.5374156                     -0.7822168
## Lag 100                           -0.4631107                     -0.6561709
## Lag 500                           -0.3115622                     -0.4297448
## Lag 1000                          -0.2502951                     -0.3378405
## Lag 5000                          -0.1757000                     -0.1812141
##            traittarsus.2:traittarsus.1.units traitbwt.2:traittarsus.1.units
## Lag 0                              0.1247101                      0.1399193
## Lag 100                            0.1426212                      0.1604774
## Lag 500                            0.1604094                      0.2063094
## Lag 1000                           0.1703454                      0.2249688
## Lag 5000                           0.1859265                      0.1911673
##            traittarsus.1:traitbwt.1.units traitbwt.1:traitbwt.1.units
## Lag 0                          -0.7822168                  -0.6444049
## Lag 100                        -0.6561709                  -0.5391921
## Lag 500                        -0.4297448                  -0.3429426
## Lag 1000                       -0.3378405                  -0.2744658
## Lag 5000                       -0.1812141                  -0.1591715
##            traittarsus.2:traitbwt.1.units traitbwt.2:traitbwt.1.units
## Lag 0                           0.1003793                   0.1067549
## Lag 100                         0.1314503                   0.1404067
## Lag 500                         0.1658186                   0.1981668
## Lag 1000                        0.1899850                   0.2354607
## Lag 5000                        0.2090708                   0.1964048
##            traittarsus.1:traittarsus.2.units traitbwt.1:traittarsus.2.units
## Lag 0                              0.1247101                      0.1003793
## Lag 100                            0.1426212                      0.1314503
## Lag 500                            0.1604094                      0.1658186
## Lag 1000                           0.1703454                      0.1899850
## Lag 5000                           0.1859265                      0.2090708
##            traittarsus.2:traittarsus.2.units traitbwt.2:traittarsus.2.units
## Lag 0                            -0.09677793                    -0.12847847
## Lag 100                          -0.06212434                    -0.10051402
## Lag 500                          -0.01671120                    -0.07130994
```

```
## Lag 1000                 -0.07460059                     -0.11790351
## Lag 5000                 -0.16171357                     -0.21125583
##          traittarsus.1:traitbwt.2.units traitbwt.1:traitbwt.2.units
## Lag 0                         0.1399193                   0.1067549
## Lag 100                       0.1604774                   0.1404067
## Lag 500                       0.2063094                   0.1981668
## Lag 1000                      0.2249688                   0.2354607
## Lag 5000                      0.1911673                   0.1964048
##          traittarsus.2:traitbwt.2.units traitbwt.2:traitbwt.2.units
## Lag 0                       -0.12847847                 -0.10947233
## Lag 100                     -0.10051402                 -0.09309607
## Lag 500                     -0.07130994                 -0.08545450
## Lag 1000                    -0.11790351                 -0.11149356
## Lag 5000                    -0.21125583                 -0.23203853
##
## , , traitbwt.1:traitbwt.1.animal
##
##          traittarsus.1:traittarsus.1.animal traitbwt.1:traittarsus.1.animal
## Lag 0                            0.23164362                      0.70010050
## Lag 100                          0.18054608                      0.54456316
## Lag 500                          0.08781934                      0.30301892
## Lag 1000                         0.03769032                      0.17531595
## Lag 5000                         0.09013727                      0.08812775
##          traittarsus.2:traittarsus.1.animal traitbwt.2:traittarsus.1.animal
## Lag 0                            0.09679049                     0.329994492
## Lag 100                          0.07358032                     0.280145064
## Lag 500                          0.03161374                     0.197610680
## Lag 1000                         0.07044623                     0.170452855
## Lag 5000                         0.09611101                     0.004847697
##          traittarsus.1:traitbwt.1.animal traitbwt.1:traitbwt.1.animal
## Lag 0                         0.70010050                    1.0000000
## Lag 100                       0.54456316                    0.6856952
## Lag 500                       0.30301892                    0.3598203
## Lag 1000                      0.17531595                    0.2634115
## Lag 5000                      0.08812775                    0.0581774
##          traittarsus.2:traitbwt.1.animal traitbwt.2:traitbwt.1.animal
## Lag 0                          0.2789729                   0.50673141
## Lag 100                        0.2383906                   0.37724913
## Lag 500                        0.1850306                   0.26913927
## Lag 1000                       0.1760392                   0.21403804
## Lag 5000                       0.1959228                   0.08822723
##          traittarsus.1:traittarsus.2.animal traitbwt.1:traittarsus.2.animal
## Lag 0                            0.09679049                       0.2789729
## Lag 100                          0.07358032                       0.2383906
## Lag 500                          0.03161374                       0.1850306
## Lag 1000                         0.07044623                       0.1760392
## Lag 5000                         0.09611101                       0.1959228
```

```
##          traittarsus.2:traittarsus.2.animal traitbwt.2:traittarsus.2.animal
## Lag 0                            0.10548333                      0.17131088
## Lag 100                          0.08666667                      0.15141502
## Lag 500                          0.03855034                      0.12592562
## Lag 1000                         0.09753802                      0.15461525
## Lag 5000                         0.05868589                      0.07881607
##          traittarsus.1:traitbwt.2.animal traitbwt.1:traitbwt.2.animal
## Lag 0                        0.329994492                   0.50673141
## Lag 100                      0.280145064                   0.37724913
## Lag 500                      0.197610680                   0.26913927
## Lag 1000                     0.170452855                   0.21403804
## Lag 5000                     0.004847697                   0.08822723
##          traittarsus.2:traitbwt.2.animal traitbwt.2:traitbwt.2.animal
## Lag 0                         0.17131088                   0.21046169
## Lag 100                       0.15141502                   0.17525516
## Lag 500                       0.12592562                   0.17738787
## Lag 1000                      0.15461525                   0.17597147
## Lag 5000                      0.07881607                   0.08328384
##          traittarsus.1.byear traitbwt.1.byear traittarsus.2.byear
## Lag 0            0.065188114     -0.054239888       -0.0315843380
## Lag 100          0.038096586     -0.064724456       -0.0570202816
## Lag 500         -0.002027739      0.020824115        0.0009269064
## Lag 1000         0.057546907      0.008429484       -0.0456402525
## Lag 5000         0.105389029      0.003598701        0.0158576632
##          traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother
## Lag 0         -0.02489988          0.063535708      -0.301057181
## Lag 100       -0.02027214          0.044670327      -0.205303237
## Lag 500       -0.01893478          0.000885945      -0.083381850
## Lag 1000      -0.01593842         -0.053672083      -0.098869582
## Lag 5000      -0.06322669          0.022199101       0.007755258
##          traittarsus.2.mother traitbwt.2.mother
## Lag 0              0.02830176       -0.06829043
## Lag 100            0.01508424       -0.03965583
## Lag 500            0.07970255       -0.07134929
## Lag 1000           0.03715760       -0.03341572
## Lag 5000           0.05894613       -0.03420041
##          traittarsus.1:traittarsus.1.units traitbwt.1:traittarsus.1.units
## Lag 0                         -0.224526532                    -0.57857216
## Lag 100                       -0.156949752                    -0.45706691
## Lag 500                       -0.038181523                    -0.25766540
## Lag 1000                      -0.006974297                    -0.17163469
## Lag 5000                      -0.082791880                    -0.06775113
##          traittarsus.2:traittarsus.1.units traitbwt.2:traittarsus.1.units
## Lag 0                           0.08095300                     0.11864383
## Lag 100                         0.08975567                     0.13271891
## Lag 500                         0.10744809                     0.16596526
## Lag 1000                        0.10586708                     0.15987797
```

```
## Lag 5000                        0.11020681                      0.08507017
##          traittarsus.1:traitbwt.1.units traitbwt.1:traitbwt.1.units
## Lag 0                       -0.57857216                 -0.72140390
## Lag 100                     -0.45706691                 -0.56413893
## Lag 500                     -0.25766540                 -0.34043397
## Lag 1000                    -0.17163469                 -0.22135712
## Lag 5000                    -0.06775113                 -0.03117589
##          traittarsus.2:traitbwt.1.units traitbwt.2:traitbwt.1.units
## Lag 0                         0.1206260                  0.15466547
## Lag 100                       0.1358748                  0.17988396
## Lag 500                       0.1545988                  0.21095632
## Lag 1000                      0.1778949                  0.23064318
## Lag 5000                      0.1189483                  0.08708938
##          traittarsus.1:traittarsus.2.units traitbwt.1:traittarsus.2.units
## Lag 0                           0.08095300                      0.1206260
## Lag 100                         0.08975567                      0.1358748
## Lag 500                         0.10744809                      0.1545988
## Lag 1000                        0.10586708                      0.1778949
## Lag 5000                        0.11020681                      0.1189483
##          traittarsus.2:traittarsus.2.units traitbwt.2:traittarsus.2.units
## Lag 0                          -0.11346055                     -0.1672807
## Lag 100                        -0.08013985                     -0.1375357
## Lag 500                        -0.05850422                     -0.1306059
## Lag 1000                       -0.11497643                     -0.1592872
## Lag 5000                       -0.07297426                     -0.0658664
##          traittarsus.1:traitbwt.2.units traitbwt.1:traitbwt.2.units
## Lag 0                        0.11864383                  0.15466547
## Lag 100                      0.13271891                  0.17988396
## Lag 500                      0.16596526                  0.21095632
## Lag 1000                     0.15987797                  0.23064318
## Lag 5000                     0.08507017                  0.08708938
##          traittarsus.2:traitbwt.2.units traitbwt.2:traitbwt.2.units
## Lag 0                        -0.1672807                  -0.1878114
## Lag 100                      -0.1375357                  -0.1655553
## Lag 500                      -0.1306059                  -0.1703498
## Lag 1000                     -0.1592872                  -0.1664878
## Lag 5000                     -0.0658664                  -0.0614103
##
## , , traittarsus.2:traitbwt.1.animal
##
##          traittarsus.1:traittarsus.1.animal traitbwt.1:traittarsus.1.animal
## Lag 0                            0.43711841                       0.4680554
## Lag 100                          0.38614287                       0.3822935
## Lag 500                          0.32973015                       0.2828059
## Lag 1000                         0.30898433                       0.3053279
## Lag 5000                         0.06068506                       0.1038801
##          traittarsus.2:traittarsus.1.animal traitbwt.2:traittarsus.1.animal
```

```
## Lag 0                          0.71265304                         0.59763628
## Lag 100                        0.64495665                         0.53517485
## Lag 500                        0.56187680                         0.46435370
## Lag 1000                       0.52770068                         0.43493174
## Lag 5000                      -0.04596197                        -0.09919957
##          traittarsus.1:traitbwt.1.animal traitbwt.1:traitbwt.1.animal
## Lag 0                          0.4680554                   0.27897287
## Lag 100                        0.3822935                   0.24804717
## Lag 500                        0.2828059                   0.18131034
## Lag 1000                       0.3053279                   0.20383689
## Lag 5000                       0.1038801                   0.07466278
##          traittarsus.2:traitbwt.1.animal traitbwt.2:traitbwt.1.animal
## Lag 0                         1.00000000                   0.75320258
## Lag 100                       0.84412396                   0.63847339
## Lag 500                       0.63408467                   0.47179404
## Lag 1000                      0.55041345                   0.40200369
## Lag 5000                      0.07989653                   0.02863099
##          traittarsus.1:traittarsus.2.animal traitbwt.1:traittarsus.2.animal
## Lag 0                          0.71265304                      1.00000000
## Lag 100                        0.64495665                      0.84412396
## Lag 500                        0.56187680                      0.63408467
## Lag 1000                       0.52770068                      0.55041345
## Lag 5000                      -0.04596197                      0.07989653
##          traittarsus.2:traittarsus.2.animal traitbwt.2:traittarsus.2.animal
## Lag 0                          0.39609257                      0.50085427
## Lag 100                        0.37249703                      0.45415166
## Lag 500                        0.36147616                      0.41592880
## Lag 1000                       0.38702161                      0.40262387
## Lag 5000                       0.05902071                      0.05027704
##          traittarsus.1:traitbwt.2.animal traitbwt.1:traitbwt.2.animal
## Lag 0                         0.59763628                   0.75320258
## Lag 100                       0.53517485                   0.63847339
## Lag 500                       0.46435370                   0.47179404
## Lag 1000                      0.43493174                   0.40200369
## Lag 5000                     -0.09919957                   0.02863099
##          traittarsus.2:traitbwt.2.animal traitbwt.2:traitbwt.2.animal
## Lag 0                         0.50085427                   0.47574281
## Lag 100                       0.45415166                   0.42373764
## Lag 500                       0.41592880                   0.36577921
## Lag 1000                      0.40262387                   0.31479935
## Lag 5000                      0.05027704                   0.04228229
##          traittarsus.1.byear traitbwt.1.byear traittarsus.2.byear
## Lag 0            0.029421346       0.01370326          0.08861601
## Lag 100          0.024425366       0.01320865          0.06508810
## Lag 500          0.050837464       0.03060238          0.05880699
## Lag 1000         0.065685010       0.04013922          0.02624809
## Lag 5000        -0.006279369       0.01390888          0.06953734
```

```
##          traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother
## Lag 0         -0.06566102          0.010266822      -0.002921727
## Lag 100       -0.05957647          0.001133316      -0.025849735
## Lag 500       -0.03310752         -0.035302602      -0.011049599
## Lag 1000      -0.01325750         -0.005132729      -0.030094999
## Lag 5000       0.07737072          0.051936326       0.028222378
##          traittarsus.2.mother traitbwt.2.mother
## Lag 0             -0.01173970       0.004891297
## Lag 100           -0.01984404       0.001495609
## Lag 500           -0.01047992       0.019305497
## Lag 1000          -0.06166849       0.035361493
## Lag 5000          -0.03572076       0.037357859
##          traittarsus.1:traittarsus.1.units traitbwt.1:traittarsus.1.units
## Lag 0                           -0.3729388                     -0.3850991
## Lag 100                         -0.3393916                     -0.3381615
## Lag 500                         -0.2662669                     -0.2603097
## Lag 1000                        -0.2581177                     -0.2862286
## Lag 5000                        -0.1138844                     -0.1255711
##          traittarsus.2:traittarsus.1.units traitbwt.2:traittarsus.1.units
## Lag 0                            0.1304165                      0.1778597
## Lag 100                          0.1523428                      0.1937314
## Lag 500                          0.1726064                      0.2144724
## Lag 1000                         0.1844905                      0.2275146
## Lag 5000                         0.1876933                      0.1730132
##          traittarsus.1:traitbwt.1.units traitbwt.1:traitbwt.1.units
## Lag 0                        -0.3850991                  -0.2793636
## Lag 100                      -0.3381615                  -0.2451230
## Lag 500                      -0.2603097                  -0.1889420
## Lag 1000                     -0.2862286                  -0.2310740
## Lag 5000                     -0.1255711                  -0.1098246
##          traittarsus.2:traitbwt.1.units traitbwt.2:traitbwt.1.units
## Lag 0                         0.1142625                   0.1618783
## Lag 100                       0.1516538                   0.1886145
## Lag 500                       0.1942499                   0.2259939
## Lag 1000                      0.1947749                   0.2314168
## Lag 5000                      0.1938069                   0.1610221
##          traittarsus.1:traittarsus.2.units traitbwt.1:traittarsus.2.units
## Lag 0                            0.1304165                      0.1142625
## Lag 100                          0.1523428                      0.1516538
## Lag 500                          0.1726064                      0.1942499
## Lag 1000                         0.1844905                      0.1947749
## Lag 5000                         0.1876933                      0.1938069
##          traittarsus.2:traittarsus.2.units traitbwt.2:traittarsus.2.units
## Lag 0                          -0.41858410                    -0.47291409
## Lag 100                        -0.40815749                    -0.45309828
## Lag 500                        -0.38612479                    -0.40783101
## Lag 1000                       -0.40349965                    -0.40278702
```

```
## Lag 5000                        -0.06617356                      -0.06076514
##          traittarsus.1:traitbwt.2.units traitbwt.1:traitbwt.2.units
## Lag 0                         0.1778597                   0.1618783
## Lag 100                       0.1937314                   0.1886145
## Lag 500                       0.2144724                   0.2259939
## Lag 1000                      0.2275146                   0.2314168
## Lag 5000                      0.1730132                   0.1610221
##          traittarsus.2:traitbwt.2.units traitbwt.2:traitbwt.2.units
## Lag 0                       -0.47291409                  -0.4396042
## Lag 100                     -0.45309828                  -0.4158969
## Lag 500                     -0.40783101                  -0.3577962
## Lag 1000                    -0.40278702                  -0.3301300
## Lag 5000                    -0.06076514                  -0.0490055
##
## , , traitbwt.2:traitbwt.1.animal
##
##          traittarsus.1:traittarsus.1.animal traitbwt.1:traittarsus.1.animal
## Lag 0                            0.23631479                      0.42935174
## Lag 100                          0.19631829                      0.33111043
## Lag 500                          0.13140023                      0.20166811
## Lag 1000                         0.13084790                      0.23051272
## Lag 5000                        -0.05046358                      0.04857134
##          traittarsus.2:traittarsus.1.animal traitbwt.2:traittarsus.1.animal
## Lag 0                             0.4651159                       0.6478170
## Lag 100                           0.4250027                       0.5751741
## Lag 500                           0.3644232                       0.4605468
## Lag 1000                          0.3695356                       0.4130944
## Lag 5000                         -0.0748654                      -0.1705451
##          traittarsus.1:traitbwt.1.animal traitbwt.1:traitbwt.1.animal
## Lag 0                         0.42935174                   0.50673141
## Lag 100                       0.33111043                   0.36623376
## Lag 500                       0.20166811                   0.24599792
## Lag 1000                      0.23051272                   0.26598499
## Lag 5000                      0.04857134                   0.06879203
##          traittarsus.2:traitbwt.1.animal traitbwt.2:traitbwt.1.animal
## Lag 0                         0.75320258                   1.00000000
## Lag 100                       0.64643730                   0.80429897
## Lag 500                       0.48359147                   0.55454840
## Lag 1000                      0.43668798                   0.44468678
## Lag 5000                      0.08606661                  -0.01807979
##          traittarsus.1:traittarsus.2.animal traitbwt.1:traittarsus.2.animal
## Lag 0                             0.4651159                      0.75320258
## Lag 100                           0.4250027                      0.64643730
## Lag 500                           0.3644232                      0.48359147
## Lag 1000                          0.3695356                      0.43668798
## Lag 5000                         -0.0748654                      0.08606661
##          traittarsus.2:traittarsus.2.animal traitbwt.2:traittarsus.2.animal
```

```
## Lag 0                         0.35637772                       0.518702070
## Lag 100                       0.34579510                       0.481108274
## Lag 500                       0.32649959                       0.434843612
## Lag 1000                      0.37931051                       0.436821292
## Lag 5000                      0.03852246                       0.006399124
##          traittarsus.1:traitbwt.2.animal traitbwt.1:traitbwt.2.animal
## Lag 0                          0.6478170                   1.00000000
## Lag 100                        0.5751741                   0.80429897
## Lag 500                        0.4605468                   0.55454840
## Lag 1000                       0.4130944                   0.44468678
## Lag 5000                      -0.1705451                  -0.01807979
##          traittarsus.2:traitbwt.2.animal traitbwt.2:traitbwt.2.animal
## Lag 0                        0.518702070                   0.64907876
## Lag 100                      0.481108274                   0.56161598
## Lag 500                      0.434843612                   0.47984513
## Lag 1000                     0.436821292                   0.40938531
## Lag 5000                     0.006399124                  -0.01977366
##          traittarsus.1.byear traitbwt.1.byear traittarsus.2.byear
## Lag 0            0.034800266      0.007431509          0.10446126
## Lag 100          0.051936557     -0.001493245          0.08007660
## Lag 500          0.071129943      0.067797207          0.05478615
## Lag 1000         0.103624443      0.063225351          0.01489821
## Lag 5000        -0.000397122      0.008471637         -0.01350094
##          traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother
## Lag 0         -0.08333568          0.100888337       -0.21005355
## Lag 100       -0.07762909          0.079323546       -0.17806133
## Lag 500       -0.03825641         -0.007478373       -0.11051022
## Lag 1000      -0.02784742          0.017077993       -0.10296388
## Lag 5000       0.04558001          0.022598106        0.02483781
##          traittarsus.2.mother traitbwt.2.mother
## Lag 0             0.018470325      -0.095372303
## Lag 100          -0.002048636      -0.029630368
## Lag 500           0.014260425      -0.034300090
## Lag 1000         -0.048567932       0.067004499
## Lag 5000         -0.025983993       0.005631837
##          traittarsus.1:traittarsus.1.units traitbwt.1:traittarsus.1.units
## Lag 0                          -0.25474138                    -0.36301593
## Lag 100                        -0.21067390                    -0.29399524
## Lag 500                        -0.11042093                    -0.17823668
## Lag 1000                       -0.13264168                    -0.21582496
## Lag 5000                        0.02716341                    -0.03930422
##          traittarsus.2:traittarsus.1.units traitbwt.2:traittarsus.1.units
## Lag 0                           0.06808542                      0.1473359
## Lag 100                         0.08333997                      0.1644163
## Lag 500                         0.11004808                      0.1967466
## Lag 1000                        0.13239890                      0.2087490
## Lag 5000                        0.14121855                      0.1213850
```

```
##           traittarsus.1:traitbwt.1.units traitbwt.1:traitbwt.1.units
## Lag 0                         -0.36301593                 -0.39024104
## Lag 100                       -0.29399524                 -0.30803165
## Lag 500                       -0.17823668                 -0.22428734
## Lag 1000                      -0.21582496                 -0.24800908
## Lag 5000                      -0.03930422                 -0.07900553
##           traittarsus.2:traitbwt.1.units traitbwt.2:traitbwt.1.units
## Lag 0                          0.09800038                   0.1786089
## Lag 100                        0.12840120                   0.2150929
## Lag 500                        0.17479984                   0.2654006
## Lag 1000                       0.19253125                   0.2644751
## Lag 5000                       0.13671344                   0.1087463
##           traittarsus.1:traittarsus.2.units traitbwt.1:traittarsus.2.units
## Lag 0                             0.06808542                     0.09800038
## Lag 100                           0.08333997                     0.12840120
## Lag 500                           0.11004808                     0.17479984
## Lag 1000                          0.13239890                     0.19253125
## Lag 5000                          0.14121855                     0.13671344
##           traittarsus.2:traittarsus.2.units traitbwt.2:traittarsus.2.units
## Lag 0                            -0.38430674                    -0.49584021
## Lag 100                          -0.36892511                    -0.47162690
## Lag 500                          -0.35875583                    -0.43506761
## Lag 1000                         -0.38190122                    -0.42199356
## Lag 5000                         -0.04674851                    -0.01287201
##           traittarsus.1:traitbwt.2.units traitbwt.1:traitbwt.2.units
## Lag 0                           0.1473359                   0.1786089
## Lag 100                         0.1644163                   0.2150929
## Lag 500                         0.1967466                   0.2654006
## Lag 1000                        0.2087490                   0.2644751
## Lag 5000                        0.1213850                   0.1087463
##           traittarsus.2:traitbwt.2.units traitbwt.2:traitbwt.2.units
## Lag 0                         -0.49584021                 -0.56988609
## Lag 100                       -0.47162690                 -0.53124887
## Lag 500                       -0.43506761                 -0.45896948
## Lag 1000                      -0.42199356                 -0.40139643
## Lag 5000                      -0.01287201                  0.01366036
##
## , , traittarsus.1:traittarsus.2.animal
##
##           traittarsus.1:traittarsus.1.animal traitbwt.1:traittarsus.1.animal
## Lag 0                            0.682164176                      0.38634307
## Lag 100                          0.591700877                      0.34935277
## Lag 500                          0.451559860                      0.32828629
## Lag 1000                         0.378373002                      0.27249926
## Lag 5000                         0.004289439                      0.08293975
##           traittarsus.2:traittarsus.1.animal traitbwt.2:traittarsus.1.animal
## Lag 0                             1.00000000                      0.78206164
```

```
## Lag 100                        0.87865696                       0.70110541
## Lag 500                        0.69161215                       0.56910648
## Lag 1000                       0.56265051                       0.44347532
## Lag 5000                      -0.04003226                       0.01712343
##          traittarsus.1:traitbwt.1.animal traitbwt.1:traitbwt.1.animal
## Lag 0                         0.38634307                   0.09679049
## Lag 100                       0.34935277                   0.10017661
## Lag 500                       0.32828629                   0.12775760
## Lag 1000                      0.27249926                   0.11433423
## Lag 5000                      0.08293975                   0.09000388
##          traittarsus.2:traitbwt.1.animal traitbwt.2:traitbwt.1.animal
## Lag 0                         0.71265304                   0.46511587
## Lag 100                       0.64354820                   0.41849123
## Lag 500                       0.54967619                   0.35510793
## Lag 1000                      0.45077032                   0.27846473
## Lag 5000                      0.02763651                   0.08826768
##          traittarsus.1:traittarsus.2.animal traitbwt.1:traittarsus.2.animal
## Lag 0                            1.00000000                      0.71265304
## Lag 100                          0.87865696                      0.64354820
## Lag 500                          0.69161215                      0.54967619
## Lag 1000                         0.56265051                      0.45077032
## Lag 5000                        -0.04003226                      0.02763651
##          traittarsus.2:traittarsus.2.animal traitbwt.2:traittarsus.2.animal
## Lag 0                             0.5942621                       0.5613010
## Lag 100                           0.5307170                       0.5141865
## Lag 500                           0.4678297                       0.4619296
## Lag 1000                          0.4001045                       0.3816713
## Lag 5000                          0.1478270                       0.1489578
##          traittarsus.1:traitbwt.2.animal traitbwt.1:traitbwt.2.animal
## Lag 0                         0.78206164                   0.46511587
## Lag 100                       0.70110541                   0.41849123
## Lag 500                       0.56910648                   0.35510793
## Lag 1000                      0.44347532                   0.27846473
## Lag 5000                      0.01712343                   0.08826768
##          traittarsus.2:traitbwt.2.animal traitbwt.2:traitbwt.2.animal
## Lag 0                          0.5613010                    0.4107260
## Lag 100                        0.5141865                    0.3793894
## Lag 500                        0.4619296                    0.3449678
## Lag 1000                       0.3816713                    0.2731469
## Lag 5000                       0.1489578                    0.1431489
##          traittarsus.1.byear traitbwt.1.byear traittarsus.2.byear
## Lag 0             0.01620495       0.04295234         0.052223393
## Lag 100           0.02029711       0.05648775         0.034069858
## Lag 500           0.04765917       0.03285861         0.007554307
## Lag 1000          0.03767470       0.07587887         0.003191847
## Lag 5000         -0.02249363       0.05599353         0.040862718
##          traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother
```

```
## Lag 0        -0.04161269        -0.102952660        0.04055573
## Lag 100      -0.05474586        -0.077407539        0.03752540
## Lag 500      -0.01536913        -0.009985327        0.02041393
## Lag 1000     -0.02242552        -0.016880479        0.02095844
## Lag 5000      0.05382429         0.093039192       -0.03853343
##           traittarsus.2.mother traitbwt.2.mother
## Lag 0              -0.15988076        0.11172969
## Lag 100            -0.14920373        0.08235912
## Lag 500            -0.10669450        0.07860308
## Lag 1000           -0.09563279        0.04882603
## Lag 5000           -0.03477033        0.03882608
##           traittarsus.1:traittarsus.1.units traitbwt.1:traittarsus.1.units
## Lag 0                           -0.48510213                    -0.35513667
## Lag 100                         -0.43884380                    -0.32128424
## Lag 500                         -0.37005382                    -0.29419691
## Lag 1000                        -0.29875897                    -0.25541065
## Lag 5000                        -0.06651357                    -0.08518695
##           traittarsus.2:traittarsus.1.units traitbwt.2:traittarsus.1.units
## Lag 0                             0.1906441                      0.2159001
## Lag 100                           0.2109187                      0.2292953
## Lag 500                           0.2433902                      0.2525070
## Lag 1000                          0.2670207                      0.2801991
## Lag 5000                          0.2055428                      0.2202544
##           traittarsus.1:traitbwt.1.units traitbwt.1:traitbwt.1.units
## Lag 0                        -0.35513667                 -0.16353731
## Lag 100                      -0.32128424                 -0.14737332
## Lag 500                      -0.29419691                 -0.14406290
## Lag 1000                     -0.25541065                 -0.15449858
## Lag 5000                     -0.08518695                 -0.09726346
##           traittarsus.2:traitbwt.1.units traitbwt.2:traitbwt.1.units
## Lag 0                          0.1588923                   0.1751169
## Lag 100                        0.1763493                   0.1863279
## Lag 500                        0.2035612                   0.2019259
## Lag 1000                       0.2408050                   0.2434815
## Lag 5000                       0.2188271                   0.2190020
##           traittarsus.1:traittarsus.2.units traitbwt.1:traittarsus.2.units
## Lag 0                             0.1906441                      0.1588923
## Lag 100                           0.2109187                      0.1763493
## Lag 500                           0.2433902                      0.2035612
## Lag 1000                          0.2670207                      0.2408050
## Lag 5000                          0.2055428                      0.2188271
##           traittarsus.2:traittarsus.2.units traitbwt.2:traittarsus.2.units
## Lag 0                            -0.5600992                     -0.5208193
## Lag 100                          -0.5263626                     -0.5010452
## Lag 500                          -0.4620756                     -0.4434018
## Lag 1000                         -0.4037773                     -0.3729971
## Lag 5000                         -0.1493219                     -0.1529356
```

```
##          traittarsus.1:traitbwt.2.units traitbwt.1:traitbwt.2.units
## Lag 0                         0.2159001                   0.1751169
## Lag 100                       0.2292953                   0.1863279
## Lag 500                       0.2525070                   0.2019259
## Lag 1000                      0.2801991                   0.2434815
## Lag 5000                      0.2202544                   0.2190020
##          traittarsus.2:traitbwt.2.units traitbwt.2:traitbwt.2.units
## Lag 0                        -0.5208193                  -0.3939711
## Lag 100                      -0.5010452                  -0.3851102
## Lag 500                      -0.4434018                  -0.3487254
## Lag 1000                     -0.3729971                  -0.2846600
## Lag 5000                     -0.1529356                  -0.1449719
##
## , , traitbwt.1:traittarsus.2.animal
##
##          traittarsus.1:traittarsus.1.animal traitbwt.1:traittarsus.1.animal
## Lag 0                            0.43711841                       0.4680554
## Lag 100                          0.38614287                       0.3822935
## Lag 500                          0.32973015                       0.2828059
## Lag 1000                         0.30898433                       0.3053279
## Lag 5000                         0.06068506                       0.1038801
##          traittarsus.2:traittarsus.1.animal traitbwt.2:traittarsus.1.animal
## Lag 0                            0.71265304                      0.59763628
## Lag 100                          0.64495665                      0.53517485
## Lag 500                          0.56187680                      0.46435370
## Lag 1000                         0.52770068                      0.43493174
## Lag 5000                        -0.04596197                     -0.09919957
##          traittarsus.1:traitbwt.1.animal traitbwt.1:traitbwt.1.animal
## Lag 0                          0.4680554                   0.27897287
## Lag 100                        0.3822935                   0.24804717
## Lag 500                        0.2828059                   0.18131034
## Lag 1000                       0.3053279                   0.20383689
## Lag 5000                       0.1038801                   0.07466278
##          traittarsus.2:traitbwt.1.animal traitbwt.2:traitbwt.1.animal
## Lag 0                         1.00000000                   0.75320258
## Lag 100                       0.84412396                   0.63847339
## Lag 500                       0.63408467                   0.47179404
## Lag 1000                      0.55041345                   0.40200369
## Lag 5000                      0.07989653                   0.02863099
##          traittarsus.1:traittarsus.2.animal traitbwt.1:traittarsus.2.animal
## Lag 0                            0.71265304                      1.00000000
## Lag 100                          0.64495665                      0.84412396
## Lag 500                          0.56187680                      0.63408467
## Lag 1000                         0.52770068                      0.55041345
## Lag 5000                        -0.04596197                      0.07989653
##          traittarsus.2:traittarsus.2.animal traitbwt.2:traittarsus.2.animal
## Lag 0                            0.39609257                      0.50085427
```

```
## Lag 100                        0.37249703                      0.45415166
## Lag 500                        0.36147616                      0.41592880
## Lag 1000                       0.38702161                      0.40262387
## Lag 5000                       0.05902071                      0.05027704
##          traittarsus.1:traitbwt.2.animal traitbwt.1:traitbwt.2.animal
## Lag 0                         0.59763628                   0.75320258
## Lag 100                       0.53517485                   0.63847339
## Lag 500                       0.46435370                   0.47179404
## Lag 1000                      0.43493174                   0.40200369
## Lag 5000                     -0.09919957                   0.02863099
##          traittarsus.2:traitbwt.2.animal traitbwt.2:traitbwt.2.animal
## Lag 0                         0.50085427                   0.47574281
## Lag 100                       0.45415166                   0.42373764
## Lag 500                       0.41592880                   0.36577921
## Lag 1000                      0.40262387                   0.31479935
## Lag 5000                      0.05027704                   0.04228229
##          traittarsus.1.byear traitbwt.1.byear traittarsus.2.byear
## Lag 0             0.029421346       0.01370326          0.08861601
## Lag 100           0.024425366       0.01320865          0.06508810
## Lag 500           0.050837464       0.03060238          0.05880699
## Lag 1000          0.065685010       0.04013922          0.02624809
## Lag 5000         -0.006279369       0.01390888          0.06953734
##          traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother
## Lag 0         -0.06566102          0.010266822      -0.002921727
## Lag 100       -0.05957647          0.001133316      -0.025849735
## Lag 500       -0.03310752         -0.035302602      -0.011049599
## Lag 1000      -0.01325750         -0.005132729      -0.030094999
## Lag 5000       0.07737072          0.051936326       0.028222378
##          traittarsus.2.mother traitbwt.2.mother
## Lag 0             -0.01173970       0.004891297
## Lag 100           -0.01984404       0.001495609
## Lag 500           -0.01047992       0.019305497
## Lag 1000          -0.06166849       0.035361493
## Lag 5000          -0.03572076       0.037357859
##          traittarsus.1:traittarsus.1.units traitbwt.1:traittarsus.1.units
## Lag 0                           -0.3729388                     -0.3850991
## Lag 100                         -0.3393916                     -0.3381615
## Lag 500                         -0.2662669                     -0.2603097
## Lag 1000                        -0.2581177                     -0.2862286
## Lag 5000                        -0.1138844                     -0.1255711
##          traittarsus.2:traittarsus.1.units traitbwt.2:traittarsus.1.units
## Lag 0                            0.1304165                      0.1778597
## Lag 100                          0.1523428                      0.1937314
## Lag 500                          0.1726064                      0.2144724
## Lag 1000                         0.1844905                      0.2275146
## Lag 5000                         0.1876933                      0.1730132
##          traittarsus.1:traitbwt.1.units traitbwt.1:traitbwt.1.units
```

```
## Lag 0                   -0.3850991                   -0.2793636
## Lag 100                 -0.3381615                   -0.2451230
## Lag 500                 -0.2603097                   -0.1889420
## Lag 1000                -0.2862286                   -0.2310740
## Lag 5000                -0.1255711                   -0.1098246
##          traittarsus.2:traitbwt.1.units traitbwt.2:traitbwt.1.units
## Lag 0                     0.1142625                   0.1618783
## Lag 100                   0.1516538                   0.1886145
## Lag 500                   0.1942499                   0.2259939
## Lag 1000                  0.1947749                   0.2314168
## Lag 5000                  0.1938069                   0.1610221
##          traittarsus.1:traittarsus.2.units traitbwt.1:traittarsus.2.units
## Lag 0                            0.1304165                      0.1142625
## Lag 100                          0.1523428                      0.1516538
## Lag 500                          0.1726064                      0.1942499
## Lag 1000                         0.1844905                      0.1947749
## Lag 5000                         0.1876933                      0.1938069
##          traittarsus.2:traittarsus.2.units traitbwt.2:traittarsus.2.units
## Lag 0                          -0.41858410                    -0.47291409
## Lag 100                        -0.40815749                    -0.45309828
## Lag 500                        -0.38612479                    -0.40783101
## Lag 1000                       -0.40349965                    -0.40278702
## Lag 5000                       -0.06617356                    -0.06076514
##          traittarsus.1:traitbwt.2.units traitbwt.1:traitbwt.2.units
## Lag 0                     0.1778597                   0.1618783
## Lag 100                   0.1937314                   0.1886145
## Lag 500                   0.2144724                   0.2259939
## Lag 1000                  0.2275146                   0.2314168
## Lag 5000                  0.1730132                   0.1610221
##          traittarsus.2:traitbwt.2.units traitbwt.2:traitbwt.2.units
## Lag 0                   -0.47291409                  -0.4396042
## Lag 100                 -0.45309828                  -0.4158969
## Lag 500                 -0.40783101                  -0.3577962
## Lag 1000                -0.40278702                  -0.3301300
## Lag 5000                -0.06076514                  -0.0490055
##
## , , traittarsus.2:traittarsus.2.animal
##
##          traittarsus.1:traittarsus.1.animal traitbwt.1:traittarsus.1.animal
## Lag 0                           0.107806440                      0.09660116
## Lag 100                         0.063335645                      0.07671143
## Lag 500                         0.015199121                      0.08067887
## Lag 1000                       -0.004286261                      0.05833877
## Lag 5000                       -0.070723679                     -0.04217947
##          traittarsus.2:traittarsus.1.animal traitbwt.2:traittarsus.1.animal
## Lag 0                             0.5942621                       0.5635407
## Lag 100                           0.5173844                       0.5077019
```

```
## Lag 500                      0.4100415                          0.4261910
## Lag 1000                     0.3053499                          0.3088610
## Lag 5000                    -0.2062339                         -0.1851005
##          traittarsus.1:traitbwt.1.animal traitbwt.1:traitbwt.1.animal
## Lag 0                         0.09660116                   0.10548333
## Lag 100                       0.07671143                   0.09974202
## Lag 500                       0.08067887                   0.11354731
## Lag 1000                      0.05833877                   0.12159525
## Lag 5000                     -0.04217947                  -0.06338610
##          traittarsus.2:traitbwt.1.animal traitbwt.2:traitbwt.1.animal
## Lag 0                          0.3960926                    0.3563777
## Lag 100                        0.3697695                    0.3333969
## Lag 500                        0.3480333                    0.3176505
## Lag 1000                       0.2823012                    0.2658600
## Lag 5000                      -0.2062348                   -0.1460308
##          traittarsus.1:traittarsus.2.animal traitbwt.1:traittarsus.2.animal
## Lag 0                             0.5942621                       0.3960926
## Lag 100                           0.5173844                       0.3697695
## Lag 500                           0.4100415                       0.3480333
## Lag 1000                          0.3053499                       0.2823012
## Lag 5000                         -0.2062339                      -0.2062348
##          traittarsus.2:traittarsus.2.animal traitbwt.2:traittarsus.2.animal
## Lag 0                            1.00000000                      0.89913093
## Lag 100                          0.90510783                      0.83322028
## Lag 500                          0.73781155                      0.70412544
## Lag 1000                         0.57269345                      0.54745411
## Lag 5000                        -0.03830606                     -0.09250669
##          traittarsus.1:traitbwt.2.animal traitbwt.1:traitbwt.2.animal
## Lag 0                          0.5635407                    0.3563777
## Lag 100                        0.5077019                    0.3333969
## Lag 500                        0.4261910                    0.3176505
## Lag 1000                       0.3088610                    0.2658600
## Lag 5000                      -0.1851005                   -0.1460308
##          traittarsus.2:traitbwt.2.animal traitbwt.2:traitbwt.2.animal
## Lag 0                         0.89913093                    0.6844205
## Lag 100                       0.83322028                    0.6434324
## Lag 500                       0.70412544                    0.5640206
## Lag 1000                      0.54745411                    0.4452587
## Lag 5000                     -0.09250669                   -0.0996112
##          traittarsus.1.byear traitbwt.1.byear traittarsus.2.byear
## Lag 0            0.035961574     -0.017469135         0.007171364
## Lag 100          0.026817555     -0.002104493         0.011633070
## Lag 500          0.008446146     -0.011130916         0.013837207
## Lag 1000         0.029054326      0.040567400         0.023793648
## Lag 5000        -0.032575030      0.020439004        -0.049218434
##          traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother
## Lag 0         -0.08333086           0.04651404       -0.06375729
```

```
## Lag 100      -0.08053153          0.06577446       -0.05659105
## Lag 500      -0.03847864          0.11200938       -0.07300512
## Lag 1000     -0.04249559          0.08134977       -0.07101148
## Lag 5000      0.07016400          0.02226530        0.03188352
##           traittarsus.2.mother traitbwt.2.mother
## Lag 0              -0.34477064        0.15871038
## Lag 100            -0.31220276        0.12040861
## Lag 500            -0.20777383        0.08824805
## Lag 1000           -0.12481403        0.05105578
## Lag 5000            0.01048624        0.01454861
##           traittarsus.1:traittarsus.1.units traitbwt.1:traittarsus.1.units
## Lag 0                           -0.10376953                    -0.10398125
## Lag 100                         -0.07294547                    -0.07699566
## Lag 500                         -0.06977230                    -0.08979287
## Lag 1000                        -0.03903802                    -0.06150263
## Lag 5000                         0.09531506                     0.08613972
##           traittarsus.2:traittarsus.1.units traitbwt.2:traittarsus.1.units
## Lag 0                            0.18812698                     0.21480017
## Lag 100                          0.19528250                     0.21914991
## Lag 500                          0.19556551                     0.21256430
## Lag 1000                         0.18892755                     0.20764610
## Lag 5000                         0.06665558                     0.07468684
##           traittarsus.1:traitbwt.1.units traitbwt.1:traitbwt.1.units
## Lag 0                        -0.10398125                 -0.10182068
## Lag 100                      -0.07699566                 -0.08777589
## Lag 500                      -0.08979287                 -0.09511315
## Lag 1000                     -0.06150263                 -0.09765668
## Lag 5000                      0.08613972                  0.05634093
##           traittarsus.2:traitbwt.1.units traitbwt.2:traitbwt.1.units
## Lag 0                         0.22270138                  0.23393547
## Lag 100                       0.22287169                  0.23382912
## Lag 500                       0.20351827                  0.21079497
## Lag 1000                      0.20537971                  0.21383439
## Lag 5000                      0.03798515                  0.03641653
##           traittarsus.1:traittarsus.2.units traitbwt.1:traittarsus.2.units
## Lag 0                            0.18812698                     0.22270138
## Lag 100                          0.19528250                     0.22287169
## Lag 500                          0.19556551                     0.20351827
## Lag 1000                         0.18892755                     0.20537971
## Lag 5000                         0.06665558                     0.03798515
##           traittarsus.2:traittarsus.2.units traitbwt.2:traittarsus.2.units
## Lag 0                            -0.9107369                    -0.84107771
## Lag 100                          -0.8633544                    -0.80717702
## Lag 500                          -0.7252004                    -0.68217338
## Lag 1000                         -0.5917870                    -0.54946518
## Lag 5000                          0.0476902                     0.09830838
##           traittarsus.1:traitbwt.2.units traitbwt.1:traitbwt.2.units
```

```
## Lag 0                     0.21480017                  0.23393547
## Lag 100                   0.21914991                  0.23382912
## Lag 500                   0.21256430                  0.21079497
## Lag 1000                  0.20764610                  0.21383439
## Lag 5000                  0.07468684                  0.03641653
##          traittarsus.2:traitbwt.2.units traitbwt.2:traitbwt.2.units
## Lag 0                    -0.84107771                  -0.6791085
## Lag 100                  -0.80717702                  -0.6539764
## Lag 500                  -0.68217338                  -0.5583969
## Lag 1000                 -0.54946518                  -0.4464232
## Lag 5000                  0.09830838                   0.1028304
##
## , , traitbwt.2:traittarsus.2.animal
##
##          traittarsus.1:traittarsus.1.animal traitbwt.1:traittarsus.1.animal
## Lag 0                            0.12397199                      0.14997594
## Lag 100                          0.08643519                      0.11314881
## Lag 500                          0.03605225                      0.09323271
## Lag 1000                         0.03084094                      0.10586940
## Lag 5000                        -0.09632022                     -0.03936224
##          traittarsus.2:traittarsus.1.animal traitbwt.2:traittarsus.1.animal
## Lag 0                             0.5613010                       0.6729793
## Lag 100                           0.5033508                       0.6010903
## Lag 500                           0.4274531                       0.5133373
## Lag 1000                          0.3517565                       0.4086869
## Lag 5000                         -0.1677216                      -0.1581302
##          traittarsus.1:traitbwt.1.animal traitbwt.1:traitbwt.1.animal
## Lag 0                         0.14997594                   0.17131088
## Lag 100                       0.11314881                   0.15721379
## Lag 500                       0.09323271                   0.15933093
## Lag 1000                      0.10586940                   0.18501406
## Lag 5000                     -0.03936224                  -0.01791672
##          traittarsus.2:traitbwt.1.animal traitbwt.2:traitbwt.1.animal
## Lag 0                          0.5008543                   0.51870207
## Lag 100                        0.4453244                   0.46669360
## Lag 500                        0.3907627                   0.41453930
## Lag 1000                       0.3366895                   0.35501264
## Lag 5000                      -0.1140445                  -0.07692479
##          traittarsus.1:traittarsus.2.animal traitbwt.1:traittarsus.2.animal
## Lag 0                             0.5613010                       0.5008543
## Lag 100                           0.5033508                       0.4453244
## Lag 500                           0.4274531                       0.3907627
## Lag 1000                          0.3517565                       0.3366895
## Lag 5000                         -0.1677216                      -0.1140445
##          traittarsus.2:traittarsus.2.animal traitbwt.2:traittarsus.2.animal
## Lag 0                             0.8991309                      1.00000000
## Lag 100                           0.8359176                      0.91646465
```

```
## Lag 500                           0.7187715                           0.77900191
## Lag 1000                          0.5982337                           0.63306113
## Lag 5000                          0.0176654                          -0.03136451
##          traittarsus.1:traitbwt.2.animal traitbwt.1:traitbwt.2.animal
## Lag 0                          0.6729793                   0.51870207
## Lag 100                        0.6010903                   0.46669360
## Lag 500                        0.5133373                   0.41453930
## Lag 1000                       0.4086869                   0.35501264
## Lag 5000                      -0.1581302                  -0.07692479
##          traittarsus.2:traitbwt.2.animal traitbwt.2:traitbwt.2.animal
## Lag 0                         1.00000000                   0.89818763
## Lag 100                       0.91646465                   0.82112793
## Lag 500                       0.77900191                   0.69592684
## Lag 1000                      0.63306113                   0.55065244
## Lag 5000                     -0.03136451                  -0.04949222
##          traittarsus.1.byear traitbwt.1.byear traittarsus.2.byear
## Lag 0             0.05124741      0.001646162          0.04068399
## Lag 100           0.04921037      0.008930910          0.03759685
## Lag 500           0.03899327      0.015514352          0.02580930
## Lag 1000          0.06406637      0.051682789          0.02147033
## Lag 5000         -0.01137788      0.015052216         -0.04729885
##          traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother
## Lag 0         -0.12402916           0.08639137       -0.09704390
## Lag 100       -0.10713277           0.09204331       -0.10427670
## Lag 500       -0.07124572           0.09145340       -0.11605857
## Lag 1000      -0.06554488           0.09437629       -0.10182520
## Lag 5000       0.06888625           0.02727995        0.01776003
##          traittarsus.2.mother traitbwt.2.mother
## Lag 0             -0.15610253        0.09891371
## Lag 100           -0.16408367        0.08304541
## Lag 500           -0.12517718        0.04261766
## Lag 1000          -0.09948987        0.04824881
## Lag 5000          -0.01179365       -0.01278893
##          traittarsus.1:traittarsus.1.units traitbwt.1:traittarsus.1.units
## Lag 0                          -0.14515627                     -0.1467921
## Lag 100                        -0.11636785                     -0.1156256
## Lag 500                        -0.08159624                     -0.1042741
## Lag 1000                       -0.07861755                     -0.1076860
## Lag 5000                        0.10186075                      0.0712461
##          traittarsus.2:traittarsus.1.units traitbwt.2:traittarsus.1.units
## Lag 0                           0.18051752                     0.23807593
## Lag 100                         0.18953377                     0.24534120
## Lag 500                         0.17920764                     0.22900261
## Lag 1000                        0.16794260                     0.21104881
## Lag 5000                        0.04389169                     0.05181362
##          traittarsus.1:traitbwt.1.units traitbwt.1:traitbwt.1.units
## Lag 0                        -0.1467921                 -0.14376430
```

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## Lag 100                  -0.1156256              -0.12366939
## Lag 500                  -0.1042741              -0.12078005
## Lag 1000                 -0.1076860              -0.15700540
## Lag 5000                  0.0712461               0.01799705
##          traittarsus.2:traitbwt.1.units traitbwt.2:traitbwt.1.units
## Lag 0                       0.21778240               0.25816273
## Lag 100                     0.22684710               0.26502282
## Lag 500                     0.20506975               0.23751874
## Lag 1000                    0.19012136               0.21960899
## Lag 5000                    0.02816484               0.03038383
##          traittarsus.1:traittarsus.2.units traitbwt.1:traittarsus.2.units
## Lag 0                          0.18051752                     0.21778240
## Lag 100                        0.18953377                     0.22684710
## Lag 500                        0.17920764                     0.20506975
## Lag 1000                       0.16794260                     0.19012136
## Lag 5000                       0.04389169                     0.02816484
##          traittarsus.2:traittarsus.2.units traitbwt.2:traittarsus.2.units
## Lag 0                       -0.8750125593                    -0.93853010
## Lag 100                     -0.8368578282                    -0.89227332
## Lag 500                     -0.7287281819                    -0.75764556
## Lag 1000                    -0.6175608959                    -0.62307537
## Lag 5000                    -0.0008665459                     0.04348967
##          traittarsus.1:traitbwt.2.units traitbwt.1:traitbwt.2.units
## Lag 0                       0.23807593               0.25816273
## Lag 100                     0.24534120               0.26502282
## Lag 500                     0.22900261               0.23751874
## Lag 1000                    0.21104881               0.21960899
## Lag 5000                    0.05181362               0.03038383
##          traittarsus.2:traitbwt.2.units traitbwt.2:traitbwt.2.units
## Lag 0                      -0.93853010              -0.85888343
## Lag 100                    -0.89227332              -0.81357341
## Lag 500                    -0.75764556              -0.67868373
## Lag 1000                   -0.62307537              -0.54366192
## Lag 5000                    0.04348967               0.05718606
##
## , , traittarsus.1:traitbwt.2.animal
##
##          traittarsus.1:traittarsus.1.animal traitbwt.1:traittarsus.1.animal
## Lag 0                            0.51576277                      0.52342220
## Lag 100                          0.44159056                      0.43580048
## Lag 500                          0.30785687                      0.33037079
## Lag 1000                         0.24390874                      0.26926704
## Lag 5000                        -0.05005481                      0.04687804
##          traittarsus.2:traittarsus.1.animal traitbwt.2:traittarsus.1.animal
## Lag 0                           0.782061640                      1.00000000
## Lag 100                         0.696299215                      0.87453824
## Lag 500                         0.538889846                      0.65219311
```

```
## Lag 1000                      0.445389577                        0.48957859
## Lag 5000                     -0.006519724                        0.01842864
##            traittarsus.1:traitbwt.1.animal traitbwt.1:traitbwt.1.animal
## Lag 0                           0.52342220                   0.32999449
## Lag 100                         0.43580048                   0.28148773
## Lag 500                         0.33037079                   0.26589289
## Lag 1000                        0.26926704                   0.24323871
## Lag 5000                        0.04687804                   0.09890983
##            traittarsus.2:traitbwt.1.animal traitbwt.2:traitbwt.1.animal
## Lag 0                           0.59763628                    0.6478170
## Lag 100                         0.52643466                    0.5573055
## Lag 500                         0.44551868                    0.4418750
## Lag 1000                        0.37736602                    0.3442054
## Lag 5000                        0.08285167                    0.1125165
##            traittarsus.1:traittarsus.2.animal traitbwt.1:traittarsus.2.animal
## Lag 0                             0.782061640                      0.59763628
## Lag 100                           0.696299215                      0.52643466
## Lag 500                           0.538889846                      0.44551868
## Lag 1000                          0.445389577                      0.37736602
## Lag 5000                         -0.006519724                      0.08285167
##            traittarsus.2:traittarsus.2.animal traitbwt.2:traittarsus.2.animal
## Lag 0                               0.5635407                       0.6729793
## Lag 100                             0.5125673                       0.6052812
## Lag 500                             0.4465910                       0.5277439
## Lag 1000                            0.4070664                       0.4538221
## Lag 5000                            0.1850370                       0.1792542
##            traittarsus.1:traitbwt.2.animal traitbwt.1:traitbwt.2.animal
## Lag 0                           1.00000000                    0.6478170
## Lag 100                         0.87453824                    0.5573055
## Lag 500                         0.65219311                    0.4418750
## Lag 1000                        0.48957859                    0.3442054
## Lag 5000                        0.01842864                    0.1125165
##            traittarsus.2:traitbwt.2.animal traitbwt.2:traitbwt.2.animal
## Lag 0                            0.6729793                    0.6191252
## Lag 100                          0.6052812                    0.5529718
## Lag 500                          0.5277439                    0.4729419
## Lag 1000                         0.4538221                    0.3884032
## Lag 5000                         0.1792542                    0.1542326
##            traittarsus.1.byear traitbwt.1.byear traittarsus.2.byear
## Lag 0              0.063463728       0.02730871         0.051964042
## Lag 100            0.066558472       0.03961464         0.040967359
## Lag 500            0.076728186       0.05374642        -0.012930939
## Lag 1000           0.100842393       0.09752083        -0.062954038
## Lag 5000          -0.006751012       0.04984406         0.002434151
##            traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother
## Lag 0           -0.09337461           0.02006907       -0.06942502
## Lag 100         -0.09001277           0.02763705       -0.07262374
```

```
## Lag 500      -0.04869538           0.02000750       -0.09505843
## Lag 1000     -0.05831890           0.02560894       -0.08617648
## Lag 5000      0.04246982           0.06392166       -0.03722137
##          traittarsus.2.mother traitbwt.2.mother
## Lag 0           -0.026436938        0.04826105
## Lag 100         -0.041329867        0.04078039
## Lag 500         -0.028290001        0.03056152
## Lag 1000        -0.036326123        0.04300492
## Lag 5000        -0.008439906        0.00653221
##          traittarsus.1:traittarsus.1.units traitbwt.1:traittarsus.1.units
## Lag 0                        -0.3969629895                    -0.44235441
## Lag 100                      -0.3457725771                    -0.37788435
## Lag 500                      -0.2409128696                    -0.27612777
## Lag 1000                     -0.2064627528                    -0.23939733
## Lag 5000                     -0.0008284304                    -0.05932951
##          traittarsus.2:traittarsus.1.units traitbwt.2:traittarsus.1.units
## Lag 0                            0.1332860                      0.1894193
## Lag 100                          0.1542105                      0.2129929
## Lag 500                          0.1772766                      0.2426247
## Lag 1000                         0.1956287                      0.2577964
## Lag 5000                         0.1561845                      0.1623293
##          traittarsus.1:traitbwt.1.units traitbwt.1:traitbwt.1.units
## Lag 0                       -0.44235441                  -0.3300209
## Lag 100                     -0.37788435                  -0.2868342
## Lag 500                     -0.27612777                  -0.2200427
## Lag 1000                    -0.23939733                  -0.2196364
## Lag 5000                    -0.05932951                  -0.1105188
##          traittarsus.2:traitbwt.1.units traitbwt.2:traitbwt.1.units
## Lag 0                         0.1392793                   0.1845588
## Lag 100                       0.1618837                   0.2068320
## Lag 500                       0.1824833                   0.2322375
## Lag 1000                      0.2062851                   0.2545405
## Lag 5000                      0.1708879                   0.1679111
##          traittarsus.1:traittarsus.2.units traitbwt.1:traittarsus.2.units
## Lag 0                            0.1332860                      0.1392793
## Lag 100                          0.1542105                      0.1618837
## Lag 500                          0.1772766                      0.1824833
## Lag 1000                         0.1956287                      0.2062851
## Lag 5000                         0.1561845                      0.1708879
##          traittarsus.2:traittarsus.2.units traitbwt.2:traittarsus.2.units
## Lag 0                           -0.5541670                     -0.6200400
## Lag 100                         -0.5163721                     -0.5823652
## Lag 500                         -0.4591717                     -0.5082023
## Lag 1000                        -0.4081394                     -0.4277328
## Lag 5000                        -0.1850899                     -0.1717978
##          traittarsus.1:traitbwt.2.units traitbwt.1:traitbwt.2.units
## Lag 0                         0.1894193                   0.1845588
```

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## Lag 100                     0.2129929                     0.2068320
## Lag 500                     0.2426247                     0.2322375
## Lag 1000                    0.2577964                     0.2545405
## Lag 5000                    0.1623293                     0.1679111
##          traittarsus.2:traitbwt.2.units traitbwt.2:traitbwt.2.units
## Lag 0                      -0.6200400                    -0.5649761
## Lag 100                    -0.5823652                    -0.5353605
## Lag 500                    -0.5082023                    -0.4627844
## Lag 1000                   -0.4277328                    -0.3777429
## Lag 5000                   -0.1717978                    -0.1507443
##
## , , traitbwt.1:traitbwt.2.animal
##
##          traittarsus.1:traittarsus.1.animal traitbwt.1:traittarsus.1.animal
## Lag 0                            0.23631479                      0.42935174
## Lag 100                          0.19631829                      0.33111043
## Lag 500                          0.13140023                      0.20166811
## Lag 1000                         0.13084790                      0.23051272
## Lag 5000                        -0.05046358                      0.04857134
##          traittarsus.2:traittarsus.1.animal traitbwt.2:traittarsus.1.animal
## Lag 0                             0.4651159                       0.6478170
## Lag 100                           0.4250027                       0.5751741
## Lag 500                           0.3644232                       0.4605468
## Lag 1000                          0.3695356                       0.4130944
## Lag 5000                         -0.0748654                      -0.1705451
##          traittarsus.1:traitbwt.1.animal traitbwt.1:traitbwt.1.animal
## Lag 0                         0.42935174                   0.50673141
## Lag 100                       0.33111043                   0.36623376
## Lag 500                       0.20166811                   0.24599792
## Lag 1000                      0.23051272                   0.26598499
## Lag 5000                      0.04857134                   0.06879203
##          traittarsus.2:traitbwt.1.animal traitbwt.2:traitbwt.1.animal
## Lag 0                         0.75320258                   1.00000000
## Lag 100                       0.64643730                   0.80429897
## Lag 500                       0.48359147                   0.55454840
## Lag 1000                      0.43668798                   0.44468678
## Lag 5000                      0.08606661                  -0.01807979
##          traittarsus.1:traittarsus.2.animal traitbwt.1:traittarsus.2.animal
## Lag 0                             0.4651159                      0.75320258
## Lag 100                           0.4250027                      0.64643730
## Lag 500                           0.3644232                      0.48359147
## Lag 1000                          0.3695356                      0.43668798
## Lag 5000                         -0.0748654                      0.08606661
##          traittarsus.2:traittarsus.2.animal traitbwt.2:traittarsus.2.animal
## Lag 0                            0.35637772                     0.518702070
## Lag 100                          0.34579510                     0.481108274
## Lag 500                          0.32649959                     0.434843612
```

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## Lag 1000                    0.37931051                      0.436821292
## Lag 5000                    0.03852246                      0.006399124
##            traittarsus.1:traitbwt.2.animal traitbwt.1:traitbwt.2.animal
## Lag 0                            0.6478170                   1.00000000
## Lag 100                          0.5751741                   0.80429897
## Lag 500                          0.4605468                   0.55454840
## Lag 1000                         0.4130944                   0.44468678
## Lag 5000                        -0.1705451                  -0.01807979
##            traittarsus.2:traitbwt.2.animal traitbwt.2:traitbwt.2.animal
## Lag 0                          0.518702070                   0.64907876
## Lag 100                        0.481108274                   0.56161598
## Lag 500                        0.434843612                   0.47984513
## Lag 1000                       0.436821292                   0.40938531
## Lag 5000                       0.006399124                  -0.01977366
##            traittarsus.1.byear traitbwt.1.byear traittarsus.2.byear
## Lag 0              0.034800266      0.007431509          0.10446126
## Lag 100            0.051936557     -0.001493245          0.08007660
## Lag 500            0.071129943      0.067797207          0.05478615
## Lag 1000           0.103624443      0.063225351          0.01489821
## Lag 5000          -0.000397122      0.008471637         -0.01350094
##            traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother
## Lag 0           -0.08333568          0.100888337       -0.21005355
## Lag 100         -0.07762909          0.079323546       -0.17806133
## Lag 500         -0.03825641         -0.007478373       -0.11051022
## Lag 1000        -0.02784742          0.017077993       -0.10296388
## Lag 5000         0.04558001          0.022598106        0.02483781
##            traittarsus.2.mother traitbwt.2.mother
## Lag 0               0.018470325      -0.095372303
## Lag 100            -0.002048636      -0.029630368
## Lag 500             0.014260425      -0.034300090
## Lag 1000           -0.048567932       0.067004499
## Lag 5000           -0.025983993       0.005631837
##            traittarsus.1:traittarsus.1.units traitbwt.1:traittarsus.1.units
## Lag 0                             -0.25474138                    -0.36301593
## Lag 100                           -0.21067390                    -0.29399524
## Lag 500                           -0.11042093                    -0.17823668
## Lag 1000                          -0.13264168                    -0.21582496
## Lag 5000                           0.02716341                    -0.03930422
##            traittarsus.2:traittarsus.1.units traitbwt.2:traittarsus.1.units
## Lag 0                              0.06808542                      0.1473359
## Lag 100                            0.08333997                      0.1644163
## Lag 500                            0.11004808                      0.1967466
## Lag 1000                           0.13239890                      0.2087490
## Lag 5000                           0.14121855                      0.1213850
##            traittarsus.1:traitbwt.1.units traitbwt.1:traitbwt.1.units
## Lag 0                         -0.36301593                 -0.39024104
## Lag 100                       -0.29399524                 -0.30803165
```

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## Lag 500                    -0.17823668                 -0.22428734
## Lag 1000                   -0.21582496                 -0.24800908
## Lag 5000                   -0.03930422                 -0.07900553
##          traittarsus.2:traitbwt.1.units traitbwt.2:traitbwt.1.units
## Lag 0                       0.09800038                   0.1786089
## Lag 100                     0.12840120                   0.2150929
## Lag 500                     0.17479984                   0.2654006
## Lag 1000                    0.19253125                   0.2644751
## Lag 5000                    0.13671344                   0.1087463
##          traittarsus.1:traittarsus.2.units traitbwt.1:traittarsus.2.units
## Lag 0                          0.06808542                     0.09800038
## Lag 100                        0.08333997                     0.12840120
## Lag 500                        0.11004808                     0.17479984
## Lag 1000                       0.13239890                     0.19253125
## Lag 5000                       0.14121855                     0.13671344
##          traittarsus.2:traittarsus.2.units traitbwt.2:traittarsus.2.units
## Lag 0                         -0.38430674                    -0.49584021
## Lag 100                       -0.36892511                    -0.47162690
## Lag 500                       -0.35875583                    -0.43506761
## Lag 1000                      -0.38190122                    -0.42199356
## Lag 5000                      -0.04674851                    -0.01287201
##          traittarsus.1:traitbwt.2.units traitbwt.1:traitbwt.2.units
## Lag 0                        0.1473359                   0.1786089
## Lag 100                      0.1644163                   0.2150929
## Lag 500                      0.1967466                   0.2654006
## Lag 1000                     0.2087490                   0.2644751
## Lag 5000                     0.1213850                   0.1087463
##          traittarsus.2:traitbwt.2.units traitbwt.2:traitbwt.2.units
## Lag 0                      -0.49584021                 -0.56988609
## Lag 100                    -0.47162690                 -0.53124887
## Lag 500                    -0.43506761                 -0.45896948
## Lag 1000                   -0.42199356                 -0.40139643
## Lag 5000                   -0.01287201                  0.01366036
##
## , , traittarsus.2:traitbwt.2.animal
##
##          traittarsus.1:traittarsus.1.animal traitbwt.1:traittarsus.1.animal
## Lag 0                            0.12397199                      0.14997594
## Lag 100                          0.08643519                      0.11314881
## Lag 500                          0.03605225                      0.09323271
## Lag 1000                         0.03084094                      0.10586940
## Lag 5000                        -0.09632022                     -0.03936224
##          traittarsus.2:traittarsus.1.animal traitbwt.2:traittarsus.1.animal
## Lag 0                             0.5613010                       0.6729793
## Lag 100                           0.5033508                       0.6010903
## Lag 500                           0.4274531                       0.5133373
## Lag 1000                          0.3517565                       0.4086869
```

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## Lag 5000                       -0.1677216                        -0.1581302
##          traittarsus.1:traitbwt.1.animal traitbwt.1:traitbwt.1.animal
## Lag 0                         0.14997594                   0.17131088
## Lag 100                       0.11314881                   0.15721379
## Lag 500                       0.09323271                   0.15933093
## Lag 1000                      0.10586940                   0.18501406
## Lag 5000                     -0.03936224                  -0.01791672
##          traittarsus.2:traitbwt.1.animal traitbwt.2:traitbwt.1.animal
## Lag 0                          0.5008543                   0.51870207
## Lag 100                        0.4453244                   0.46669360
## Lag 500                        0.3907627                   0.41453930
## Lag 1000                       0.3366895                   0.35501264
## Lag 5000                      -0.1140445                  -0.07692479
##          traittarsus.1:traittarsus.2.animal traitbwt.1:traittarsus.2.animal
## Lag 0                             0.5613010                       0.5008543
## Lag 100                           0.5033508                       0.4453244
## Lag 500                           0.4274531                       0.3907627
## Lag 1000                          0.3517565                       0.3366895
## Lag 5000                         -0.1677216                      -0.1140445
##          traittarsus.2:traittarsus.2.animal traitbwt.2:traittarsus.2.animal
## Lag 0                             0.8991309                      1.00000000
## Lag 100                           0.8359176                      0.91646465
## Lag 500                           0.7187715                      0.77900191
## Lag 1000                          0.5982337                      0.63306113
## Lag 5000                          0.0176654                     -0.03136451
##          traittarsus.1:traitbwt.2.animal traitbwt.1:traitbwt.2.animal
## Lag 0                          0.6729793                   0.51870207
## Lag 100                        0.6010903                   0.46669360
## Lag 500                        0.5133373                   0.41453930
## Lag 1000                       0.4086869                   0.35501264
## Lag 5000                      -0.1581302                  -0.07692479
##          traittarsus.2:traitbwt.2.animal traitbwt.2:traitbwt.2.animal
## Lag 0                         1.00000000                   0.89818763
## Lag 100                       0.91646465                   0.82112793
## Lag 500                       0.77900191                   0.69592684
## Lag 1000                      0.63306113                   0.55065244
## Lag 5000                     -0.03136451                  -0.04949222
##          traittarsus.1.byear traitbwt.1.byear traittarsus.2.byear
## Lag 0             0.05124741      0.001646162          0.04068399
## Lag 100           0.04921037      0.008930910          0.03759685
## Lag 500           0.03899327      0.015514352          0.02580930
## Lag 1000          0.06406637      0.051682789          0.02147033
## Lag 5000         -0.01137788      0.015052216         -0.04729885
##          traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother
## Lag 0         -0.12402916           0.08639137       -0.09704390
## Lag 100       -0.10713277           0.09204331       -0.10427670
## Lag 500       -0.07124572           0.09145340       -0.11605857
```

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## Lag 1000      -0.06554488          0.09437629       -0.10182520
## Lag 5000       0.06888625          0.02727995        0.01776003
##           traittarsus.2.mother traitbwt.2.mother
## Lag 0              -0.15610253        0.09891371
## Lag 100            -0.16408367        0.08304541
## Lag 500            -0.12517718        0.04261766
## Lag 1000           -0.09948987        0.04824881
## Lag 5000           -0.01179365       -0.01278893
##           traittarsus.1:traittarsus.1.units traitbwt.1:traittarsus.1.units
## Lag 0                           -0.14515627                     -0.1467921
## Lag 100                         -0.11636785                     -0.1156256
## Lag 500                         -0.08159624                     -0.1042741
## Lag 1000                        -0.07861755                     -0.1076860
## Lag 5000                         0.10186075                      0.0712461
##           traittarsus.2:traittarsus.1.units traitbwt.2:traittarsus.1.units
## Lag 0                            0.18051752                     0.23807593
## Lag 100                          0.18953377                     0.24534120
## Lag 500                          0.17920764                     0.22900261
## Lag 1000                         0.16794260                     0.21104881
## Lag 5000                         0.04389169                     0.05181362
##           traittarsus.1:traitbwt.1.units traitbwt.1:traitbwt.1.units
## Lag 0                         -0.1467921                 -0.14376430
## Lag 100                       -0.1156256                 -0.12366939
## Lag 500                       -0.1042741                 -0.12078005
## Lag 1000                      -0.1076860                 -0.15700540
## Lag 5000                       0.0712461                  0.01799705
##           traittarsus.2:traitbwt.1.units traitbwt.2:traitbwt.1.units
## Lag 0                         0.21778240                  0.25816273
## Lag 100                       0.22684710                  0.26502282
## Lag 500                       0.20506975                  0.23751874
## Lag 1000                      0.19012136                  0.21960899
## Lag 5000                      0.02816484                  0.03038383
##           traittarsus.1:traittarsus.2.units traitbwt.1:traittarsus.2.units
## Lag 0                            0.18051752                     0.21778240
## Lag 100                          0.18953377                     0.22684710
## Lag 500                          0.17920764                     0.20506975
## Lag 1000                         0.16794260                     0.19012136
## Lag 5000                         0.04389169                     0.02816484
##           traittarsus.2:traittarsus.2.units traitbwt.2:traittarsus.2.units
## Lag 0                         -0.8750125593                    -0.93853010
## Lag 100                       -0.8368578282                    -0.89227332
## Lag 500                       -0.7287281819                    -0.75764556
## Lag 1000                      -0.6175608959                    -0.62307537
## Lag 5000                      -0.0008665459                     0.04348967
##           traittarsus.1:traitbwt.2.units traitbwt.1:traitbwt.2.units
## Lag 0                         0.23807593                  0.25816273
## Lag 100                       0.24534120                  0.26502282
```

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## Lag 500                    0.22900261                   0.23751874
## Lag 1000                   0.21104881                   0.21960899
## Lag 5000                   0.05181362                   0.03038383
##          traittarsus.2:traitbwt.2.units traitbwt.2:traitbwt.2.units
## Lag 0                     -0.93853010                  -0.85888343
## Lag 100                   -0.89227332                  -0.81357341
## Lag 500                   -0.75764556                  -0.67868373
## Lag 1000                  -0.62307537                  -0.54366192
## Lag 5000                   0.04348967                   0.05718606
##
## , , traitbwt.2:traitbwt.2.animal
##
##          traittarsus.1:traittarsus.1.animal traitbwt.1:traittarsus.1.animal
## Lag 0                          0.07790198                      0.14180302
## Lag 100                        0.04618642                      0.09666633
## Lag 500                        0.01084756                      0.06603768
## Lag 1000                       0.02267992                      0.11225922
## Lag 5000                      -0.11897702                     -0.02765292
##          traittarsus.2:traittarsus.1.animal traitbwt.2:traittarsus.1.animal
## Lag 0                           0.4107260                       0.6191252
## Lag 100                         0.3762287                       0.5533278
## Lag 500                         0.3541228                       0.4906565
## Lag 1000                        0.3161080                       0.4110850
## Lag 5000                       -0.1301409                      -0.1457415
##          traittarsus.1:traitbwt.1.animal traitbwt.1:traitbwt.1.animal
## Lag 0                       0.14180302                   0.21046169
## Lag 100                     0.09666633                   0.16894953
## Lag 500                     0.06603768                   0.16336058
## Lag 1000                    0.11225922                   0.19977861
## Lag 5000                   -0.02765292                   0.02292947
##          traittarsus.2:traitbwt.1.animal traitbwt.2:traitbwt.1.animal
## Lag 0                       0.47574281                   0.64907876
## Lag 100                     0.42046513                   0.55150494
## Lag 500                     0.36650261                   0.46465819
## Lag 1000                    0.33756450                   0.39404623
## Lag 5000                   -0.04573143                  -0.05021868
##          traittarsus.1:traittarsus.2.animal traitbwt.1:traittarsus.2.animal
## Lag 0                           0.4107260                      0.47574281
## Lag 100                         0.3762287                      0.42046513
## Lag 500                         0.3541228                      0.36650261
## Lag 1000                        0.3161080                      0.33756450
## Lag 5000                       -0.1301409                     -0.04573143
##          traittarsus.2:traittarsus.2.animal traitbwt.2:traittarsus.2.animal
## Lag 0                           0.6844205                      0.89818763
## Lag 100                         0.6509791                      0.82577566
## Lag 500                         0.5935139                      0.71300098
## Lag 1000                        0.5428655                      0.62246323
```

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## Lag 5000                    0.0305572                   -0.02000725
##          traittarsus.1:traitbwt.2.animal traitbwt.1:traitbwt.2.animal
## Lag 0                          0.6191252                    0.64907876
## Lag 100                        0.5533278                    0.55150494
## Lag 500                        0.4906565                    0.46465819
## Lag 1000                       0.4110850                    0.39404623
## Lag 5000                      -0.1457415                   -0.05021868
##          traittarsus.2:traitbwt.2.animal traitbwt.2:traitbwt.2.animal
## Lag 0                         0.89818763                    1.00000000
## Lag 100                       0.82577566                    0.87344161
## Lag 500                       0.71300098                    0.71296418
## Lag 1000                      0.62246323                    0.58027397
## Lag 5000                     -0.02000725                   -0.05065402
##          traittarsus.1.byear traitbwt.1.byear traittarsus.2.byear
## Lag 0             0.05353374      0.007606345          0.07295919
## Lag 100           0.05915538      0.016873424          0.06649764
## Lag 500           0.05495199      0.034153584          0.05087275
## Lag 1000          0.08867289      0.063336260          0.03210710
## Lag 5000          0.01157646      0.010648297         -0.07267030
##          traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother
## Lag 0         -0.11303991          0.128729447      -0.162810059
## Lag 100       -0.10682241          0.132664466      -0.165762472
## Lag 500       -0.06622430          0.082749840      -0.142795999
## Lag 1000      -0.06796661          0.092840268      -0.120838816
## Lag 5000       0.07422776          0.007625067       0.007301082
##          traittarsus.2.mother traitbwt.2.mother
## Lag 0             -0.04298505      -0.033866092
## Lag 100           -0.06870971       0.016347544
## Lag 500           -0.06335390       0.003806205
## Lag 1000          -0.06335680       0.042702082
## Lag 5000          -0.03319016      -0.022982672
##          traittarsus.1:traittarsus.1.units traitbwt.1:traittarsus.1.units
## Lag 0                          -0.13106867                    -0.13241719
## Lag 100                        -0.10278270                    -0.09227117
## Lag 500                        -0.06959318                    -0.07769390
## Lag 1000                       -0.08442761                    -0.10813364
## Lag 5000                        0.12643968                     0.06443195
##          traittarsus.2:traittarsus.1.units traitbwt.2:traittarsus.1.units
## Lag 0                           0.13071885                     0.21162923
## Lag 100                         0.13765665                     0.22039206
## Lag 500                         0.12262833                     0.19792348
## Lag 1000                        0.11563474                     0.17509971
## Lag 5000                        0.01775142                     0.02534375
##          traittarsus.1:traitbwt.1.units traitbwt.1:traitbwt.1.units
## Lag 0                       -0.13241719                  -0.1400636
## Lag 100                     -0.09227117                  -0.1032594
## Lag 500                     -0.07769390                  -0.1120628
```

```
## Lag 1000                   -0.10813364                   -0.1695827
## Lag 5000                    0.06443195                   -0.0137381
##          traittarsus.2:traitbwt.1.units traitbwt.2:traitbwt.1.units
## Lag 0                     0.172783869                   0.24161056
## Lag 100                   0.184368154                   0.25618384
## Lag 500                   0.169565117                   0.23188706
## Lag 1000                  0.152615170                   0.20023901
## Lag 5000                  0.008979599                   0.01431812
##          traittarsus.1:traittarsus.2.units traitbwt.1:traittarsus.2.units
## Lag 0                          0.13071885                    0.172783869
## Lag 100                        0.13765665                    0.184368154
## Lag 500                        0.12262833                    0.169565117
## Lag 1000                       0.11563474                    0.152615170
## Lag 5000                       0.01775142                    0.008979599
##          traittarsus.2:traittarsus.2.units traitbwt.2:traittarsus.2.units
## Lag 0                         -0.70436348                    -0.85484247
## Lag 100                       -0.67503813                    -0.80874929
## Lag 500                       -0.61496101                    -0.69869786
## Lag 1000                      -0.55915090                    -0.60389172
## Lag 5000                      -0.01252908                     0.03149869
##          traittarsus.1:traitbwt.2.units traitbwt.1:traitbwt.2.units
## Lag 0                      0.21162923                   0.24161056
## Lag 100                    0.22039206                   0.25618384
## Lag 500                    0.19792348                   0.23188706
## Lag 1000                   0.17509971                   0.20023901
## Lag 5000                   0.02534375                   0.01431812
##          traittarsus.2:traitbwt.2.units traitbwt.2:traitbwt.2.units
## Lag 0                     -0.85484247                  -0.90703776
## Lag 100                   -0.80874929                  -0.84260101
## Lag 500                   -0.69869786                  -0.68593227
## Lag 1000                  -0.60389172                  -0.56191283
## Lag 5000                   0.03149869                   0.05571691
##
## , , traittarsus.1.byear
##
##          traittarsus.1:traittarsus.1.animal traitbwt.1:traittarsus.1.animal
## Lag 0                        -0.0001991343                      0.06781216
## Lag 100                       0.0149599532                      0.07212249
## Lag 500                      -0.0052702707                      0.06733748
## Lag 1000                      0.0022177857                      0.01064963
## Lag 5000                     -0.0477855881                     -0.02770227
##          traittarsus.2:traittarsus.1.animal traitbwt.2:traittarsus.1.animal
## Lag 0                          0.016204947                      0.06346373
## Lag 100                        0.029428446                      0.06520358
## Lag 500                        0.003988555                      0.04831408
## Lag 1000                      -0.009687121                     -0.01510108
## Lag 5000                      -0.057748697                     -0.07984786
```

```
##          traittarsus.1:traitbwt.1.animal traitbwt.1:traitbwt.1.animal
## Lag 0                         0.06781216                   0.06518811
## Lag 100                       0.07212249                   0.07480376
## Lag 500                       0.06733748                   0.11082992
## Lag 1000                      0.01064963                   0.05008650
## Lag 5000                     -0.02770227                  -0.01341916
##          traittarsus.2:traitbwt.1.animal traitbwt.2:traitbwt.1.animal
## Lag 0                         0.02942135                  0.034800266
## Lag 100                       0.02240012                  0.032507546
## Lag 500                       0.02748906                  0.041726424
## Lag 1000                      0.01673477                  0.007404418
## Lag 5000                     -0.04116453                 -0.064540096
##          traittarsus.1:traittarsus.2.animal traitbwt.1:traittarsus.2.animal
## Lag 0                           0.016204947                      0.02942135
## Lag 100                         0.029428446                      0.02240012
## Lag 500                         0.003988555                      0.02748906
## Lag 1000                       -0.009687121                      0.01673477
## Lag 5000                       -0.057748697                     -0.04116453
##          traittarsus.2:traittarsus.2.animal traitbwt.2:traittarsus.2.animal
## Lag 0                           0.035961574                      0.05124741
## Lag 100                         0.039140531                      0.04519151
## Lag 500                        -0.008894598                      0.03130914
## Lag 1000                       -0.036681278                     -0.01447981
## Lag 5000                       -0.088569223                     -0.10213928
##          traittarsus.1:traitbwt.2.animal traitbwt.1:traitbwt.2.animal
## Lag 0                         0.06346373                  0.034800266
## Lag 100                       0.06520358                  0.032507546
## Lag 500                       0.04831408                  0.041726424
## Lag 1000                     -0.01510108                  0.007404418
## Lag 5000                     -0.07984786                 -0.064540096
##          traittarsus.2:traitbwt.2.animal traitbwt.2:traitbwt.2.animal
## Lag 0                         0.05124741                   0.05353374
## Lag 100                       0.04519151                   0.03671240
## Lag 500                       0.03130914                   0.04212493
## Lag 1000                     -0.01447981                  -0.01321894
## Lag 5000                     -0.10213928                  -0.09784272
##          traittarsus.1.byear traitbwt.1.byear traittarsus.2.byear
## Lag 0             1.00000000     -0.011500754        -0.014207130
## Lag 100           0.29498964      0.032775932         0.007424037
## Lag 500           0.01534486     -0.007063004        -0.008141387
## Lag 1000         -0.00531817      0.074940752        -0.088872220
## Lag 5000         -0.04617778     -0.015458692        -0.020304988
##          traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother
## Lag 0       -0.0081906518          0.107143639       -0.06029833
## Lag 100     -0.0458427594          0.096733446       -0.08150148
## Lag 500      0.0004877642          0.068025342       -0.06046456
## Lag 1000     0.0105349484         -0.002189929       -0.01019378
```

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## Lag 5000    -0.0644916207         -0.020934152        0.04368155
##          traittarsus.2.mother traitbwt.2.mother
## Lag 0             -0.03378213       0.028992058
## Lag 100           -0.04096317       0.005259162
## Lag 500            0.04192974      -0.033349969
## Lag 1000          -0.02480675      -0.011058052
## Lag 5000           0.04747283      -0.001107231
##          traittarsus.1:traittarsus.1.units traitbwt.1:traittarsus.1.units
## Lag 0                         -0.145066040                   -0.104716754
## Lag 100                       -0.089626633                   -0.078525674
## Lag 500                       -0.055797909                   -0.064960700
## Lag 1000                      -0.002415045                   -0.025253406
## Lag 5000                       0.031464141                    0.006356867
##          traittarsus.2:traittarsus.1.units traitbwt.2:traittarsus.1.units
## Lag 0                         -0.038470154                    -0.03236997
## Lag 100                       -0.037857054                    -0.03429257
## Lag 500                       -0.023813333                    -0.02985769
## Lag 1000                      -0.004466145                    -0.01855463
## Lag 5000                       0.031916697                     0.01037899
##          traittarsus.1:traitbwt.1.units traitbwt.1:traitbwt.1.units
## Lag 0                      -0.104716754                -0.071954690
## Lag 100                    -0.078525674                -0.071715488
## Lag 500                    -0.064960700                -0.078535410
## Lag 1000                   -0.025253406                -0.053257563
## Lag 5000                    0.006356867                -0.008584678
##          traittarsus.2:traitbwt.1.units traitbwt.2:traitbwt.1.units
## Lag 0                       -0.02749973                 -0.02370119
## Lag 100                     -0.02036580                 -0.01896999
## Lag 500                     -0.02537270                 -0.03447923
## Lag 1000                     0.01650965                  0.00885959
## Lag 5000                     0.03965003                  0.01362772
##          traittarsus.1:traittarsus.2.units traitbwt.1:traittarsus.2.units
## Lag 0                         -0.038470154                    -0.02749973
## Lag 100                       -0.037857054                    -0.02036580
## Lag 500                       -0.023813333                    -0.02537270
## Lag 1000                      -0.004466145                     0.01650965
## Lag 5000                       0.031916697                     0.03965003
##          traittarsus.2:traittarsus.2.units traitbwt.2:traittarsus.2.units
## Lag 0                         -0.029532571                    -0.04533921
## Lag 100                       -0.006520508                    -0.01935854
## Lag 500                        0.015074249                    -0.01914032
## Lag 1000                       0.040326869                     0.01182073
## Lag 5000                       0.077261030                     0.09163015
##          traittarsus.1:traitbwt.2.units traitbwt.1:traitbwt.2.units
## Lag 0                       -0.03236997                 -0.02370119
## Lag 100                     -0.03429257                 -0.01896999
## Lag 500                     -0.02985769                 -0.03447923
```

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## Lag 1000                -0.01855463                 0.00885959
## Lag 5000                 0.01037899                 0.01362772
##            traittarsus.2:traitbwt.2.units traitbwt.2:traitbwt.2.units
## Lag 0                   -0.04533921                -0.044815839
## Lag 100                 -0.01935854                -0.018188105
## Lag 500                 -0.01914032                -0.044430332
## Lag 1000                 0.01182073                 0.006995154
## Lag 5000                 0.09163015                 0.087372099
##
## , , traitbwt.1.byear
##
##            traittarsus.1:traittarsus.1.animal traitbwt.1:traittarsus.1.animal
## Lag 0                          0.02533600                    -0.048571545
## Lag 100                        0.04296781                    -0.011259967
## Lag 500                        0.04385496                     0.001433897
## Lag 1000                       0.00311012                    -0.028185947
## Lag 5000                      -0.03791093                    -0.035032491
##            traittarsus.2:traittarsus.1.animal traitbwt.2:traittarsus.1.animal
## Lag 0                         0.042952342                     0.027308707
## Lag 100                       0.053766787                     0.050479200
## Lag 500                       0.061397390                     0.045799389
## Lag 1000                      0.026376244                     0.045575916
## Lag 5000                     -0.007467705                     0.004959177
##            traittarsus.1:traitbwt.1.animal traitbwt.1:traitbwt.1.animal
## Lag 0                      -0.048571545                 -0.054239888
## Lag 100                    -0.011259967                 -0.013618719
## Lag 500                     0.001433897                 -0.023666680
## Lag 1000                   -0.028185947                 -0.035975542
## Lag 5000                   -0.035032491                 -0.004849703
##            traittarsus.2:traitbwt.1.animal traitbwt.2:traitbwt.1.animal
## Lag 0                        0.01370326                  0.007431509
## Lag 100                      0.02573311                  0.031124056
## Lag 500                      0.01003935                 -0.020817482
## Lag 1000                    -0.01201110                 -0.011831635
## Lag 5000                    -0.03020983                  0.005318089
##            traittarsus.1:traittarsus.2.animal traitbwt.1:traittarsus.2.animal
## Lag 0                         0.042952342                      0.01370326
## Lag 100                       0.053766787                      0.02573311
## Lag 500                       0.061397390                      0.01003935
## Lag 1000                      0.026376244                     -0.01201110
## Lag 5000                     -0.007467705                     -0.03020983
##            traittarsus.2:traittarsus.2.animal traitbwt.2:traittarsus.2.animal
## Lag 0                         -0.01746914                     0.001646162
## Lag 100                       -0.00918084                     0.014660207
## Lag 500                        0.03727433                     0.029738658
## Lag 1000                       0.05233753                     0.058558627
## Lag 5000                       0.05442837                     0.036237222
```

```
##           traittarsus.1:traitbwt.2.animal traitbwt.1:traitbwt.2.animal
## Lag 0                         0.027308707                  0.007431509
## Lag 100                       0.050479200                  0.031124056
## Lag 500                       0.045799389                 -0.020817482
## Lag 1000                      0.045575916                 -0.011831635
## Lag 5000                      0.004959177                  0.005318089
##           traittarsus.2:traitbwt.2.animal traitbwt.2:traitbwt.2.animal
## Lag 0                         0.001646162                  0.007606345
## Lag 100                       0.014660207                  0.025027029
## Lag 500                       0.029738658                  0.007127126
## Lag 1000                      0.058558627                  0.051997571
## Lag 5000                      0.036237222                  0.030982100
##           traittarsus.1.byear traitbwt.1.byear traittarsus.2.byear
## Lag 0            -0.011500754       1.00000000        -0.032565228
## Lag 100          -0.008778968       0.12997956        -0.003228198
## Lag 500          -0.004505343       0.03863671        -0.017827698
## Lag 1000          0.025463698      -0.01655625         0.013769326
## Lag 5000          0.001254535      -0.04239004         0.001901775
##           traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother
## Lag 0         -0.039257246          -0.02879748       0.065880688
## Lag 100        0.015007558          -0.03208555       0.058933430
## Lag 500       -0.005393351           0.03210587       0.004743831
## Lag 1000       0.043913747           0.05551756       0.012244934
## Lag 5000      -0.026820593           0.05843803       0.010088100
##           traittarsus.2.mother traitbwt.2.mother
## Lag 0              0.008939011       0.059268463
## Lag 100           -0.001571382       0.086064468
## Lag 500           -0.023366713       0.008732966
## Lag 1000           0.002165536      -0.002113612
## Lag 5000          -0.038345540      -0.007683096
##           traittarsus.1:traittarsus.1.units traitbwt.1:traittarsus.1.units
## Lag 0                         -0.0435586501                    0.010219509
## Lag 100                       -0.0505048908                   -0.031324102
## Lag 500                       -0.0630828149                   -0.004357406
## Lag 1000                       0.0199630207                    0.069957559
## Lag 5000                       0.0005522977                   -0.005454216
##           traittarsus.2:traittarsus.1.units traitbwt.2:traittarsus.1.units
## Lag 0                            0.05293519                     0.05768879
## Lag 100                          0.04858011                     0.05892110
## Lag 500                          0.05854491                     0.06372575
## Lag 1000                         0.04969484                     0.03639502
## Lag 5000                         0.02832954                     0.02784365
##           traittarsus.1:traitbwt.1.units traitbwt.1:traitbwt.1.units
## Lag 0                        0.010219509                -0.028183637
## Lag 100                     -0.031324102                -0.040106071
## Lag 500                     -0.004357406                 0.006591277
## Lag 1000                     0.069957559                 0.063937711
```

```
## Lag 5000                -0.005454216                -0.027544320
##          traittarsus.2:traitbwt.1.units traitbwt.2:traitbwt.1.units
## Lag 0                      0.04996250                  0.04700881
## Lag 100                    0.04397513                  0.04673808
## Lag 500                    0.04695403                  0.04531904
## Lag 1000                   0.03436998                  0.02563582
## Lag 5000                   0.02256523                  0.02398399
##          traittarsus.1:traittarsus.2.units traitbwt.1:traittarsus.2.units
## Lag 0                         0.05293519                     0.04996250
## Lag 100                       0.04858011                     0.04397513
## Lag 500                       0.05854491                     0.04695403
## Lag 1000                      0.04969484                     0.03436998
## Lag 5000                      0.02832954                     0.02256523
##          traittarsus.2:traittarsus.2.units traitbwt.2:traittarsus.2.units
## Lag 0                         0.01013932                   -0.001638125
## Lag 100                       0.01806400                    0.001129150
## Lag 500                      -0.01420490                   -0.017077159
## Lag 1000                     -0.04995245                   -0.056833617
## Lag 5000                     -0.04322171                   -0.023913807
##          traittarsus.1:traitbwt.2.units traitbwt.1:traitbwt.2.units
## Lag 0                      0.05768879                  0.04700881
## Lag 100                    0.05892110                  0.04673808
## Lag 500                    0.06372575                  0.04531904
## Lag 1000                   0.03639502                  0.02563582
## Lag 5000                   0.02784365                  0.02398399
##          traittarsus.2:traitbwt.2.units traitbwt.2:traitbwt.2.units
## Lag 0                    -0.001638125                -0.007601342
## Lag 100                   0.001129150                -0.013307489
## Lag 500                  -0.017077159                -0.008568690
## Lag 1000                 -0.056833617                -0.049677065
## Lag 5000                 -0.023913807                -0.009694337
##
## , , traittarsus.2.byear
##
##          traittarsus.1:traittarsus.1.animal traitbwt.1:traittarsus.1.animal
## Lag 0                          0.02726198                     -0.00111586
## Lag 100                        0.05357730                      0.01828074
## Lag 500                        0.04315378                      0.02964535
## Lag 1000                       0.08991282                      0.06959065
## Lag 5000                       0.05518086                      0.09966305
##          traittarsus.2:traittarsus.1.animal traitbwt.2:traittarsus.1.animal
## Lag 0                          0.05222339                      0.05196404
## Lag 100                        0.07930026                      0.07496121
## Lag 500                        0.04558008                      0.04893690
## Lag 1000                       0.07097163                      0.08902753
## Lag 5000                       0.06038135                      0.02474492
##          traittarsus.1:traitbwt.1.animal traitbwt.1:traitbwt.1.animal
```

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## Lag 0                  -0.00111586                -0.03158434
## Lag 100                 0.01828074                -0.03831807
## Lag 500                 0.02964535                 0.03186606
## Lag 1000                0.06959065                 0.06084561
## Lag 5000                0.09966305                 0.04703834
##          traittarsus.2:traitbwt.1.animal traitbwt.2:traitbwt.1.animal
## Lag 0                   0.08861601                 0.10446126
## Lag 100                 0.08291699                 0.08928353
## Lag 500                 0.07447628                 0.09304440
## Lag 1000                0.05734586                 0.08937241
## Lag 5000                0.08247995                 0.05423744
##          traittarsus.1:traittarsus.2.animal traitbwt.1:traittarsus.2.animal
## Lag 0                      0.05222339                      0.08861601
## Lag 100                    0.07930026                      0.08291699
## Lag 500                    0.04558008                      0.07447628
## Lag 1000                   0.07097163                      0.05734586
## Lag 5000                   0.06038135                      0.08247995
##          traittarsus.2:traittarsus.2.animal traitbwt.2:traittarsus.2.animal
## Lag 0                     0.007171364                      0.04068399
## Lag 100                   0.043732946                      0.05987656
## Lag 500                   0.015444417                      0.03370999
## Lag 1000                  0.019544081                      0.04502976
## Lag 5000                  0.006685864                     -0.01642810
##          traittarsus.1:traitbwt.2.animal traitbwt.1:traitbwt.2.animal
## Lag 0                   0.05196404                 0.10446126
## Lag 100                 0.07496121                 0.08928353
## Lag 500                 0.04893690                 0.09304440
## Lag 1000                0.08902753                 0.08937241
## Lag 5000                0.02474492                 0.05423744
##          traittarsus.2:traitbwt.2.animal traitbwt.2:traitbwt.2.animal
## Lag 0                   0.04068399                 0.07295919
## Lag 100                 0.05987656                 0.07152626
## Lag 500                 0.03370999                 0.07468887
## Lag 1000                0.04502976                 0.05593692
## Lag 5000               -0.01642810                -0.02210630
##          traittarsus.1.byear traitbwt.1.byear traittarsus.2.byear
## Lag 0           -0.014207130      -0.03256523          1.00000000
## Lag 100          0.004989327       0.01606065          0.26418064
## Lag 500          0.044052804       0.03428138          0.09537772
## Lag 1000        -0.001440518       0.01039861          0.10874833
## Lag 5000         0.022958892      -0.01931981         -0.01473189
##          traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother
## Lag 0        0.0396353651           0.00119313       0.009996629
## Lag 100      0.0105436230           0.04327018       0.062928368
## Lag 500     -0.0175690949           0.04625644       0.018026408
## Lag 1000    -0.0005183552           0.06289415      -0.081508956
## Lag 5000     0.0441472029          -0.04105115       0.035686320
```

```
##           traittarsus.2.mother traitbwt.2.mother
## Lag 0              0.04535223       0.002495676
## Lag 100            0.02030029       0.045447997
## Lag 500            0.02446377       0.009649222
## Lag 1000           0.03899831       0.024762534
## Lag 5000          -0.06415993       0.094134035
##           traittarsus.1:traittarsus.1.units traitbwt.1:traittarsus.1.units
## Lag 0                           -0.04924174                   0.0004983836
## Lag 100                         -0.07260472                  -0.0274666354
## Lag 500                         -0.08762084                  -0.0545545565
## Lag 1000                        -0.11600745                  -0.0941075726
## Lag 5000                        -0.01429942                  -0.0306094192
##           traittarsus.2:traittarsus.1.units traitbwt.2:traittarsus.1.units
## Lag 0                            0.06126409                     0.06054337
## Lag 100                          0.06861858                     0.06794736
## Lag 500                          0.06487160                     0.06219436
## Lag 1000                         0.05154526                     0.06299063
## Lag 5000                        -0.03961272                    -0.02077759
##           traittarsus.1:traitbwt.1.units traitbwt.1:traitbwt.1.units
## Lag 0                       0.0004983836                 0.045243199
## Lag 100                    -0.0274666354                 0.002618325
## Lag 500                    -0.0545545565                -0.045086068
## Lag 1000                   -0.0941075726                -0.078265909
## Lag 5000                   -0.0306094192                -0.039652118
##           traittarsus.2:traitbwt.1.units traitbwt.2:traitbwt.1.units
## Lag 0                         0.04569537                  0.05361674
## Lag 100                       0.05790943                  0.06228633
## Lag 500                       0.06629817                  0.07181673
## Lag 1000                      0.05677668                  0.07820270
## Lag 5000                     -0.04900870                 -0.01725220
##           traittarsus.1:traittarsus.2.units traitbwt.1:traittarsus.2.units
## Lag 0                            0.06126409                     0.04569537
## Lag 100                          0.06861858                     0.05790943
## Lag 500                          0.06487160                     0.06629817
## Lag 1000                         0.05154526                     0.05677668
## Lag 5000                        -0.03961272                    -0.04900870
##           traittarsus.2:traittarsus.2.units traitbwt.2:traittarsus.2.units
## Lag 0                           -0.05907849                    -0.07410803
## Lag 100                         -0.06985906                    -0.08123809
## Lag 500                         -0.02440940                    -0.02862324
## Lag 1000                        -0.03153841                    -0.04394287
## Lag 5000                         0.01609465                     0.02558327
##           traittarsus.1:traitbwt.2.units traitbwt.1:traitbwt.2.units
## Lag 0                         0.06054337                  0.05361674
## Lag 100                       0.06794736                  0.06228633
## Lag 500                       0.06219436                  0.07181673
## Lag 1000                      0.06299063                  0.07820270
```

```
## Lag 5000                  -0.02077759                  -0.01725220
##          traittarsus.2:traitbwt.2.units traitbwt.2:traitbwt.2.units
## Lag 0                     -0.07410803                  -0.09539294
## Lag 100                   -0.08123809                  -0.10192651
## Lag 500                   -0.02862324                  -0.04787149
## Lag 1000                  -0.04394287                  -0.05696449
## Lag 5000                   0.02558327                   0.02318439
##
## , , traitbwt.2.byear
##
##          traittarsus.1:traittarsus.1.animal traitbwt.1:traittarsus.1.animal
## Lag 0                          -0.012312644                    -0.026101857
## Lag 100                         0.001679568                    -0.022719854
## Lag 500                        -0.022095064                     0.036781391
## Lag 1000                       -0.044649058                     0.008440477
## Lag 5000                        0.012471911                     0.017412057
##          traittarsus.2:traittarsus.1.animal traitbwt.2:traittarsus.1.animal
## Lag 0                          -0.041612693                    -0.093374609
## Lag 100                        -0.044670676                    -0.085938138
## Lag 500                        -0.073851310                    -0.057467051
## Lag 1000                       -0.112427556                    -0.073729661
## Lag 5000                       -0.002302422                    -0.007211525
##          traittarsus.1:traitbwt.1.animal traitbwt.1:traitbwt.1.animal
## Lag 0                       -0.026101857                 -0.024899884
## Lag 100                     -0.022719854                 -0.008317247
## Lag 500                      0.036781391                  0.041716499
## Lag 1000                     0.008440477                 -0.015226273
## Lag 5000                     0.017412057                 -0.007915616
##          traittarsus.2:traitbwt.1.animal traitbwt.2:traitbwt.1.animal
## Lag 0                        -0.06566102                  -0.08333568
## Lag 100                      -0.07750349                  -0.08378159
## Lag 500                      -0.08329811                  -0.05814502
## Lag 1000                     -0.08817705                  -0.08501262
## Lag 5000                      0.01626488                  -0.01063817
##          traittarsus.1:traittarsus.2.animal traitbwt.1:traittarsus.2.animal
## Lag 0                          -0.041612693                      -0.06566102
## Lag 100                        -0.044670676                      -0.07750349
## Lag 500                        -0.073851310                      -0.08329811
## Lag 1000                       -0.112427556                      -0.08817705
## Lag 5000                       -0.002302422                       0.01626488
##          traittarsus.2:traittarsus.2.animal traitbwt.2:traittarsus.2.animal
## Lag 0                           -0.08333086                      -0.12402916
## Lag 100                         -0.07538028                      -0.10747454
## Lag 500                         -0.05024835                      -0.08333129
## Lag 1000                        -0.08252216                      -0.09539109
## Lag 5000                        -0.05270947                      -0.04030638
##          traittarsus.1:traitbwt.2.animal traitbwt.1:traitbwt.2.animal
```

```
## Lag 0                     -0.093374609                 -0.08333568
## Lag 100                   -0.085938138                 -0.08378159
## Lag 500                   -0.057467051                 -0.05814502
## Lag 1000                  -0.073729661                 -0.08501262
## Lag 5000                  -0.007211525                 -0.01063817
##          traittarsus.2:traitbwt.2.animal traitbwt.2:traitbwt.2.animal
## Lag 0                      -0.12402916                 -0.11303991
## Lag 100                    -0.10747454                 -0.09513886
## Lag 500                    -0.08333129                 -0.08666156
## Lag 1000                   -0.09539109                 -0.10675958
## Lag 5000                   -0.04030638                 -0.02380443
##          traittarsus.1.byear traitbwt.1.byear traittarsus.2.byear
## Lag 0         -0.008190652     -0.039257246         0.03963537
## Lag 100       -0.031080960     -0.037426765         0.00903900
## Lag 500        0.006051004     -0.020419576        -0.06809153
## Lag 1000       0.018314138     -0.002583670        -0.02323337
## Lag 5000      -0.026798307     -0.007024901        -0.01177870
##          traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother
## Lag 0       1.000000000         -0.03484939       0.019595061
## Lag 100     0.148773685         -0.05262924       0.013805361
## Lag 500     0.023071337          0.01145834       0.001042167
## Lag 1000    0.001235911          0.02017891       0.034032045
## Lag 5000   -0.035993191         -0.01462895      -0.011384188
##          traittarsus.2.mother traitbwt.2.mother
## Lag 0           0.015981233      -0.007859673
## Lag 100        -0.022156260      -0.004707385
## Lag 500        -0.006728665      -0.029061201
## Lag 1000       -0.021805472       0.003816387
## Lag 5000       -0.009007212       0.012478432
##          traittarsus.1:traittarsus.1.units traitbwt.1:traittarsus.1.units
## Lag 0                           0.01051817                     0.02175859
## Lag 100                         0.02304329                     0.01564866
## Lag 500                         0.01520723                    -0.00804956
## Lag 1000                        0.04140673                     0.03546143
## Lag 5000                       -0.01488195                    -0.01947941
##          traittarsus.2:traittarsus.1.units traitbwt.2:traittarsus.1.units
## Lag 0                          -0.04179855                    -0.03235648
## Lag 100                        -0.04317226                    -0.03935256
## Lag 500                        -0.03459143                    -0.04109499
## Lag 1000                       -0.03581518                    -0.03377959
## Lag 5000                       -0.04487869                    -0.06427439
##          traittarsus.1:traitbwt.1.units traitbwt.1:traitbwt.1.units
## Lag 0                        0.02175859                0.008779544
## Lag 100                      0.01564866                0.004367987
## Lag 500                     -0.00804956               -0.020584034
## Lag 1000                     0.03546143                0.024592354
## Lag 5000                    -0.01947941               -0.008436479
```

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##          traittarsus.2:traitbwt.1.units traitbwt.2:traitbwt.1.units
## Lag 0                       -0.05587517                 -0.03458419
## Lag 100                     -0.04924453                 -0.03546666
## Lag 500                     -0.03327777                 -0.03542884
## Lag 1000                    -0.02872355                 -0.01384796
## Lag 5000                    -0.05472119                 -0.06947879
##          traittarsus.1:traittarsus.2.units traitbwt.1:traittarsus.2.units
## Lag 0                          -0.04179855                    -0.05587517
## Lag 100                        -0.04317226                    -0.04924453
## Lag 500                        -0.03459143                    -0.03327777
## Lag 1000                       -0.03581518                    -0.02872355
## Lag 5000                       -0.04487869                    -0.05472119
##          traittarsus.2:traittarsus.2.units traitbwt.2:traittarsus.2.units
## Lag 0                           0.07499456                     0.09224924
## Lag 100                         0.07208086                     0.09762890
## Lag 500                         0.07251351                     0.09224810
## Lag 1000                        0.08656386                     0.08963227
## Lag 5000                        0.01938132                     0.01875251
##          traittarsus.1:traitbwt.2.units traitbwt.1:traitbwt.2.units
## Lag 0                       -0.03235648                 -0.03458419
## Lag 100                     -0.03935256                 -0.03546666
## Lag 500                     -0.04109499                 -0.03542884
## Lag 1000                    -0.03377959                 -0.01384796
## Lag 5000                    -0.06427439                 -0.06947879
##          traittarsus.2:traitbwt.2.units traitbwt.2:traitbwt.2.units
## Lag 0                        0.09224924                  0.07926090
## Lag 100                      0.09762890                  0.09616451
## Lag 500                      0.09224810                  0.09549623
## Lag 1000                     0.08963227                  0.09029398
## Lag 5000                     0.01875251                  0.01366050
##
## , , traittarsus.1.mother
##
##          traittarsus.1:traittarsus.1.animal traitbwt.1:traittarsus.1.animal
## Lag 0                           -0.15078835                     0.015326642
## Lag 100                         -0.14463422                     0.003365171
## Lag 500                         -0.15804338                    -0.076509373
## Lag 1000                        -0.09886124                    -0.083743318
## Lag 5000                        -0.10523556                    -0.044881123
##          traittarsus.2:traittarsus.1.animal traitbwt.2:traittarsus.1.animal
## Lag 0                           -0.10295266                     0.020069065
## Lag 100                         -0.08557369                     0.024944654
## Lag 500                         -0.09200768                    -0.007032787
## Lag 1000                        -0.07176616                    -0.035638619
## Lag 5000                        -0.04022520                    -0.053311401
##          traittarsus.1:traitbwt.1.animal traitbwt.1:traitbwt.1.animal
## Lag 0                        0.015326642                  0.063535708
```

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## Lag 100                  0.003365171                  0.050510724
## Lag 500                 -0.076509373                  0.005284771
## Lag 1000                -0.083743318                 -0.009316143
## Lag 5000                -0.044881123                  0.017585405
##          traittarsus.2:traitbwt.1.animal traitbwt.2:traitbwt.1.animal
## Lag 0                        0.01026682                   0.10088834
## Lag 100                      0.02777302                   0.10524313
## Lag 500                     -0.02208151                   0.06189318
## Lag 1000                    -0.03691548                   0.02840216
## Lag 5000                    -0.05057754                  -0.05628831
##          traittarsus.1:traittarsus.2.animal traitbwt.1:traittarsus.2.animal
## Lag 0                           -0.10295266                      0.01026682
## Lag 100                         -0.08557369                      0.02777302
## Lag 500                         -0.09200768                     -0.02208151
## Lag 1000                        -0.07176616                     -0.03691548
## Lag 5000                        -0.04022520                     -0.05057754
##          traittarsus.2:traittarsus.2.animal traitbwt.2:traittarsus.2.animal
## Lag 0                           0.046514036                     0.086391373
## Lag 100                         0.041591585                     0.092682345
## Lag 500                         0.014159903                     0.054749349
## Lag 1000                       -0.006046443                     0.037148101
## Lag 5000                        0.023770495                    -0.002799893
##          traittarsus.1:traitbwt.2.animal traitbwt.1:traitbwt.2.animal
## Lag 0                       0.020069065                   0.10088834
## Lag 100                     0.024944654                   0.10524313
## Lag 500                    -0.007032787                   0.06189318
## Lag 1000                   -0.035638619                   0.02840216
## Lag 5000                   -0.053311401                  -0.05628831
##          traittarsus.2:traitbwt.2.animal traitbwt.2:traitbwt.2.animal
## Lag 0                       0.086391373                  0.128729447
## Lag 100                     0.092682345                  0.137837082
## Lag 500                     0.054749349                  0.091445074
## Lag 1000                    0.037148101                  0.065510680
## Lag 5000                   -0.002799893                 -0.009892994
##          traittarsus.1.byear traitbwt.1.byear traittarsus.2.byear
## Lag 0             0.10714364     -0.028797482         0.001193130
## Lag 100           0.12475726     -0.002859105         0.017423692
## Lag 500           0.05635178      0.024729770         0.044602685
## Lag 1000         -0.01346005      0.015026664        -0.004151145
## Lag 5000         -0.03482857     -0.062611057        -0.134069816
##          traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother
## Lag 0         -0.03484939           1.00000000      -0.271213796
## Lag 100       -0.06696141           0.63404978      -0.170737492
## Lag 500       -0.04137534           0.29008219      -0.136893424
## Lag 1000       0.02864811           0.07345948      -0.100567641
## Lag 5000       0.02750431          -0.03892620       0.007641615
##          traittarsus.2.mother traitbwt.2.mother
```

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## Lag 0            0.03387619      -0.05622667
## Lag 100          0.07299528      -0.04780327
## Lag 500          0.04150672      -0.03149897
## Lag 1000         0.02244428       0.03981911
## Lag 5000        -0.02167543       0.03773247
##          traittarsus.1:traittarsus.1.units traitbwt.1:traittarsus.1.units
## Lag 0                          -0.28511353                   -0.039522955
## Lag 100                        -0.16904760                   -0.001067247
## Lag 500                        -0.02585760                    0.071889419
## Lag 1000                        0.03550783                    0.091662892
## Lag 5000                        0.11461631                    0.071952509
##          traittarsus.2:traittarsus.1.units traitbwt.2:traittarsus.1.units
## Lag 0                            0.1697424                     0.17038749
## Lag 100                          0.1698287                     0.16772504
## Lag 500                          0.1774711                     0.18621633
## Lag 1000                         0.1539551                     0.18005891
## Lag 5000                         0.1039239                     0.09992436
##          traittarsus.1:traitbwt.1.units traitbwt.1:traitbwt.1.units
## Lag 0                      -0.039522955                  0.02826569
## Lag 100                    -0.001067247                  0.01968611
## Lag 500                     0.071889419                  0.06722240
## Lag 1000                    0.091662892                  0.06515118
## Lag 5000                    0.071952509                 -0.00146006
##          traittarsus.2:traitbwt.1.units traitbwt.2:traitbwt.1.units
## Lag 0                         0.1570314                  0.15014199
## Lag 100                       0.1589658                  0.15363210
## Lag 500                       0.1753944                  0.19214621
## Lag 1000                      0.1525229                  0.17920894
## Lag 5000                      0.0981355                  0.09929337
##          traittarsus.1:traittarsus.2.units traitbwt.1:traittarsus.2.units
## Lag 0                            0.1697424                      0.1570314
## Lag 100                          0.1698287                      0.1589658
## Lag 500                          0.1774711                      0.1753944
## Lag 1000                         0.1539551                      0.1525229
## Lag 5000                         0.1039239                      0.0981355
##          traittarsus.2:traittarsus.2.units traitbwt.2:traittarsus.2.units
## Lag 0                          -0.05365944                    -0.08507034
## Lag 100                        -0.05114312                    -0.08650307
## Lag 500                        -0.03294118                    -0.06365200
## Lag 1000                       -0.01342963                    -0.04929539
## Lag 5000                       -0.03255967                    -0.00364547
##          traittarsus.1:traitbwt.2.units traitbwt.1:traitbwt.2.units
## Lag 0                        0.17038749                  0.15014199
## Lag 100                      0.16772504                  0.15363210
## Lag 500                      0.18621633                  0.19214621
## Lag 1000                     0.18005891                  0.17920894
## Lag 5000                     0.09992436                  0.09929337
```

```
##           traittarsus.2:traitbwt.2.units traitbwt.2:traitbwt.2.units
## Lag 0                       -0.08507034                 -0.11755479
## Lag 100                     -0.08650307                 -0.11806828
## Lag 500                     -0.06365200                 -0.08269424
## Lag 1000                    -0.04929539                 -0.07064952
## Lag 5000                    -0.00364547                  0.01527502
##
## , , traitbwt.1.mother
##
##           traittarsus.1:traittarsus.1.animal traitbwt.1:traittarsus.1.animal
## Lag 0                             0.10750858                    -0.015001711
## Lag 100                           0.11345621                    -0.018373787
## Lag 500                           0.12529867                     0.019269248
## Lag 1000                          0.09676891                     0.063965485
## Lag 5000                          0.03295446                     0.002551181
##           traittarsus.2:traittarsus.1.animal traitbwt.2:traittarsus.1.animal
## Lag 0                             0.04055573                     -0.06942502
## Lag 100                           0.04246078                     -0.06694784
## Lag 500                           0.05073917                     -0.04628001
## Lag 1000                          0.02033431                     -0.02832344
## Lag 5000                          0.02405793                      0.06116511
##           traittarsus.1:traitbwt.1.animal traitbwt.1:traitbwt.1.animal
## Lag 0                        -0.015001711                 -0.301057181
## Lag 100                      -0.018373787                 -0.217367082
## Lag 500                       0.019269248                 -0.084030109
## Lag 1000                      0.063965485                  0.016600029
## Lag 5000                      0.002551181                  0.006633359
##           traittarsus.2:traitbwt.1.animal traitbwt.2:traitbwt.1.animal
## Lag 0                        -0.002921727                  -0.21005355
## Lag 100                      -0.017967358                  -0.17453411
## Lag 500                      -0.048665239                  -0.13167639
## Lag 1000                     -0.013679253                  -0.06743430
## Lag 5000                     -0.015338823                   0.06036364
##           traittarsus.1:traittarsus.2.animal traitbwt.1:traittarsus.2.animal
## Lag 0                             0.04055573                    -0.002921727
## Lag 100                           0.04246078                    -0.017967358
## Lag 500                           0.05073917                    -0.048665239
## Lag 1000                          0.02033431                    -0.013679253
## Lag 5000                          0.02405793                    -0.015338823
##           traittarsus.2:traittarsus.2.animal traitbwt.2:traittarsus.2.animal
## Lag 0                           -0.063757286                     -0.09704390
## Lag 100                         -0.078555235                     -0.11278771
## Lag 500                         -0.075850107                     -0.13102396
## Lag 1000                        -0.051714924                     -0.09839159
## Lag 5000                         0.004416861                      0.02809940
##           traittarsus.1:traitbwt.2.animal traitbwt.1:traitbwt.2.animal
## Lag 0                         -0.06942502                  -0.21005355
```

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## Lag 100                   -0.06694784                 -0.17453411
## Lag 500                   -0.04628001                 -0.13167639
## Lag 1000                  -0.02832344                 -0.06743430
## Lag 5000                   0.06116511                  0.06036364
##          traittarsus.2:traitbwt.2.animal traitbwt.2:traitbwt.2.animal
## Lag 0                     -0.09704390                 -0.16281006
## Lag 100                   -0.11278771                 -0.15402583
## Lag 500                   -0.13102396                 -0.18417663
## Lag 1000                  -0.09839159                 -0.13265931
## Lag 5000                   0.02809940                  0.06774942
##          traittarsus.1.byear traitbwt.1.byear traittarsus.2.byear
## Lag 0            -0.06029833      0.065880688         0.009996629
## Lag 100          -0.06060175      0.002155759         0.013541244
## Lag 500           0.02852613     -0.001260087         0.019839054
## Lag 1000         -0.02910626      0.001290157         0.048245645
## Lag 5000         -0.01024266      0.050399045         0.056737041
##          traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother
## Lag 0        0.0195950614        -0.2712137958       1.000000000
## Lag 100     -0.0008933777        -0.1720110752       0.379551682
## Lag 500      0.0366638614        -0.0393624856       0.041329213
## Lag 1000    -0.0151426446         0.0476618317       0.002159042
## Lag 5000     0.0123140414         0.0001252644      -0.018222262
##          traittarsus.2.mother traitbwt.2.mother
## Lag 0             0.031492934        0.14519001
## Lag 100           0.002534347        0.07587057
## Lag 500          -0.013284762        0.04165749
## Lag 1000         -0.031081556       -0.02212041
## Lag 5000          0.013850724       -0.02074787
##          traittarsus.1:traittarsus.1.units traitbwt.1:traittarsus.1.units
## Lag 0                           0.01973629                     0.03665672
## Lag 100                        -0.02293101                     0.01498518
## Lag 500                        -0.11066356                    -0.05474960
## Lag 1000                       -0.09135360                    -0.03226117
## Lag 5000                       -0.07860493                    -0.07560389
##          traittarsus.2:traittarsus.1.units traitbwt.2:traittarsus.1.units
## Lag 0                           0.04294093                    0.012376673
## Lag 100                         0.03955764                    0.010683501
## Lag 500                         0.01752126                   -0.006221666
## Lag 1000                        0.02219142                   -0.001297180
## Lag 5000                        0.01239642                    0.030951874
##          traittarsus.1:traitbwt.1.units traitbwt.1:traitbwt.1.units
## Lag 0                        0.03665672                -0.007047622
## Lag 100                      0.01498518                 0.037977225
## Lag 500                     -0.05474960                 0.019970710
## Lag 1000                    -0.03226117                -0.007739455
## Lag 5000                    -0.07560389                -0.062919612
##          traittarsus.2:traitbwt.1.units traitbwt.2:traitbwt.1.units
```

```
## Lag 0                     -0.002752353               -0.03097991
## Lag 100                   -0.003093096               -0.03192449
## Lag 500                   -0.009027187               -0.04102552
## Lag 1000                  -0.020527419               -0.03483856
## Lag 5000                   0.006886321                0.02535835
##          traittarsus.1:traittarsus.2.units traitbwt.1:traittarsus.2.units
## Lag 0                              0.04294093                   -0.002752353
## Lag 100                            0.03955764                   -0.003093096
## Lag 500                            0.01752126                   -0.009027187
## Lag 1000                           0.02219142                   -0.020527419
## Lag 5000                           0.01239642                    0.006886321
##          traittarsus.2:traittarsus.2.units traitbwt.2:traittarsus.2.units
## Lag 0                              0.08205572                     0.11704839
## Lag 100                            0.07607819                     0.11403531
## Lag 500                            0.10265484                     0.14762922
## Lag 1000                           0.06476226                     0.10125717
## Lag 5000                          -0.03096688                    -0.06021103
##          traittarsus.1:traitbwt.2.units traitbwt.1:traitbwt.2.units
## Lag 0                       0.012376673                 -0.03097991
## Lag 100                     0.010683501                 -0.03192449
## Lag 500                    -0.006221666                 -0.04102552
## Lag 1000                   -0.001297180                 -0.03483856
## Lag 5000                    0.030951874                  0.02535835
##          traittarsus.2:traitbwt.2.units traitbwt.2:traitbwt.2.units
## Lag 0                        0.11704839                  0.15336397
## Lag 100                      0.11403531                  0.15628950
## Lag 500                      0.14762922                  0.17953508
## Lag 1000                     0.10125717                  0.12282290
## Lag 5000                    -0.06021103                 -0.09027737
##
## , , traittarsus.2.mother
##
##          traittarsus.1:traittarsus.1.animal traitbwt.1:traittarsus.1.animal
## Lag 0                                0.01502226                     0.051714153
## Lag 100                              0.02971209                     0.049905332
## Lag 500                              0.07537838                     0.055173503
## Lag 1000                             0.12660306                     0.083736831
## Lag 5000                             0.02592685                     0.003920255
##          traittarsus.2:traittarsus.1.animal traitbwt.2:traittarsus.1.animal
## Lag 0                               -0.15988076                    -0.026436938
## Lag 100                             -0.12481132                    -0.008713726
## Lag 500                             -0.06365003                    -0.003368880
## Lag 1000                            -0.01077423                     0.048477788
## Lag 5000                             0.17321257                     0.100587628
##          traittarsus.1:traitbwt.1.animal traitbwt.1:traitbwt.1.animal
## Lag 0                         0.051714153                   0.02830176
## Lag 100                       0.049905332                   0.03057360
```

```
## Lag 500                 0.055173503                   0.03073470
## Lag 1000                0.083736831                   0.04723145
## Lag 5000                0.003920255                   0.01299831
##          traittarsus.2:traitbwt.1.animal traitbwt.2:traitbwt.1.animal
## Lag 0                      -0.01173970                 0.0184703252
## Lag 100                    -0.01697136                 0.0251626879
## Lag 500                    -0.05188574                -0.0005911452
## Lag 1000                   -0.04833371                 0.0163990890
## Lag 5000                    0.24669771                 0.1785739883
##          traittarsus.1:traittarsus.2.animal traitbwt.1:traittarsus.2.animal
## Lag 0                           -0.15988076                     -0.01173970
## Lag 100                         -0.12481132                     -0.01697136
## Lag 500                         -0.06365003                     -0.05188574
## Lag 1000                        -0.01077423                     -0.04833371
## Lag 5000                         0.17321257                      0.24669771
##          traittarsus.2:traittarsus.2.animal traitbwt.2:traittarsus.2.animal
## Lag 0                            -0.3447706                      -0.1561025
## Lag 100                          -0.2981644                      -0.1438613
## Lag 500                          -0.2223198                      -0.1486635
## Lag 1000                         -0.1932667                      -0.1478947
## Lag 5000                          0.1277913                       0.1562519
##          traittarsus.1:traitbwt.2.animal traitbwt.1:traitbwt.2.animal
## Lag 0                     -0.026436938                 0.0184703252
## Lag 100                   -0.008713726                 0.0251626879
## Lag 500                   -0.003368880                -0.0005911452
## Lag 1000                   0.048477788                 0.0163990890
## Lag 5000                   0.100587628                 0.1785739883
##          traittarsus.2:traitbwt.2.animal traitbwt.2:traitbwt.2.animal
## Lag 0                       -0.1561025                  -0.04298505
## Lag 100                     -0.1438613                  -0.03256173
## Lag 500                     -0.1486635                  -0.08441125
## Lag 1000                    -0.1478947                  -0.11538109
## Lag 5000                     0.1562519                   0.16485805
##          traittarsus.1.byear traitbwt.1.byear traittarsus.2.byear
## Lag 0           -0.033782129     0.0089390110          0.04535223
## Lag 100          0.009970602    -0.0185988821          0.06005459
## Lag 500         -0.031227653     0.0075697533         -0.02997353
## Lag 1000         0.011336122    -0.0006296073         -0.05122879
## Lag 5000         0.049341702    -0.0529101788          0.11732582
##          traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother
## Lag 0         0.015981233          0.033876186       0.031492934
## Lag 100      -0.001350435          0.027458021      -0.034002906
## Lag 500      -0.067109166         -0.078872225      -0.017665845
## Lag 1000     -0.038517473         -0.030003877      -0.040451967
## Lag 5000     -0.086683580         -0.004367187       0.002148712
##          traittarsus.2.mother traitbwt.2.mother
## Lag 0              1.00000000       -0.32918284
```

```
## Lag 100          0.57125197       -0.19561543
## Lag 500          0.26951589       -0.09671746
## Lag 1000         0.09211216       -0.01393679
## Lag 5000        -0.02238888       -0.04415446
##          traittarsus.1:traittarsus.1.units traitbwt.1:traittarsus.1.units
## Lag 0                         -0.003303414                   -0.033595784
## Lag 100                       -0.026601660                   -0.053415941
## Lag 500                        0.023989474                   -0.005220881
## Lag 1000                      -0.059547268                   -0.037570106
## Lag 5000                      -0.043225022                   -0.018285255
##          traittarsus.2:traittarsus.1.units traitbwt.2:traittarsus.1.units
## Lag 0                         -0.032394558                   -0.038463991
## Lag 100                       -0.025527001                   -0.031296257
## Lag 500                       -0.026572307                   -0.025766415
## Lag 1000                      -0.039244262                   -0.042965449
## Lag 5000                      -0.005888125                   -0.008787816
##          traittarsus.1:traitbwt.1.units traitbwt.1:traitbwt.1.units
## Lag 0                      -0.033595784                -0.047856148
## Lag 100                    -0.053415941                -0.036979690
## Lag 500                    -0.005220881                 0.004374636
## Lag 1000                   -0.037570106                -0.014564806
## Lag 5000                   -0.018285255                -0.019587618
##          traittarsus.2:traitbwt.1.units traitbwt.2:traitbwt.1.units
## Lag 0                      -0.044767110                -0.050917805
## Lag 100                    -0.038505551                -0.046892201
## Lag 500                    -0.026544619                -0.030053092
## Lag 1000                   -0.047964926                -0.058484565
## Lag 5000                    0.005513663                 0.008103974
##          traittarsus.1:traittarsus.2.units traitbwt.1:traittarsus.2.units
## Lag 0                         -0.032394558                   -0.044767110
## Lag 100                       -0.025527001                   -0.038505551
## Lag 500                       -0.026572307                   -0.026544619
## Lag 1000                      -0.039244262                   -0.047964926
## Lag 5000                      -0.005888125                    0.005513663
##          traittarsus.2:traittarsus.2.units traitbwt.2:traittarsus.2.units
## Lag 0                            0.1360740                      0.1159929
## Lag 100                          0.1741515                      0.1418886
## Lag 500                          0.1700049                      0.1445076
## Lag 1000                         0.1777767                      0.1521923
## Lag 5000                        -0.1463666                     -0.1686025
##          traittarsus.1:traitbwt.2.units traitbwt.1:traitbwt.2.units
## Lag 0                      -0.038463991                -0.050917805
## Lag 100                    -0.031296257                -0.046892201
## Lag 500                    -0.025766415                -0.030053092
## Lag 1000                   -0.042965449                -0.058484565
## Lag 5000                   -0.008787816                 0.008103974
##          traittarsus.2:traitbwt.2.units traitbwt.2:traitbwt.2.units
```

```
## Lag 0                    0.1159929                   0.0979877
## Lag 100                  0.1418886                   0.1021546
## Lag 500                  0.1445076                   0.1134636
## Lag 1000                 0.1521923                   0.1278208
## Lag 5000                -0.1686025                  -0.1687524
##
## , , traitbwt.2.mother
##
##            traittarsus.1:traittarsus.1.animal traitbwt.1:traittarsus.1.animal
## Lag 0                              0.05082067                    -0.011552553
## Lag 100                            0.04450359                    -0.023686867
## Lag 500                            0.04179199                     0.004658431
## Lag 1000                           0.02883236                    -0.006496015
## Lag 5000                           0.04112469                     0.028334393
##            traittarsus.2:traittarsus.1.animal traitbwt.2:traittarsus.1.animal
## Lag 0                              0.11172969                      0.04826105
## Lag 100                            0.10951168                      0.03784269
## Lag 500                            0.08924566                      0.03087286
## Lag 1000                           0.05576158                      0.03858511
## Lag 5000                          -0.02612490                      0.02719676
##            traittarsus.1:traitbwt.1.animal traitbwt.1:traitbwt.1.animal
## Lag 0                         -0.011552553                 -0.068290432
## Lag 100                       -0.023686867                 -0.061106862
## Lag 500                        0.004658431                 -0.008368994
## Lag 1000                      -0.006496015                  0.002748701
## Lag 5000                       0.028334393                  0.008620918
##            traittarsus.2:traitbwt.1.animal traitbwt.2:traitbwt.1.animal
## Lag 0                          0.004891297                 -0.095372303
## Lag 100                        0.018900269                 -0.050527725
## Lag 500                        0.034858608                 -0.018316704
## Lag 1000                       0.021136189                 -0.004218270
## Lag 5000                      -0.083516144                  0.008525728
##            traittarsus.1:traittarsus.2.animal traitbwt.1:traittarsus.2.animal
## Lag 0                              0.11172969                     0.004891297
## Lag 100                            0.10951168                     0.018900269
## Lag 500                            0.08924566                     0.034858608
## Lag 1000                           0.05576158                     0.021136189
## Lag 5000                          -0.02612490                    -0.083516144
##            traittarsus.2:traittarsus.2.animal traitbwt.2:traittarsus.2.animal
## Lag 0                              0.15871038                      0.09891371
## Lag 100                            0.13316302                      0.07837814
## Lag 500                            0.10976919                      0.06061434
## Lag 1000                           0.08100730                      0.06929365
## Lag 5000                          -0.02040836                     -0.01741179
##            traittarsus.1:traitbwt.2.animal traitbwt.1:traitbwt.2.animal
## Lag 0                           0.04826105                 -0.095372303
## Lag 100                         0.03784269                 -0.050527725
```

```
## Lag 500                    0.03087286                   -0.018316704
## Lag 1000                   0.03858511                   -0.004218270
## Lag 5000                   0.02719676                    0.008525728
##          traittarsus.2:traitbwt.2.animal traitbwt.2:traitbwt.2.animal
## Lag 0                      0.09891371                   -0.033866092
## Lag 100                    0.07837814                   -0.011360083
## Lag 500                    0.06061434                    0.012969192
## Lag 1000                   0.06929365                    0.045752648
## Lag 5000                  -0.01741179                   -0.001193243
##          traittarsus.1.byear traitbwt.1.byear traittarsus.2.byear
## Lag 0             0.02899206       0.05926846        0.0024956756
## Lag 100          -0.01583481       0.05520016        0.0239528518
## Lag 500           0.03917478       0.01148328        0.0002419691
## Lag 1000         -0.03694049       0.02504159        0.0667961149
## Lag 5000         -0.06196001       0.02957462        0.0049061407
##          traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother
## Lag 0        -0.007859673          -0.05622667        0.14519001
## Lag 100       0.010189964          -0.05585546        0.13743423
## Lag 500       0.007357905           0.02124383        0.03427438
## Lag 1000      0.029340288           0.06934074       -0.01797194
## Lag 5000      0.011164278           0.01230641        0.01184408
##          traittarsus.2.mother traitbwt.2.mother
## Lag 0           -0.329182837       1.000000000
## Lag 100         -0.235728358       0.284175599
## Lag 500         -0.148665968       0.029162936
## Lag 1000        -0.007592145      -0.008559910
## Lag 5000         0.006615767       0.006917489
##          traittarsus.1:traittarsus.1.units traitbwt.1:traittarsus.1.units
## Lag 0                          -0.04849521                    -0.01247903
## Lag 100                        -0.04229095                    -0.01179876
## Lag 500                        -0.06190225                    -0.03479262
## Lag 1000                       -0.06244621                    -0.01333269
## Lag 5000                       -0.04472803                    -0.03405548
##          traittarsus.2:traittarsus.1.units traitbwt.2:traittarsus.1.units
## Lag 0                           0.06299708                     0.07575889
## Lag 100                         0.05582189                     0.06465068
## Lag 500                         0.05304268                     0.04802379
## Lag 1000                        0.07638864                     0.07282218
## Lag 5000                        0.04062409                     0.05791562
##          traittarsus.1:traitbwt.1.units traitbwt.1:traitbwt.1.units
## Lag 0                       -0.01247903                -0.009223763
## Lag 100                     -0.01179876                -0.004801511
## Lag 500                     -0.03479262                -0.021159851
## Lag 1000                    -0.01333269                -0.005423005
## Lag 5000                    -0.03405548                -0.040128813
##          traittarsus.2:traitbwt.1.units traitbwt.2:traitbwt.1.units
## Lag 0                        0.07595500                  0.08248472
```

```
## Lag 100                    0.06741840                    0.07062568
## Lag 500                    0.04493967                    0.04348999
## Lag 1000                   0.05963657                    0.06140170
## Lag 5000                   0.05397711                    0.06956257
##          traittarsus.1:traittarsus.2.units traitbwt.1:traittarsus.2.units
## Lag 0                             0.06299708                     0.07595500
## Lag 100                           0.05582189                     0.06741840
## Lag 500                           0.05304268                     0.04493967
## Lag 1000                          0.07638864                     0.05963657
## Lag 5000                          0.04062409                     0.05397711
##          traittarsus.2:traittarsus.2.units traitbwt.2:traittarsus.2.units
## Lag 0                            -0.063098741                   -0.063844474
## Lag 100                          -0.069885333                   -0.060995678
## Lag 500                          -0.075115678                   -0.052589081
## Lag 1000                         -0.091682781                   -0.072696501
## Lag 5000                          0.004523339                    0.009847437
##          traittarsus.1:traitbwt.2.units traitbwt.1:traitbwt.2.units
## Lag 0                         0.07575889                  0.08248472
## Lag 100                       0.06465068                  0.07062568
## Lag 500                       0.04802379                  0.04348999
## Lag 1000                      0.07282218                  0.06140170
## Lag 5000                      0.05791562                  0.06956257
##          traittarsus.2:traitbwt.2.units traitbwt.2:traitbwt.2.units
## Lag 0                       -0.063844474                -0.079128573
## Lag 100                     -0.060995678                -0.038220443
## Lag 500                     -0.052589081                -0.022953575
## Lag 1000                    -0.072696501                -0.037549862
## Lag 5000                     0.009847437                -0.001314642
##
## , , traittarsus.1:traittarsus.1.units
##
##          traittarsus.1:traittarsus.1.animal traitbwt.1:traittarsus.1.animal
## Lag 0                              -0.69647928                     -0.53741563
## Lag 100                            -0.62623971                     -0.47900505
## Lag 500                            -0.45854096                     -0.35990127
## Lag 1000                           -0.34465891                     -0.24167598
## Lag 5000                           -0.04540565                     -0.08362331
##          traittarsus.2:traittarsus.1.animal traitbwt.2:traittarsus.1.animal
## Lag 0                               -0.4851021                      -0.3969630
## Lag 100                             -0.4391087                      -0.3672331
## Lag 500                             -0.3514192                      -0.3303341
## Lag 1000                            -0.2817756                      -0.2606715
## Lag 5000                            -0.1379797                      -0.1850268
##          traittarsus.1:traitbwt.1.animal traitbwt.1:traitbwt.1.animal
## Lag 0                           -0.53741563                   -0.2245265
## Lag 100                         -0.47900505                   -0.1935129
## Lag 500                         -0.35990127                   -0.1387130
```

```
## Lag 1000              -0.24167598                -0.1103208
## Lag 5000              -0.08362331                -0.1059888
##           traittarsus.2:traitbwt.1.animal traitbwt.2:traitbwt.1.animal
## Lag 0                      -0.3729388                   -0.2547414
## Lag 100                    -0.3377067                   -0.2223712
## Lag 500                    -0.2941086                   -0.2173660
## Lag 1000                   -0.2338232                   -0.1759256
## Lag 5000                   -0.1733008                   -0.1754188
##           traittarsus.1:traittarsus.2.animal traitbwt.1:traittarsus.2.animal
## Lag 0                         -0.4851021                      -0.3729388
## Lag 100                       -0.4391087                      -0.3377067
## Lag 500                       -0.3514192                      -0.2941086
## Lag 1000                      -0.2817756                      -0.2338232
## Lag 5000                      -0.1379797                      -0.1733008
##           traittarsus.2:traittarsus.2.animal traitbwt.2:traittarsus.2.animal
## Lag 0                        -0.10376953                      -0.1451563
## Lag 100                      -0.07852837                      -0.1303753
## Lag 500                      -0.06730801                      -0.1313359
## Lag 1000                     -0.06713014                      -0.1425029
## Lag 5000                     -0.15697371                      -0.2346428
##           traittarsus.1:traitbwt.2.animal traitbwt.1:traitbwt.2.animal
## Lag 0                      -0.3969630                   -0.2547414
## Lag 100                    -0.3672331                   -0.2223712
## Lag 500                    -0.3303341                   -0.2173660
## Lag 1000                   -0.2606715                   -0.1759256
## Lag 5000                   -0.1850268                   -0.1754188
##           traittarsus.2:traitbwt.2.animal traitbwt.2:traitbwt.2.animal
## Lag 0                      -0.1451563                   -0.1310687
## Lag 100                    -0.1303753                   -0.1210976
## Lag 500                    -0.1313359                   -0.1454273
## Lag 1000                   -0.1425029                   -0.1484290
## Lag 5000                   -0.2346428                   -0.2608162
##           traittarsus.1.byear traitbwt.1.byear traittarsus.2.byear
## Lag 0             -0.14506604     -0.043558650         -0.04924174
## Lag 100           -0.12498034     -0.053994536         -0.03871946
## Lag 500           -0.05225308     -0.005205432         -0.05590755
## Lag 1000          -0.05643316     -0.037921140          0.00532337
## Lag 5000          -0.01904738     -0.070857345          0.03761236
##           traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother
## Lag 0           0.01051817          -0.28511353        0.01973629
## Lag 100         0.03224747          -0.21849925        0.02374680
## Lag 500         0.03546917          -0.12897815        0.01858679
## Lag 1000        0.01230618          -0.03335119        0.03274960
## Lag 5000        0.02825979          -0.05125552        0.04540862
##           traittarsus.2.mother traitbwt.2.mother
## Lag 0             -0.003303414      -0.048495208
## Lag 100           -0.027103529      -0.040346222
```

```
## Lag 500        -0.025758939       0.002369226
## Lag 1000       -0.025407178      -0.024008377
## Lag 5000       -0.010658268       0.012747460
##          traittarsus.1:traittarsus.1.units traitbwt.1:traittarsus.1.units
## Lag 0                           1.00000000                     0.71266479
## Lag 100                         0.69601632                     0.48602800
## Lag 500                         0.44391095                     0.33331074
## Lag 1000                        0.32879898                     0.24626220
## Lag 5000                        0.09190517                     0.09278524
##          traittarsus.2:traittarsus.1.units traitbwt.2:traittarsus.1.units
## Lag 0                           -0.2592850                     -0.2645685
## Lag 100                         -0.2655767                     -0.2702771
## Lag 500                         -0.2886811                     -0.2950022
## Lag 1000                        -0.2858651                     -0.3159051
## Lag 5000                        -0.2005196                     -0.2351461
##          traittarsus.1:traitbwt.1.units traitbwt.1:traitbwt.1.units
## Lag 0                        0.71266479                   0.3606694
## Lag 100                      0.48602800                   0.2474550
## Lag 500                      0.33331074                   0.1595171
## Lag 1000                     0.24626220                   0.1323001
## Lag 5000                     0.09278524                   0.1142750
##          traittarsus.2:traitbwt.1.units traitbwt.2:traitbwt.1.units
## Lag 0                        -0.2009925                  -0.1971901
## Lag 100                      -0.2133808                  -0.2127295
## Lag 500                      -0.2513257                  -0.2534202
## Lag 1000                     -0.2644654                  -0.2860502
## Lag 5000                     -0.2208762                  -0.2453635
##          traittarsus.1:traittarsus.2.units traitbwt.1:traittarsus.2.units
## Lag 0                           -0.2592850                     -0.2009925
## Lag 100                         -0.2655767                     -0.2133808
## Lag 500                         -0.2886811                     -0.2513257
## Lag 1000                        -0.2858651                     -0.2644654
## Lag 5000                        -0.2005196                     -0.2208762
##          traittarsus.2:traittarsus.2.units traitbwt.2:traittarsus.2.units
## Lag 0                           0.09543017                     0.11602826
## Lag 100                         0.06131639                     0.09650511
## Lag 500                         0.06137108                     0.11179013
## Lag 1000                        0.08079826                     0.13634360
## Lag 5000                        0.18979188                     0.24893895
##          traittarsus.1:traitbwt.2.units traitbwt.1:traitbwt.2.units
## Lag 0                        -0.2645685                  -0.1971901
## Lag 100                      -0.2702771                  -0.2127295
## Lag 500                      -0.2950022                  -0.2534202
## Lag 1000                     -0.3159051                  -0.2860502
## Lag 5000                     -0.2351461                  -0.2453635
##          traittarsus.2:traitbwt.2.units traitbwt.2:traitbwt.2.units
## Lag 0                        0.11602826                  0.10062986
```

```
## Lag 100                     0.09650511                  0.09093566
## Lag 500                     0.11179013                  0.12421446
## Lag 1000                    0.13634360                  0.14583460
## Lag 5000                    0.24893895                  0.25949670
##
## , , traitbwt.1:traittarsus.1.units
##
##            traittarsus.1:traittarsus.1.animal traitbwt.1:traittarsus.1.animal
## Lag 0                              -0.5806661                      -0.7822168
## Lag 100                            -0.5195230                      -0.6845208
## Lag 500                            -0.3880444                      -0.4391722
## Lag 1000                           -0.2850697                      -0.3219049
## Lag 5000                           -0.1858774                      -0.1615545
##            traittarsus.2:traittarsus.1.animal traitbwt.2:traittarsus.1.animal
## Lag 0                              -0.3551367                      -0.4423544
## Lag 100                            -0.3116917                      -0.4053917
## Lag 500                            -0.2504438                      -0.3222535
## Lag 1000                           -0.2164808                      -0.2714011
## Lag 5000                           -0.1964028                      -0.1739972
##            traittarsus.1:traitbwt.1.animal traitbwt.1:traitbwt.1.animal
## Lag 0                           -0.7822168                   -0.5785722
## Lag 100                         -0.6845208                   -0.5036377
## Lag 500                         -0.4391722                   -0.3105590
## Lag 1000                        -0.3219049                   -0.2500610
## Lag 5000                        -0.1615545                   -0.1051180
##            traittarsus.2:traitbwt.1.animal traitbwt.2:traitbwt.1.animal
## Lag 0                           -0.3850991                   -0.3630159
## Lag 100                         -0.3306453                   -0.3097920
## Lag 500                         -0.2840530                   -0.2549302
## Lag 1000                        -0.2403468                   -0.2124423
## Lag 5000                        -0.2587649                   -0.2036370
##            traittarsus.1:traittarsus.2.animal traitbwt.1:traittarsus.2.animal
## Lag 0                              -0.3551367                      -0.3850991
## Lag 100                            -0.3116917                      -0.3306453
## Lag 500                            -0.2504438                      -0.2840530
## Lag 1000                           -0.2164808                      -0.2403468
## Lag 5000                           -0.1964028                      -0.2587649
##            traittarsus.2:traittarsus.2.animal traitbwt.2:traittarsus.2.animal
## Lag 0                             -0.10398125                      -0.1467921
## Lag 100                           -0.07656994                      -0.1228344
## Lag 500                           -0.05666776                      -0.1265197
## Lag 1000                          -0.08628503                      -0.1605079
## Lag 5000                          -0.11080574                      -0.1945688
##            traittarsus.1:traitbwt.2.animal traitbwt.1:traitbwt.2.animal
## Lag 0                           -0.4423544                   -0.3630159
## Lag 100                         -0.4053917                   -0.3097920
## Lag 500                         -0.3222535                   -0.2549302
```

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## Lag 1000                    -0.2714011                    -0.2124423
## Lag 5000                    -0.1739972                    -0.2036370
##          traittarsus.2:traitbwt.2.animal traitbwt.2:traitbwt.2.animal
## Lag 0                       -0.1467921                    -0.1324172
## Lag 100                     -0.1228344                    -0.1123196
## Lag 500                     -0.1265197                    -0.1443413
## Lag 1000                    -0.1605079                    -0.1717954
## Lag 5000                    -0.1945688                    -0.2243561
##          traittarsus.1.byear traitbwt.1.byear traittarsus.2.byear
## Lag 0            -0.10471675       0.01021951        0.0004983836
## Lag 100          -0.08194667       0.01380504       -0.0044687157
## Lag 500          -0.01278894       0.03290932       -0.0005650915
## Lag 1000         -0.06407190      -0.02170329        0.0530406940
## Lag 5000         -0.07516029      -0.06130238       -0.0224119290
##          traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother
## Lag 0          0.02175859         -0.039522955        0.03665672
## Lag 100        0.03477326         -0.019056605        0.05315654
## Lag 500       -0.01973469         -0.002626844        0.03028858
## Lag 1000       0.04003712          0.003169525        0.06449203
## Lag 5000       0.02550062         -0.010727363        0.04503907
##          traittarsus.2.mother traitbwt.2.mother
## Lag 0             -0.03359578      -0.012479028
## Lag 100           -0.04488434      -0.002934766
## Lag 500           -0.06697376       0.021613573
## Lag 1000          -0.08457909       0.019481160
## Lag 5000          -0.08600099       0.051485249
##          traittarsus.1:traittarsus.1.units traitbwt.1:traittarsus.1.units
## Lag 0                            0.7126648                      1.0000000
## Lag 100                          0.4891102                      0.6680602
## Lag 500                          0.3020606                      0.3997173
## Lag 1000                         0.2345067                      0.2999511
## Lag 5000                         0.1759098                      0.1561292
##          traittarsus.2:traittarsus.1.units traitbwt.2:traittarsus.1.units
## Lag 0                           -0.1706739                     -0.1801399
## Lag 100                         -0.1802375                     -0.1994176
## Lag 500                         -0.2103921                     -0.2440747
## Lag 1000                        -0.2087782                     -0.2510893
## Lag 5000                        -0.1812853                     -0.1905911
##          traittarsus.1:traitbwt.1.units traitbwt.1:traitbwt.1.units
## Lag 0                         1.0000000                   0.8197350
## Lag 100                       0.6680602                   0.5536026
## Lag 500                       0.3997173                   0.3326177
## Lag 1000                      0.2999511                   0.2334663
## Lag 5000                      0.1561292                   0.1202757
##          traittarsus.2:traitbwt.1.units traitbwt.2:traitbwt.1.units
## Lag 0                        -0.1666030                  -0.1700866
## Lag 100                      -0.1812316                  -0.1939150
```

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## Lag 500                    -0.2194596                  -0.2430469
## Lag 1000                   -0.2384353                  -0.2743602
## Lag 5000                   -0.2008085                  -0.2014312
##          traittarsus.1:traittarsus.2.units traitbwt.1:traittarsus.2.units
## Lag 0                           -0.1706739                     -0.1666030
## Lag 100                         -0.1802375                     -0.1812316
## Lag 500                         -0.2103921                     -0.2194596
## Lag 1000                        -0.2087782                     -0.2384353
## Lag 5000                        -0.1812853                     -0.2008085
##          traittarsus.2:traittarsus.2.units traitbwt.2:traittarsus.2.units
## Lag 0                           0.10875399                     0.13276682
## Lag 100                         0.05904373                     0.09500984
## Lag 500                         0.06612909                     0.11639092
## Lag 1000                        0.10572947                     0.15285062
## Lag 5000                        0.15545551                     0.20383203
##          traittarsus.1:traitbwt.2.units traitbwt.1:traitbwt.2.units
## Lag 0                        -0.1801399                  -0.1700866
## Lag 100                      -0.1994176                  -0.1939150
## Lag 500                      -0.2440747                  -0.2430469
## Lag 1000                     -0.2510893                  -0.2743602
## Lag 5000                     -0.1905911                  -0.2014312
##          traittarsus.2:traitbwt.2.units traitbwt.2:traitbwt.2.units
## Lag 0                        0.13276682                  0.11344391
## Lag 100                      0.09500984                  0.08651744
## Lag 500                      0.11639092                  0.13209239
## Lag 1000                     0.15285062                  0.15588819
## Lag 5000                     0.20383203                  0.21723655
##
## , , traittarsus.2:traittarsus.1.units
##
##          traittarsus.1:traittarsus.1.animal traitbwt.1:traittarsus.1.animal
## Lag 0                             0.1834123                     0.124710076
## Lag 100                           0.1968309                     0.130500544
## Lag 500                           0.2068864                     0.139328738
## Lag 1000                          0.1939570                     0.142277480
## Lag 5000                          0.1325680                     0.009474997
##          traittarsus.2:traittarsus.1.animal traitbwt.2:traittarsus.1.animal
## Lag 0                             0.1906441                      0.13328596
## Lag 100                           0.2063827                      0.13989222
## Lag 500                           0.2249905                      0.15953298
## Lag 1000                          0.2243627                      0.17422740
## Lag 5000                          0.1612708                      0.09845918
##          traittarsus.1:traitbwt.1.animal traitbwt.1:traitbwt.1.animal
## Lag 0                        0.124710076                   0.08095300
## Lag 100                      0.130500544                   0.07950890
## Lag 500                      0.139328738                   0.07894049
## Lag 1000                     0.142277480                   0.08409986
```

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## Lag 5000                 0.009474997                     -0.03476503
##          traittarsus.2:traitbwt.1.animal traitbwt.2:traitbwt.1.animal
## Lag 0                     0.13041646                     0.06808542
## Lag 100                   0.13619199                     0.07439607
## Lag 500                   0.15236746                     0.10133254
## Lag 1000                  0.16354531                     0.12513909
## Lag 5000                  0.09727094                     0.09702098
##          traittarsus.1:traittarsus.2.animal traitbwt.1:traittarsus.2.animal
## Lag 0                             0.1906441                      0.13041646
## Lag 100                           0.2063827                      0.13619199
## Lag 500                           0.2249905                      0.15236746
## Lag 1000                          0.2243627                      0.16354531
## Lag 5000                          0.1612708                      0.09727094
##          traittarsus.2:traittarsus.2.animal traitbwt.2:traittarsus.2.animal
## Lag 0                             0.1881270                       0.1805175
## Lag 100                           0.2019192                       0.1895957
## Lag 500                           0.2143083                       0.2038416
## Lag 1000                          0.2049762                       0.2031078
## Lag 5000                          0.2015150                       0.2236163
##          traittarsus.1:traitbwt.2.animal traitbwt.1:traitbwt.2.animal
## Lag 0                     0.13328596                     0.06808542
## Lag 100                   0.13989222                     0.07439607
## Lag 500                   0.15953298                     0.10133254
## Lag 1000                  0.17422740                     0.12513909
## Lag 5000                  0.09845918                     0.09702098
##          traittarsus.2:traitbwt.2.animal traitbwt.2:traitbwt.2.animal
## Lag 0                      0.1805175                      0.1307188
## Lag 100                    0.1895957                      0.1387545
## Lag 500                    0.2038416                      0.1596754
## Lag 1000                   0.2031078                      0.1718471
## Lag 5000                   0.2236163                      0.2388384
##          traittarsus.1.byear traitbwt.1.byear traittarsus.2.byear
## Lag 0             -0.03847015       0.05293519          0.06126409
## Lag 100           -0.03144044       0.04956734          0.06250612
## Lag 500           -0.01780154       0.05591029          0.07921148
## Lag 1000          -0.02643841       0.04337011          0.09113494
## Lag 5000          -0.01140358       0.03031863         -0.02594409
##          traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother
## Lag 0        -0.041798551            0.1697424        0.04294093
## Lag 100      -0.034073821            0.1688986        0.04145441
## Lag 500      -0.048890409            0.1720568        0.02794912
## Lag 1000     -0.040999443            0.1790535        0.02144402
## Lag 5000     -0.002784642            0.1836021       -0.02796491
##          traittarsus.2.mother traitbwt.2.mother
## Lag 0              -0.03239456        0.06299708
## Lag 100            -0.03271179        0.06442310
## Lag 500            -0.02932124        0.06841853
```

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## Lag 1000         -0.01370787        0.05547883
## Lag 5000         -0.04156138        0.02258640
##          traittarsus.1:traittarsus.1.units traitbwt.1:traittarsus.1.units
## Lag 0                           -0.2592850                    -0.17067395
## Lag 100                         -0.2666810                    -0.16983312
## Lag 500                         -0.2761829                    -0.17499382
## Lag 1000                        -0.2748628                    -0.18004636
## Lag 5000                        -0.2185399                    -0.04226407
##          traittarsus.2:traittarsus.1.units traitbwt.2:traittarsus.1.units
## Lag 0                            1.0000000                      0.9603400
## Lag 100                          0.9783825                      0.9444274
## Lag 500                          0.9365031                      0.9054416
## Lag 1000                         0.8964880                      0.8617258
## Lag 5000                         0.6039003                      0.6022291
##          traittarsus.1:traitbwt.1.units traitbwt.1:traitbwt.1.units
## Lag 0                       -0.17067395                 -0.12741602
## Lag 100                     -0.16983312                 -0.12362277
## Lag 500                     -0.17499382                 -0.11972769
## Lag 1000                    -0.18004636                 -0.12502460
## Lag 5000                    -0.04226407                  0.01790192
##          traittarsus.2:traitbwt.1.units traitbwt.2:traitbwt.1.units
## Lag 0                         0.9609935                   0.9034487
## Lag 100                       0.9411829                   0.8893146
## Lag 500                       0.8990207                   0.8539291
## Lag 1000                      0.8622161                   0.8157349
## Lag 5000                      0.5753236                   0.5773694
##          traittarsus.1:traittarsus.2.units traitbwt.1:traittarsus.2.units
## Lag 0                            1.0000000                      0.9609935
## Lag 100                          0.9783825                      0.9411829
## Lag 500                          0.9365031                      0.8990207
## Lag 1000                         0.8964880                      0.8622161
## Lag 5000                         0.6039003                      0.5753236
##          traittarsus.2:traittarsus.2.units traitbwt.2:traittarsus.2.units
## Lag 0                           -0.1856903                     -0.1801544
## Lag 100                         -0.1921763                     -0.1830867
## Lag 500                         -0.2110415                     -0.2009371
## Lag 1000                        -0.2033807                     -0.1989511
## Lag 5000                        -0.1866476                     -0.2075534
##          traittarsus.1:traitbwt.2.units traitbwt.1:traitbwt.2.units
## Lag 0                         0.9603400                   0.9034487
## Lag 100                       0.9444274                   0.8893146
## Lag 500                       0.9054416                   0.8539291
## Lag 1000                      0.8617258                   0.8157349
## Lag 5000                      0.6022291                   0.5773694
##          traittarsus.2:traitbwt.2.units traitbwt.2:traitbwt.2.units
## Lag 0                        -0.1801544                  -0.1345421
## Lag 100                      -0.1830867                  -0.1370653
```

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## Lag 500                    -0.2009371                   -0.1566901
## Lag 1000                   -0.1989511                   -0.1643648
## Lag 5000                   -0.2075534                   -0.2123302
##
## , , traitbwt.2:traittarsus.1.units
##
##           traittarsus.1:traittarsus.1.animal traitbwt.1:traittarsus.1.animal
## Lag 0                              0.1843936                      0.13991929
## Lag 100                            0.1916063                      0.14051238
## Lag 500                            0.1997384                      0.15350375
## Lag 1000                           0.1779242                      0.14333349
## Lag 5000                           0.1059309                      0.02408511
##           traittarsus.2:traittarsus.1.animal traitbwt.2:traittarsus.1.animal
## Lag 0                              0.2159001                      0.18941930
## Lag 100                            0.2292097                      0.19756460
## Lag 500                            0.2470830                      0.21294438
## Lag 1000                           0.2430281                      0.21181509
## Lag 5000                           0.1564420                      0.09549646
##           traittarsus.1:traitbwt.1.animal traitbwt.1:traitbwt.1.animal
## Lag 0                          0.13991929                   0.11864383
## Lag 100                        0.14051238                   0.11475981
## Lag 500                        0.15350375                   0.12191537
## Lag 1000                       0.14333349                   0.12719171
## Lag 5000                       0.02408511                  -0.00131242
##           traittarsus.2:traitbwt.1.animal traitbwt.2:traitbwt.1.animal
## Lag 0                           0.1778597                    0.1473359
## Lag 100                         0.1832967                    0.1558541
## Lag 500                         0.2035349                    0.1829320
## Lag 1000                        0.2085231                    0.1947599
## Lag 5000                        0.1096782                    0.1076230
##           traittarsus.1:traittarsus.2.animal traitbwt.1:traittarsus.2.animal
## Lag 0                              0.2159001                       0.1778597
## Lag 100                            0.2292097                       0.1832967
## Lag 500                            0.2470830                       0.2035349
## Lag 1000                           0.2430281                       0.2085231
## Lag 5000                           0.1564420                       0.1096782
##           traittarsus.2:traittarsus.2.animal traitbwt.2:traittarsus.2.animal
## Lag 0                              0.2148002                       0.2380759
## Lag 100                            0.2260582                       0.2490150
## Lag 500                            0.2434250                       0.2659527
## Lag 1000                           0.2396319                       0.2621966
## Lag 5000                           0.2311987                       0.2321063
##           traittarsus.1:traitbwt.2.animal traitbwt.1:traitbwt.2.animal
## Lag 0                          0.18941930                    0.1473359
## Lag 100                        0.19756460                    0.1558541
## Lag 500                        0.21294438                    0.1829320
## Lag 1000                       0.21181509                    0.1947599
```

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## Lag 5000                     0.09549646                    0.1076230
##          traittarsus.2:traitbwt.2.animal traitbwt.2:traitbwt.2.animal
## Lag 0                         0.2380759                    0.2116292
## Lag 100                       0.2490150                    0.2231338
## Lag 500                       0.2659527                    0.2429222
## Lag 1000                      0.2621966                    0.2441661
## Lag 5000                      0.2321063                    0.2236298
##          traittarsus.1.byear traitbwt.1.byear traittarsus.2.byear
## Lag 0          -0.032369970       0.05768879          0.06054337
## Lag 100        -0.031641858       0.05864059          0.06580478
## Lag 500        -0.001530924       0.04503326          0.07399288
## Lag 1000       -0.016005519       0.03161375          0.08585903
## Lag 5000        0.010619935       0.01730446         -0.02417570
##          traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother
## Lag 0       -0.032356483            0.1703875       0.012376673
## Lag 100     -0.034654911            0.1647608       0.013581085
## Lag 500     -0.052597308            0.1600416       0.005553001
## Lag 1000    -0.039591608            0.1872703      -0.009042770
## Lag 5000     0.004455343            0.1972374      -0.027185781
##          traittarsus.2.mother traitbwt.2.mother
## Lag 0             -0.03846399        0.07575889
## Lag 100           -0.03390447        0.06853459
## Lag 500           -0.02862102        0.06274714
## Lag 1000          -0.01799649        0.06065063
## Lag 5000          -0.05555704        0.02202828
##          traittarsus.1:traittarsus.1.units traitbwt.1:traittarsus.1.units
## Lag 0                           -0.2645685                    -0.18013988
## Lag 100                         -0.2616234                    -0.17607364
## Lag 500                         -0.2652457                    -0.18034511
## Lag 1000                        -0.2671219                    -0.17702256
## Lag 5000                        -0.2093233                    -0.06028968
##          traittarsus.2:traittarsus.1.units traitbwt.2:traittarsus.1.units
## Lag 0                            0.9603400                      1.0000000
## Lag 100                          0.9432077                      0.9762869
## Lag 500                          0.9124477                      0.9252632
## Lag 1000                         0.8838890                      0.8792611
## Lag 5000                         0.6117319                      0.6007465
##          traittarsus.1:traitbwt.1.units traitbwt.1:traitbwt.1.units
## Lag 0                       -0.18013988                 -0.15026999
## Lag 100                     -0.17607364                 -0.14749648
## Lag 500                     -0.18034511                 -0.15145709
## Lag 1000                    -0.17702256                 -0.15538707
## Lag 5000                    -0.06028968                 -0.02621414
##          traittarsus.2:traitbwt.1.units traitbwt.2:traitbwt.1.units
## Lag 0                         0.9303986                   0.9527160
## Lag 100                       0.9147001                   0.9321247
## Lag 500                       0.8850543                   0.8884276
```

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## Lag 1000                     0.8576398                    0.8431799
## Lag 5000                     0.5876791                    0.5807055
##          traittarsus.1:traittarsus.2.units traitbwt.1:traittarsus.2.units
## Lag 0                              0.9603400                      0.9303986
## Lag 100                            0.9432077                      0.9147001
## Lag 500                            0.9124477                      0.8850543
## Lag 1000                           0.8838890                      0.8576398
## Lag 5000                           0.6117319                      0.5876791
##          traittarsus.2:traittarsus.2.units traitbwt.2:traittarsus.2.units
## Lag 0                             -0.2006563                     -0.2276707
## Lag 100                           -0.2124295                     -0.2354203
## Lag 500                           -0.2379446                     -0.2556157
## Lag 1000                          -0.2389714                     -0.2561306
## Lag 5000                          -0.2130152                     -0.2137306
##          traittarsus.1:traitbwt.2.units traitbwt.1:traitbwt.2.units
## Lag 0                         1.0000000                   0.9527160
## Lag 100                       0.9762869                   0.9321247
## Lag 500                       0.9252632                   0.8884276
## Lag 1000                      0.8792611                   0.8431799
## Lag 5000                      0.6007465                   0.5807055
##          traittarsus.2:traitbwt.2.units traitbwt.2:traitbwt.2.units
## Lag 0                        -0.2276707                  -0.2128094
## Lag 100                      -0.2354203                  -0.2168142
## Lag 500                      -0.2556157                  -0.2324758
## Lag 1000                     -0.2561306                  -0.2373888
## Lag 5000                     -0.2137306                  -0.1974646
##
## , , traittarsus.1:traitbwt.1.units
##
##          traittarsus.1:traittarsus.1.animal traitbwt.1:traittarsus.1.animal
## Lag 0                               -0.5806661                      -0.7822168
## Lag 100                             -0.5195230                      -0.6845208
## Lag 500                             -0.3880444                      -0.4391722
## Lag 1000                            -0.2850697                      -0.3219049
## Lag 5000                            -0.1858774                      -0.1615545
##          traittarsus.2:traittarsus.1.animal traitbwt.2:traittarsus.1.animal
## Lag 0                               -0.3551367                      -0.4423544
## Lag 100                             -0.3116917                      -0.4053917
## Lag 500                             -0.2504438                      -0.3222535
## Lag 1000                            -0.2164808                      -0.2714011
## Lag 5000                            -0.1964028                      -0.1739972
##          traittarsus.1:traitbwt.1.animal traitbwt.1:traitbwt.1.animal
## Lag 0                         -0.7822168                   -0.5785722
## Lag 100                       -0.6845208                   -0.5036377
## Lag 500                       -0.4391722                   -0.3105590
## Lag 1000                      -0.3219049                   -0.2500610
## Lag 5000                      -0.1615545                   -0.1051180
```

```
##          traittarsus.2:traitbwt.1.animal traitbwt.2:traitbwt.1.animal
## Lag 0                        -0.3850991                   -0.3630159
## Lag 100                      -0.3306453                   -0.3097920
## Lag 500                      -0.2840530                   -0.2549302
## Lag 1000                     -0.2403468                   -0.2124423
## Lag 5000                     -0.2587649                   -0.2036370
##          traittarsus.1:traittarsus.2.animal traitbwt.1:traittarsus.2.animal
## Lag 0                           -0.3551367                      -0.3850991
## Lag 100                         -0.3116917                      -0.3306453
## Lag 500                         -0.2504438                      -0.2840530
## Lag 1000                        -0.2164808                      -0.2403468
## Lag 5000                        -0.1964028                      -0.2587649
##          traittarsus.2:traittarsus.2.animal traitbwt.2:traittarsus.2.animal
## Lag 0                          -0.10398125                      -0.1467921
## Lag 100                        -0.07656994                      -0.1228344
## Lag 500                        -0.05666776                      -0.1265197
## Lag 1000                       -0.08628503                      -0.1605079
## Lag 5000                       -0.11080574                      -0.1945688
##          traittarsus.1:traitbwt.2.animal traitbwt.1:traitbwt.2.animal
## Lag 0                        -0.4423544                   -0.3630159
## Lag 100                      -0.4053917                   -0.3097920
## Lag 500                      -0.3222535                   -0.2549302
## Lag 1000                     -0.2714011                   -0.2124423
## Lag 5000                     -0.1739972                   -0.2036370
##          traittarsus.2:traitbwt.2.animal traitbwt.2:traitbwt.2.animal
## Lag 0                        -0.1467921                   -0.1324172
## Lag 100                      -0.1228344                   -0.1123196
## Lag 500                      -0.1265197                   -0.1443413
## Lag 1000                     -0.1605079                   -0.1717954
## Lag 5000                     -0.1945688                   -0.2243561
##          traittarsus.1.byear traitbwt.1.byear traittarsus.2.byear
## Lag 0            -0.10471675       0.01021951        0.0004983836
## Lag 100          -0.08194667       0.01380504       -0.0044687157
## Lag 500          -0.01278894       0.03290932       -0.0005650915
## Lag 1000         -0.06407190      -0.02170329        0.0530406940
## Lag 5000         -0.07516029      -0.06130238       -0.0224119290
##          traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother
## Lag 0          0.02175859         -0.039522955        0.03665672
## Lag 100        0.03477326         -0.019056605        0.05315654
## Lag 500       -0.01973469         -0.002626844        0.03028858
## Lag 1000       0.04003712          0.003169525        0.06449203
## Lag 5000       0.02550062         -0.010727363        0.04503907
##          traittarsus.2.mother traitbwt.2.mother
## Lag 0             -0.03359578      -0.012479028
## Lag 100           -0.04488434      -0.002934766
## Lag 500           -0.06697376       0.021613573
## Lag 1000          -0.08457909       0.019481160
```

```
## Lag 5000          -0.08600099       0.051485249
##          traittarsus.1:traittarsus.1.units traitbwt.1:traittarsus.1.units
## Lag 0                            0.7126648                      1.0000000
## Lag 100                          0.4891102                      0.6680602
## Lag 500                          0.3020606                      0.3997173
## Lag 1000                         0.2345067                      0.2999511
## Lag 5000                         0.1759098                      0.1561292
##          traittarsus.2:traittarsus.1.units traitbwt.2:traittarsus.1.units
## Lag 0                           -0.1706739                     -0.1801399
## Lag 100                         -0.1802375                     -0.1994176
## Lag 500                         -0.2103921                     -0.2440747
## Lag 1000                        -0.2087782                     -0.2510893
## Lag 5000                        -0.1812853                     -0.1905911
##          traittarsus.1:traitbwt.1.units traitbwt.1:traitbwt.1.units
## Lag 0                         1.0000000                   0.8197350
## Lag 100                       0.6680602                   0.5536026
## Lag 500                       0.3997173                   0.3326177
## Lag 1000                      0.2999511                   0.2334663
## Lag 5000                      0.1561292                   0.1202757
##          traittarsus.2:traitbwt.1.units traitbwt.2:traitbwt.1.units
## Lag 0                        -0.1666030                  -0.1700866
## Lag 100                      -0.1812316                  -0.1939150
## Lag 500                      -0.2194596                  -0.2430469
## Lag 1000                     -0.2384353                  -0.2743602
## Lag 5000                     -0.2008085                  -0.2014312
##          traittarsus.1:traittarsus.2.units traitbwt.1:traittarsus.2.units
## Lag 0                           -0.1706739                     -0.1666030
## Lag 100                         -0.1802375                     -0.1812316
## Lag 500                         -0.2103921                     -0.2194596
## Lag 1000                        -0.2087782                     -0.2384353
## Lag 5000                        -0.1812853                     -0.2008085
##          traittarsus.2:traittarsus.2.units traitbwt.2:traittarsus.2.units
## Lag 0                           0.10875399                     0.13276682
## Lag 100                         0.05904373                     0.09500984
## Lag 500                         0.06612909                     0.11639092
## Lag 1000                        0.10572947                     0.15285062
## Lag 5000                        0.15545551                     0.20383203
##          traittarsus.1:traitbwt.2.units traitbwt.1:traitbwt.2.units
## Lag 0                        -0.1801399                  -0.1700866
## Lag 100                      -0.1994176                  -0.1939150
## Lag 500                      -0.2440747                  -0.2430469
## Lag 1000                     -0.2510893                  -0.2743602
## Lag 5000                     -0.1905911                  -0.2014312
##          traittarsus.2:traitbwt.2.units traitbwt.2:traitbwt.2.units
## Lag 0                        0.13276682                  0.11344391
## Lag 100                      0.09500984                  0.08651744
## Lag 500                      0.11639092                  0.13209239
```

```
## Lag 1000                     0.15285062                    0.15588819
## Lag 5000                     0.20383203                    0.21723655
##
## , , traitbwt.1:traitbwt.1.units
##
##            traittarsus.1:traittarsus.1.animal traitbwt.1:traittarsus.1.animal
## Lag 0                             -0.29723299                      -0.6444049
## Lag 100                           -0.26194069                      -0.5583089
## Lag 500                           -0.17460653                      -0.3429615
## Lag 1000                          -0.09216281                      -0.2402326
## Lag 5000                          -0.14907830                      -0.1125298
##            traittarsus.2:traittarsus.1.animal traitbwt.2:traittarsus.1.animal
## Lag 0                             -0.16353731                     -0.33002093
## Lag 100                           -0.13444098                     -0.30242196
## Lag 500                           -0.07860312                     -0.20182430
## Lag 1000                          -0.07437860                     -0.16489835
## Lag 5000                          -0.15240021                     -0.07855392
##            traittarsus.1:traitbwt.1.animal traitbwt.1:traitbwt.1.animal
## Lag 0                          -0.6444049                 -0.72140390
## Lag 100                        -0.5583089                 -0.60150571
## Lag 500                        -0.3429615                 -0.35781515
## Lag 1000                       -0.2402326                 -0.29870892
## Lag 5000                       -0.1125298                 -0.04717998
##            traittarsus.2:traitbwt.1.animal traitbwt.2:traitbwt.1.animal
## Lag 0                          -0.2793636                   -0.3902410
## Lag 100                        -0.2441693                   -0.3411243
## Lag 500                        -0.1881361                   -0.2431591
## Lag 1000                       -0.1803300                   -0.2025644
## Lag 5000                       -0.2243905                   -0.1275516
##            traittarsus.1:traittarsus.2.animal traitbwt.1:traittarsus.2.animal
## Lag 0                             -0.16353731                      -0.2793636
## Lag 100                           -0.13444098                      -0.2441693
## Lag 500                           -0.07860312                      -0.1881361
## Lag 1000                          -0.07437860                      -0.1803300
## Lag 5000                          -0.15240021                      -0.2243905
##            traittarsus.2:traittarsus.2.animal traitbwt.2:traittarsus.2.animal
## Lag 0                             -0.10182068                     -0.14376430
## Lag 100                           -0.07461870                     -0.12129614
## Lag 500                           -0.03475445                     -0.09690301
## Lag 1000                          -0.07582375                     -0.13287333
## Lag 5000                          -0.06172035                     -0.10552070
##            traittarsus.1:traitbwt.2.animal traitbwt.1:traitbwt.2.animal
## Lag 0                         -0.33002093                   -0.3902410
## Lag 100                       -0.30242196                   -0.3411243
## Lag 500                       -0.20182430                   -0.2431591
## Lag 1000                      -0.16489835                   -0.2025644
## Lag 5000                      -0.07855392                   -0.1275516
```

```
##           traittarsus.2:traitbwt.2.animal traitbwt.2:traitbwt.2.animal
## Lag 0                         -0.14376430                   -0.1400636
## Lag 100                       -0.12129614                   -0.1267043
## Lag 500                       -0.09690301                   -0.1357567
## Lag 1000                      -0.13287333                   -0.1570152
## Lag 5000                      -0.10552070                   -0.1203712
##           traittarsus.1.byear traitbwt.1.byear traittarsus.2.byear
## Lag 0            -0.071954690     -0.028183637          0.04524320
## Lag 100          -0.044770596      0.002882978          0.03767827
## Lag 500          -0.005911696      0.003838461          0.01619977
## Lag 1000         -0.056263708      0.008443638          0.05346543
## Lag 5000         -0.087263536     -0.023015448         -0.01948411
##           traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother
## Lag 0          0.008779544          0.028265685      -0.007047622
## Lag 100        0.013764785          0.026135300       0.054993361
## Lag 500       -0.033989612          0.002688467       0.096589744
## Lag 1000       0.025220721          0.005441149       0.099042795
## Lag 5000       0.047628522         -0.007718921       0.047775710
##           traittarsus.2.mother traitbwt.2.mother
## Lag 0              -0.04785615      -0.009223763
## Lag 100            -0.05001172       0.003907093
## Lag 500            -0.07099090       0.044036802
## Lag 1000           -0.05777658       0.037746309
## Lag 5000           -0.09694236       0.069793617
##           traittarsus.1:traittarsus.1.units traitbwt.1:traittarsus.1.units
## Lag 0                            0.36066940                      0.8197350
## Lag 100                          0.25257032                      0.5640460
## Lag 500                          0.11373127                      0.3085415
## Lag 1000                         0.07190253                      0.2121382
## Lag 5000                         0.13152446                      0.1159014
##           traittarsus.2:traittarsus.1.units traitbwt.2:traittarsus.1.units
## Lag 0                            -0.1274160                     -0.1502700
## Lag 100                          -0.1314926                     -0.1663342
## Lag 500                          -0.1561690                     -0.2058338
## Lag 1000                         -0.1493199                     -0.1963753
## Lag 5000                         -0.1353839                     -0.1194476
##           traittarsus.1:traitbwt.1.units traitbwt.1:traitbwt.1.units
## Lag 0                          0.8197350                  1.00000000
## Lag 100                        0.5640460                  0.66059880
## Lag 500                        0.3085415                  0.35457689
## Lag 1000                       0.2121382                  0.23677816
## Lag 5000                       0.1159014                  0.06278176
##           traittarsus.2:traitbwt.1.units traitbwt.2:traitbwt.1.units
## Lag 0                         -0.1670809                  -0.1902055
## Lag 100                       -0.1716919                  -0.2107271
## Lag 500                       -0.1984597                  -0.2462995
## Lag 1000                      -0.2124167                  -0.2635936
```

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## Lag 5000                     -0.1444361                    -0.1252641
##          traittarsus.1:traittarsus.2.units traitbwt.1:traittarsus.2.units
## Lag 0                           -0.1274160                     -0.1670809
## Lag 100                         -0.1314926                     -0.1716919
## Lag 500                         -0.1561690                     -0.1984597
## Lag 1000                        -0.1493199                     -0.2124167
## Lag 5000                        -0.1353839                     -0.1444361
##          traittarsus.2:traittarsus.2.units traitbwt.2:traittarsus.2.units
## Lag 0                           0.11081955                     0.13741353
## Lag 100                         0.06249231                     0.09952814
## Lag 500                         0.04779758                     0.10118050
## Lag 1000                        0.09619023                     0.13533567
## Lag 5000                        0.09963826                     0.10989738
##          traittarsus.1:traitbwt.2.units traitbwt.1:traitbwt.2.units
## Lag 0                        -0.1502700                  -0.1902055
## Lag 100                      -0.1663342                  -0.2107271
## Lag 500                      -0.2058338                  -0.2462995
## Lag 1000                     -0.1963753                  -0.2635936
## Lag 5000                     -0.1194476                  -0.1252641
##          traittarsus.2:traitbwt.2.units traitbwt.2:traitbwt.2.units
## Lag 0                        0.13741353                   0.1314508
## Lag 100                      0.09952814                   0.1030693
## Lag 500                      0.10118050                   0.1373268
## Lag 1000                     0.13533567                   0.1500819
## Lag 5000                     0.10989738                   0.1138216
##
## , , traittarsus.2:traitbwt.1.units
##
##          traittarsus.1:traittarsus.1.animal traitbwt.1:traittarsus.1.animal
## Lag 0                             0.1148525                      0.10037928
## Lag 100                           0.1303566                      0.10703233
## Lag 500                           0.1453432                      0.12751184
## Lag 1000                          0.1449075                      0.12663225
## Lag 5000                          0.1652756                      0.03681818
##          traittarsus.2:traittarsus.1.animal traitbwt.2:traittarsus.1.animal
## Lag 0                             0.1588923                       0.1392793
## Lag 100                           0.1783256                       0.1463284
## Lag 500                           0.2040736                       0.1612874
## Lag 1000                          0.2230315                       0.1896293
## Lag 5000                          0.1750420                       0.0827739
##          traittarsus.1:traitbwt.1.animal traitbwt.1:traitbwt.1.animal
## Lag 0                         0.10037928                   0.12062597
## Lag 100                       0.10703233                   0.11559443
## Lag 500                       0.12751184                   0.11837717
## Lag 1000                      0.12663225                   0.10630852
## Lag 5000                      0.03681818                  -0.04309778
##          traittarsus.2:traitbwt.1.animal traitbwt.2:traitbwt.1.animal
```

```
## Lag 0                    0.1142625                   0.09800038
## Lag 100                  0.1363961                   0.11259128
## Lag 500                  0.1781857                   0.14358029
## Lag 1000                 0.1973172                   0.16595148
## Lag 5000                 0.1261037                   0.08832747
##            traittarsus.1:traittarsus.2.animal traitbwt.1:traittarsus.2.animal
## Lag 0                               0.1588923                       0.1142625
## Lag 100                             0.1783256                       0.1363961
## Lag 500                             0.2040736                       0.1781857
## Lag 1000                            0.2230315                       0.1973172
## Lag 5000                            0.1750420                       0.1261037
##            traittarsus.2:traittarsus.2.animal traitbwt.2:traittarsus.2.animal
## Lag 0                               0.2227014                       0.2177824
## Lag 100                             0.2383512                       0.2331011
## Lag 500                             0.2644369                       0.2625082
## Lag 1000                            0.2577927                       0.2670893
## Lag 5000                            0.1772736                       0.1885761
##            traittarsus.1:traitbwt.2.animal traitbwt.1:traitbwt.2.animal
## Lag 0                            0.1392793                   0.09800038
## Lag 100                          0.1463284                   0.11259128
## Lag 500                          0.1612874                   0.14358029
## Lag 1000                         0.1896293                   0.16595148
## Lag 5000                         0.0827739                   0.08832747
##            traittarsus.2:traitbwt.2.animal traitbwt.2:traitbwt.2.animal
## Lag 0                            0.2177824                    0.1727839
## Lag 100                          0.2331011                    0.1869982
## Lag 500                          0.2625082                    0.2195418
## Lag 1000                         0.2670893                    0.2381230
## Lag 5000                         0.1885761                    0.1980800
##            traittarsus.1.byear traitbwt.1.byear traittarsus.2.byear
## Lag 0             -0.027499725       0.04996250          0.04569537
## Lag 100           -0.023937020       0.05747431          0.04863214
## Lag 500           -0.009997799       0.05757848          0.05649481
## Lag 1000          -0.028336813       0.03932991          0.08794045
## Lag 5000          -0.028421868       0.02850733         -0.02604903
##            traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother
## Lag 0         -0.0558751650            0.1570314      -0.002752353
## Lag 100       -0.0390036691            0.1577619      -0.005577721
## Lag 500       -0.0604361094            0.1762753      -0.008689304
## Lag 1000      -0.0544777158            0.1711484      -0.003879605
## Lag 5000       0.0009703848            0.1611550       0.001378773
##            traittarsus.2.mother traitbwt.2.mother
## Lag 0               -0.04476711        0.07595500
## Lag 100             -0.04782246        0.07837204
## Lag 500             -0.04024464        0.07773574
## Lag 1000            -0.01332984        0.04580976
## Lag 5000            -0.03731338        0.02497852
```

```
##           traittarsus.1:traittarsus.1.units traitbwt.1:traittarsus.1.units
## Lag 0                            -0.2009925                     -0.16660301
## Lag 100                          -0.2135650                     -0.16581994
## Lag 500                          -0.2387289                     -0.17888627
## Lag 1000                         -0.2382720                     -0.17175572
## Lag 5000                         -0.2290178                     -0.06304922
##           traittarsus.2:traittarsus.1.units traitbwt.2:traittarsus.1.units
## Lag 0                             0.9609935                       0.9303986
## Lag 100                           0.9414150                       0.9167945
## Lag 500                           0.9016587                       0.8805530
## Lag 1000                          0.8646228                       0.8343108
## Lag 5000                          0.5874768                       0.5773601
##           traittarsus.1:traitbwt.1.units traitbwt.1:traitbwt.1.units
## Lag 0                        -0.16660301                -0.167080898
## Lag 100                      -0.16581994                -0.156138622
## Lag 500                      -0.17888627                -0.151199166
## Lag 1000                     -0.17175572                -0.139083793
## Lag 5000                     -0.06304922                 0.007994506
##           traittarsus.2:traitbwt.1.units traitbwt.2:traitbwt.1.units
## Lag 0                          1.0000000                   0.9457989
## Lag 100                        0.9647777                   0.9182192
## Lag 500                        0.8967026                   0.8587466
## Lag 1000                       0.8499110                   0.8058180
## Lag 5000                       0.5555747                   0.5516644
##           traittarsus.1:traittarsus.2.units traitbwt.1:traittarsus.2.units
## Lag 0                             0.9609935                       1.0000000
## Lag 100                           0.9414150                       0.9647777
## Lag 500                           0.9016587                       0.8967026
## Lag 1000                          0.8646228                       0.8499110
## Lag 5000                          0.5874768                       0.5555747
##           traittarsus.2:traittarsus.2.units traitbwt.2:traittarsus.2.units
## Lag 0                            -0.2146171                      -0.2167857
## Lag 100                          -0.2184104                      -0.2221790
## Lag 500                          -0.2572470                      -0.2584745
## Lag 1000                         -0.2569503                      -0.2596379
## Lag 5000                         -0.1645148                      -0.1699811
##           traittarsus.1:traitbwt.2.units traitbwt.1:traitbwt.2.units
## Lag 0                          0.9303986                   0.9457989
## Lag 100                        0.9167945                   0.9182192
## Lag 500                        0.8805530                   0.8587466
## Lag 1000                       0.8343108                   0.8058180
## Lag 5000                       0.5773601                   0.5516644
##           traittarsus.2:traitbwt.2.units traitbwt.2:traitbwt.2.units
## Lag 0                         -0.2167857                  -0.1800172
## Lag 100                       -0.2221790                  -0.1849007
## Lag 500                       -0.2584745                  -0.2183863
## Lag 1000                      -0.2596379                  -0.2235166
```

```
## Lag 5000                    -0.1699811                          -0.1684397
##
## , , traitbwt.2:traitbwt.1.units
##
##           traittarsus.1:traittarsus.1.animal traitbwt.1:traittarsus.1.animal
## Lag 0                              0.1045202                      0.10675486
## Lag 100                            0.1144301                      0.10909010
## Lag 500                            0.1244192                      0.13415361
## Lag 1000                           0.1101292                      0.11544191
## Lag 5000                           0.1331335                      0.04367713
##           traittarsus.2:traittarsus.1.animal traitbwt.2:traittarsus.1.animal
## Lag 0                              0.1751169                      0.18455878
## Lag 100                            0.1936998                      0.19497627
## Lag 500                            0.2199790                      0.20989089
## Lag 1000                           0.2292872                      0.21238609
## Lag 5000                           0.1693953                      0.06254965
##           traittarsus.1:traitbwt.1.animal traitbwt.1:traitbwt.1.animal
## Lag 0                          0.10675486                   0.15466547
## Lag 100                        0.10909010                   0.15753844
## Lag 500                        0.13415361                   0.17187977
## Lag 1000                       0.11544191                   0.14889411
## Lag 5000                       0.04367713                  -0.01393939
##           traittarsus.2:traitbwt.1.animal traitbwt.2:traitbwt.1.animal
## Lag 0                           0.1618783                   0.17860886
## Lag 100                         0.1807130                   0.20406604
## Lag 500                         0.2315550                   0.24587070
## Lag 1000                        0.2433453                   0.24000705
## Lag 5000                        0.1313066                   0.07959284
##           traittarsus.1:traittarsus.2.animal traitbwt.1:traittarsus.2.animal
## Lag 0                              0.1751169                       0.1618783
## Lag 100                            0.1936998                       0.1807130
## Lag 500                            0.2199790                       0.2315550
## Lag 1000                           0.2292872                       0.2433453
## Lag 5000                           0.1693953                       0.1313066
##           traittarsus.2:traittarsus.2.animal traitbwt.2:traittarsus.2.animal
## Lag 0                              0.2339355                       0.2581627
## Lag 100                            0.2476485                       0.2736295
## Lag 500                            0.2790724                       0.3078386
## Lag 1000                           0.2842308                       0.3166841
## Lag 5000                           0.2101542                       0.1923682
##           traittarsus.1:traitbwt.2.animal traitbwt.1:traitbwt.2.animal
## Lag 0                          0.18455878                   0.17860886
## Lag 100                        0.19497627                   0.20406604
## Lag 500                        0.20989089                   0.24587070
## Lag 1000                       0.21238609                   0.24000705
## Lag 5000                       0.06254965                   0.07959284
##           traittarsus.2:traitbwt.2.animal traitbwt.2:traitbwt.2.animal
```

```
## Lag 0                         0.2581627                    0.2416106
## Lag 100                       0.2736295                    0.2608676
## Lag 500                       0.3078386                    0.2963880
## Lag 1000                      0.3166841                    0.3068141
## Lag 5000                      0.1923682                    0.1712560
##          traittarsus.1.byear traitbwt.1.byear traittarsus.2.byear
## Lag 0           -0.023701193       0.04700881          0.05361674
## Lag 100         -0.021944414       0.05837761          0.06114321
## Lag 500         -0.004019018       0.04124133          0.05472308
## Lag 1000        -0.014592442       0.02897141          0.08299624
## Lag 5000        -0.001455363       0.01713092         -0.03330245
##          traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother
## Lag 0         -0.03458419            0.1501420      -0.030979909
## Lag 100       -0.02882752            0.1495980      -0.034573917
## Lag 500       -0.05044049            0.1542703      -0.037881298
## Lag 1000      -0.04326520            0.1753867      -0.049179995
## Lag 5000       0.01976572            0.1700994      -0.002621514
##          traittarsus.2.mother traitbwt.2.mother
## Lag 0             -0.05091781        0.08248472
## Lag 100           -0.04612708        0.07643625
## Lag 500           -0.04592155        0.07211789
## Lag 1000          -0.02428388        0.04810929
## Lag 5000          -0.05454058        0.02230047
##          traittarsus.1:traittarsus.1.units traitbwt.1:traittarsus.1.units
## Lag 0                           -0.1971901                    -0.17008659
## Lag 100                         -0.2006748                    -0.16466175
## Lag 500                         -0.2146434                    -0.17764629
## Lag 1000                        -0.2152829                    -0.15594317
## Lag 5000                        -0.2163189                    -0.07951097
##          traittarsus.2:traittarsus.1.units traitbwt.2:traittarsus.1.units
## Lag 0                            0.9034487                      0.9527160
## Lag 100                          0.8867034                      0.9318204
## Lag 500                          0.8558412                      0.8820862
## Lag 1000                         0.8281770                      0.8332104
## Lag 5000                         0.5777198                      0.5582022
##          traittarsus.1:traitbwt.1.units traitbwt.1:traitbwt.1.units
## Lag 0                       -0.17008659                  -0.1902055
## Lag 100                     -0.16466175                  -0.1881759
## Lag 500                     -0.17764629                  -0.1918480
## Lag 1000                    -0.15594317                  -0.1592987
## Lag 5000                    -0.07951097                  -0.0307547
##          traittarsus.2:traitbwt.1.units traitbwt.2:traitbwt.1.units
## Lag 0                         0.9457989                   1.0000000
## Lag 100                       0.9171312                   0.9591397
## Lag 500                       0.8650556                   0.8846934
## Lag 1000                      0.8286470                   0.8252821
## Lag 5000                      0.5520607                   0.5384118
```

```
##          traittarsus.1:traittarsus.2.units traitbwt.1:traittarsus.2.units
## Lag 0                            0.9034487                      0.9457989
## Lag 100                          0.8867034                      0.9171312
## Lag 500                          0.8558412                      0.8650556
## Lag 1000                         0.8281770                      0.8286470
## Lag 5000                         0.5777198                      0.5520607
##          traittarsus.2:traittarsus.2.units traitbwt.2:traittarsus.2.units
## Lag 0                           -0.2187484                     -0.2507033
## Lag 100                         -0.2283894                     -0.2593514
## Lag 500                         -0.2686154                     -0.2983604
## Lag 1000                        -0.2818961                     -0.3082824
## Lag 5000                        -0.1951997                     -0.1732268
##          traittarsus.1:traitbwt.2.units traitbwt.1:traitbwt.2.units
## Lag 0                         0.9527160                   1.0000000
## Lag 100                       0.9318204                   0.9591397
## Lag 500                       0.8820862                   0.8846934
## Lag 1000                      0.8332104                   0.8252821
## Lag 5000                      0.5582022                   0.5384118
##          traittarsus.2:traitbwt.2.units traitbwt.2:traitbwt.2.units
## Lag 0                        -0.2507033                  -0.2443613
## Lag 100                      -0.2593514                  -0.2551879
## Lag 500                      -0.2983604                  -0.2884325
## Lag 1000                     -0.3082824                  -0.2942164
## Lag 5000                     -0.1732268                  -0.1455134
##
## , , traittarsus.1:traittarsus.2.units
##
##          traittarsus.1:traittarsus.1.animal traitbwt.1:traittarsus.1.animal
## Lag 0                             0.1834123                     0.124710076
## Lag 100                           0.1968309                     0.130500544
## Lag 500                           0.2068864                     0.139328738
## Lag 1000                          0.1939570                     0.142277480
## Lag 5000                          0.1325680                     0.009474997
##          traittarsus.2:traittarsus.1.animal traitbwt.2:traittarsus.1.animal
## Lag 0                             0.1906441                      0.13328596
## Lag 100                           0.2063827                      0.13989222
## Lag 500                           0.2249905                      0.15953298
## Lag 1000                          0.2243627                      0.17422740
## Lag 5000                          0.1612708                      0.09845918
##          traittarsus.1:traitbwt.1.animal traitbwt.1:traitbwt.1.animal
## Lag 0                        0.124710076                   0.08095300
## Lag 100                      0.130500544                   0.07950890
## Lag 500                      0.139328738                   0.07894049
## Lag 1000                     0.142277480                   0.08409986
## Lag 5000                     0.009474997                  -0.03476503
##          traittarsus.2:traitbwt.1.animal traitbwt.2:traitbwt.1.animal
## Lag 0                         0.13041646                   0.06808542
```

```
## Lag 100                    0.13619199                  0.07439607
## Lag 500                    0.15236746                  0.10133254
## Lag 1000                   0.16354531                  0.12513909
## Lag 5000                   0.09727094                  0.09702098
##          traittarsus.1:traittarsus.2.animal traitbwt.1:traittarsus.2.animal
## Lag 0                               0.1906441                      0.13041646
## Lag 100                             0.2063827                      0.13619199
## Lag 500                             0.2249905                      0.15236746
## Lag 1000                            0.2243627                      0.16354531
## Lag 5000                            0.1612708                      0.09727094
##          traittarsus.2:traittarsus.2.animal traitbwt.2:traittarsus.2.animal
## Lag 0                               0.1881270                       0.1805175
## Lag 100                             0.2019192                       0.1895957
## Lag 500                             0.2143083                       0.2038416
## Lag 1000                            0.2049762                       0.2031078
## Lag 5000                            0.2015150                       0.2236163
##          traittarsus.1:traitbwt.2.animal traitbwt.1:traitbwt.2.animal
## Lag 0                         0.13328596                   0.06808542
## Lag 100                       0.13989222                   0.07439607
## Lag 500                       0.15953298                   0.10133254
## Lag 1000                      0.17422740                   0.12513909
## Lag 5000                      0.09845918                   0.09702098
##          traittarsus.2:traitbwt.2.animal traitbwt.2:traitbwt.2.animal
## Lag 0                          0.1805175                    0.1307188
## Lag 100                        0.1895957                    0.1387545
## Lag 500                        0.2038416                    0.1596754
## Lag 1000                       0.2031078                    0.1718471
## Lag 5000                       0.2236163                    0.2388384
##          traittarsus.1.byear traitbwt.1.byear traittarsus.2.byear
## Lag 0            -0.03847015       0.05293519          0.06126409
## Lag 100          -0.03144044       0.04956734          0.06250612
## Lag 500          -0.01780154       0.05591029          0.07921148
## Lag 1000         -0.02643841       0.04337011          0.09113494
## Lag 5000         -0.01140358       0.03031863         -0.02594409
##          traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother
## Lag 0        -0.041798551            0.1697424        0.04294093
## Lag 100      -0.034073821            0.1688986        0.04145441
## Lag 500      -0.048890409            0.1720568        0.02794912
## Lag 1000     -0.040999443            0.1790535        0.02144402
## Lag 5000     -0.002784642            0.1836021       -0.02796491
##          traittarsus.2.mother traitbwt.2.mother
## Lag 0             -0.03239456        0.06299708
## Lag 100           -0.03271179        0.06442310
## Lag 500           -0.02932124        0.06841853
## Lag 1000          -0.01370787        0.05547883
## Lag 5000          -0.04156138        0.02258640
##          traittarsus.1:traittarsus.1.units traitbwt.1:traittarsus.1.units
```

```
## Lag 0                     -0.2592850                      -0.17067395
## Lag 100                   -0.2666810                      -0.16983312
## Lag 500                   -0.2761829                      -0.17499382
## Lag 1000                  -0.2748628                      -0.18004636
## Lag 5000                  -0.2185399                      -0.04226407
##         traittarsus.2:traittarsus.1.units traitbwt.2:traittarsus.1.units
## Lag 0                      1.0000000                       0.9603400
## Lag 100                    0.9783825                       0.9444274
## Lag 500                    0.9365031                       0.9054416
## Lag 1000                   0.8964880                       0.8617258
## Lag 5000                   0.6039003                       0.6022291
##         traittarsus.1:traitbwt.1.units traitbwt.1:traitbwt.1.units
## Lag 0                  -0.17067395                 -0.12741602
## Lag 100                -0.16983312                 -0.12362277
## Lag 500                -0.17499382                 -0.11972769
## Lag 1000               -0.18004636                 -0.12502460
## Lag 5000               -0.04226407                  0.01790192
##         traittarsus.2:traitbwt.1.units traitbwt.2:traitbwt.1.units
## Lag 0                    0.9609935                   0.9034487
## Lag 100                  0.9411829                   0.8893146
## Lag 500                  0.8990207                   0.8539291
## Lag 1000                 0.8622161                   0.8157349
## Lag 5000                 0.5753236                   0.5773694
##         traittarsus.1:traittarsus.2.units traitbwt.1:traittarsus.2.units
## Lag 0                      1.0000000                       0.9609935
## Lag 100                    0.9783825                       0.9411829
## Lag 500                    0.9365031                       0.8990207
## Lag 1000                   0.8964880                       0.8622161
## Lag 5000                   0.6039003                       0.5753236
##         traittarsus.2:traittarsus.2.units traitbwt.2:traittarsus.2.units
## Lag 0                     -0.1856903                      -0.1801544
## Lag 100                   -0.1921763                      -0.1830867
## Lag 500                   -0.2110415                      -0.2009371
## Lag 1000                  -0.2033807                      -0.1989511
## Lag 5000                  -0.1866476                      -0.2075534
##         traittarsus.1:traitbwt.2.units traitbwt.1:traitbwt.2.units
## Lag 0                    0.9603400                   0.9034487
## Lag 100                  0.9444274                   0.8893146
## Lag 500                  0.9054416                   0.8539291
## Lag 1000                 0.8617258                   0.8157349
## Lag 5000                 0.6022291                   0.5773694
##         traittarsus.2:traitbwt.2.units traitbwt.2:traitbwt.2.units
## Lag 0                   -0.1801544                  -0.1345421
## Lag 100                 -0.1830867                  -0.1370653
## Lag 500                 -0.2009371                  -0.1566901
## Lag 1000                -0.1989511                  -0.1643648
## Lag 5000                -0.2075534                  -0.2123302
```

```
##
## , , traitbwt.1:traittarsus.2.units
##
##          traittarsus.1:traittarsus.1.animal traitbwt.1:traittarsus.1.animal
## Lag 0                             0.1148525                      0.10037928
## Lag 100                           0.1303566                      0.10703233
## Lag 500                           0.1453432                      0.12751184
## Lag 1000                          0.1449075                      0.12663225
## Lag 5000                          0.1652756                      0.03681818
##          traittarsus.2:traittarsus.1.animal traitbwt.2:traittarsus.1.animal
## Lag 0                             0.1588923                       0.1392793
## Lag 100                           0.1783256                       0.1463284
## Lag 500                           0.2040736                       0.1612874
## Lag 1000                          0.2230315                       0.1896293
## Lag 5000                          0.1750420                       0.0827739
##          traittarsus.1:traitbwt.1.animal traitbwt.1:traitbwt.1.animal
## Lag 0                        0.10037928                   0.12062597
## Lag 100                      0.10703233                   0.11559443
## Lag 500                      0.12751184                   0.11837717
## Lag 1000                     0.12663225                   0.10630852
## Lag 5000                     0.03681818                  -0.04309778
##          traittarsus.2:traitbwt.1.animal traitbwt.2:traitbwt.1.animal
## Lag 0                         0.1142625                   0.09800038
## Lag 100                       0.1363961                   0.11259128
## Lag 500                       0.1781857                   0.14358029
## Lag 1000                      0.1973172                   0.16595148
## Lag 5000                      0.1261037                   0.08832747
##          traittarsus.1:traittarsus.2.animal traitbwt.1:traittarsus.2.animal
## Lag 0                             0.1588923                       0.1142625
## Lag 100                           0.1783256                       0.1363961
## Lag 500                           0.2040736                       0.1781857
## Lag 1000                          0.2230315                       0.1973172
## Lag 5000                          0.1750420                       0.1261037
##          traittarsus.2:traittarsus.2.animal traitbwt.2:traittarsus.2.animal
## Lag 0                             0.2227014                       0.2177824
## Lag 100                           0.2383512                       0.2331011
## Lag 500                           0.2644369                       0.2625082
## Lag 1000                          0.2577927                       0.2670893
## Lag 5000                          0.1772736                       0.1885761
##          traittarsus.1:traitbwt.2.animal traitbwt.1:traitbwt.2.animal
## Lag 0                         0.1392793                   0.09800038
## Lag 100                       0.1463284                   0.11259128
## Lag 500                       0.1612874                   0.14358029
## Lag 1000                      0.1896293                   0.16595148
## Lag 5000                      0.0827739                   0.08832747
##          traittarsus.2:traitbwt.2.animal traitbwt.2:traitbwt.2.animal
## Lag 0                         0.2177824                    0.1727839
```

```
## Lag 100                   0.2331011                     0.1869982
## Lag 500                   0.2625082                     0.2195418
## Lag 1000                  0.2670893                     0.2381230
## Lag 5000                  0.1885761                     0.1980800
##          traittarsus.1.byear traitbwt.1.byear traittarsus.2.byear
## Lag 0           -0.027499725       0.04996250          0.04569537
## Lag 100         -0.023937020       0.05747431          0.04863214
## Lag 500         -0.009997799       0.05757848          0.05649481
## Lag 1000        -0.028336813       0.03932991          0.08794045
## Lag 5000        -0.028421868       0.02850733         -0.02604903
##          traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother
## Lag 0       -0.0558751650            0.1570314      -0.002752353
## Lag 100     -0.0390036691            0.1577619      -0.005577721
## Lag 500     -0.0604361094            0.1762753      -0.008689304
## Lag 1000    -0.0544777158            0.1711484      -0.003879605
## Lag 5000     0.0009703848            0.1611550       0.001378773
##          traittarsus.2.mother traitbwt.2.mother
## Lag 0             -0.04476711        0.07595500
## Lag 100           -0.04782246        0.07837204
## Lag 500           -0.04024464        0.07773574
## Lag 1000          -0.01332984        0.04580976
## Lag 5000          -0.03731338        0.02497852
##          traittarsus.1:traittarsus.1.units traitbwt.1:traittarsus.1.units
## Lag 0                           -0.2009925                    -0.16660301
## Lag 100                         -0.2135650                    -0.16581994
## Lag 500                         -0.2387289                    -0.17888627
## Lag 1000                        -0.2382720                    -0.17175572
## Lag 5000                        -0.2290178                    -0.06304922
##          traittarsus.2:traittarsus.1.units traitbwt.2:traittarsus.1.units
## Lag 0                            0.9609935                      0.9303986
## Lag 100                          0.9414150                      0.9167945
## Lag 500                          0.9016587                      0.8805530
## Lag 1000                         0.8646228                      0.8343108
## Lag 5000                         0.5874768                      0.5773601
##          traittarsus.1:traitbwt.1.units traitbwt.1:traitbwt.1.units
## Lag 0                       -0.16660301                -0.167080898
## Lag 100                     -0.16581994                -0.156138622
## Lag 500                     -0.17888627                -0.151199166
## Lag 1000                    -0.17175572                -0.139083793
## Lag 5000                    -0.06304922                 0.007994506
##          traittarsus.2:traitbwt.1.units traitbwt.2:traitbwt.1.units
## Lag 0                         1.0000000                   0.9457989
## Lag 100                       0.9647777                   0.9182192
## Lag 500                       0.8967026                   0.8587466
## Lag 1000                      0.8499110                   0.8058180
## Lag 5000                      0.5555747                   0.5516644
##          traittarsus.1:traittarsus.2.units traitbwt.1:traittarsus.2.units
```

```
## Lag 0                         0.9609935                      1.0000000
## Lag 100                       0.9414150                      0.9647777
## Lag 500                       0.9016587                      0.8967026
## Lag 1000                      0.8646228                      0.8499110
## Lag 5000                      0.5874768                      0.5555747
##          traittarsus.2:traittarsus.2.units traitbwt.2:traittarsus.2.units
## Lag 0                        -0.2146171                     -0.2167857
## Lag 100                      -0.2184104                     -0.2221790
## Lag 500                      -0.2572470                     -0.2584745
## Lag 1000                     -0.2569503                     -0.2596379
## Lag 5000                     -0.1645148                     -0.1699811
##          traittarsus.1:traitbwt.2.units traitbwt.1:traitbwt.2.units
## Lag 0                        0.9303986                   0.9457989
## Lag 100                      0.9167945                   0.9182192
## Lag 500                      0.8805530                   0.8587466
## Lag 1000                     0.8343108                   0.8058180
## Lag 5000                     0.5773601                   0.5516644
##          traittarsus.2:traitbwt.2.units traitbwt.2:traitbwt.2.units
## Lag 0                       -0.2167857                  -0.1800172
## Lag 100                     -0.2221790                  -0.1849007
## Lag 500                     -0.2584745                  -0.2183863
## Lag 1000                    -0.2596379                  -0.2235166
## Lag 5000                    -0.1699811                  -0.1684397
##
## , , traittarsus.2:traittarsus.2.units
##
##          traittarsus.1:traittarsus.1.animal traitbwt.1:traittarsus.1.animal
## Lag 0                         -0.09279221                     -0.09677793
## Lag 100                       -0.06813005                     -0.09295582
## Lag 500                       -0.02512501                     -0.08099239
## Lag 1000                      -0.02287160                     -0.08741368
## Lag 5000                       0.07141747                      0.05570893
##          traittarsus.2:traittarsus.1.animal traitbwt.2:traittarsus.1.animal
## Lag 0                          -0.5600992                      -0.5541670
## Lag 100                        -0.5121175                      -0.5169149
## Lag 500                        -0.4106125                      -0.4295480
## Lag 1000                       -0.3066655                      -0.3332778
## Lag 5000                        0.2026604                       0.1966380
##          traittarsus.1:traitbwt.1.animal traitbwt.1:traitbwt.1.animal
## Lag 0                       -0.09677793                  -0.11346055
## Lag 100                     -0.09295582                  -0.11622763
## Lag 500                     -0.08099239                  -0.09958123
## Lag 1000                    -0.08741368                  -0.12997232
## Lag 5000                     0.05570893                   0.07322980
##          traittarsus.2:traitbwt.1.animal traitbwt.2:traitbwt.1.animal
## Lag 0                        -0.4185841                   -0.3843067
## Lag 100                      -0.3914286                   -0.3603585
```

```
## Lag 500                      -0.3364209                   -0.3074805
## Lag 1000                     -0.2650097                   -0.2595029
## Lag 5000                      0.1809913                    0.1272979
##          traittarsus.1:traittarsus.2.animal traitbwt.1:traittarsus.2.animal
## Lag 0                           -0.5600992                      -0.4185841
## Lag 100                         -0.5121175                      -0.3914286
## Lag 500                         -0.4106125                      -0.3364209
## Lag 1000                        -0.3066655                      -0.2650097
## Lag 5000                         0.2026604                       0.1809913
##          traittarsus.2:traittarsus.2.animal traitbwt.2:traittarsus.2.animal
## Lag 0                          -0.91073694                     -0.87501256
## Lag 100                        -0.86504036                     -0.83310883
## Lag 500                        -0.70973046                     -0.68729285
## Lag 1000                       -0.55757696                     -0.54103224
## Lag 5000                        0.02356453                      0.08002102
##          traittarsus.1:traitbwt.2.animal traitbwt.1:traitbwt.2.animal
## Lag 0                        -0.5541670                   -0.3843067
## Lag 100                      -0.5169149                   -0.3603585
## Lag 500                      -0.4295480                   -0.3074805
## Lag 1000                     -0.3332778                   -0.2595029
## Lag 5000                      0.1966380                    0.1272979
##          traittarsus.2:traitbwt.2.animal traitbwt.2:traitbwt.2.animal
## Lag 0                       -0.87501256                  -0.70436348
## Lag 100                     -0.83310883                  -0.67114014
## Lag 500                     -0.68729285                  -0.55786587
## Lag 1000                    -0.54103224                  -0.43429408
## Lag 5000                     0.08002102                   0.08588843
##          traittarsus.1.byear traitbwt.1.byear traittarsus.2.byear
## Lag 0          -0.0295325711       0.01013932         -0.05907849
## Lag 100        -0.0258002546       0.01023903         -0.03799824
## Lag 500        -0.0008409219       0.01222834         -0.02632830
## Lag 1000       -0.0645850913      -0.04476975         -0.04078215
## Lag 5000        0.0499883850      -0.01870262          0.03463537
##          traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother
## Lag 0          0.07499456          -0.05365944        0.08205572
## Lag 100        0.07846166          -0.07198121        0.07982740
## Lag 500        0.06122895          -0.08239796        0.07480035
## Lag 1000       0.04893466          -0.08171638        0.06996265
## Lag 5000      -0.05752959          -0.01133586       -0.02071995
##          traittarsus.2.mother traitbwt.2.mother
## Lag 0              0.13607402      -0.063098741
## Lag 100            0.16280409      -0.056620767
## Lag 500            0.14111652      -0.077496866
## Lag 1000           0.12664216      -0.055395330
## Lag 5000           0.01649277      -0.003196996
##          traittarsus.1:traittarsus.1.units traitbwt.1:traittarsus.1.units
## Lag 0                           0.09543017                     0.10875399
```

```
## Lag 100                      0.06598285                      0.08293245
## Lag 500                      0.05295587                      0.08321338
## Lag 1000                     0.06481928                      0.08697241
## Lag 5000                    -0.09911194                     -0.09382365
##          traittarsus.2:traittarsus.1.units traitbwt.2:traittarsus.1.units
## Lag 0                       -0.18569026                     -0.20065634
## Lag 100                     -0.19134621                     -0.20598290
## Lag 500                     -0.19158726                     -0.20439959
## Lag 1000                    -0.17346895                     -0.18874412
## Lag 5000                    -0.04965337                     -0.05447094
##          traittarsus.1:traitbwt.1.units traitbwt.1:traitbwt.1.units
## Lag 0                       0.10875399                  0.11081955
## Lag 100                     0.08293245                  0.09377309
## Lag 500                     0.08321338                  0.07955802
## Lag 1000                    0.08697241                  0.10737966
## Lag 5000                   -0.09382365                 -0.07165472
##          traittarsus.2:traitbwt.1.units traitbwt.2:traitbwt.1.units
## Lag 0                      -0.21461708                  -0.2187484
## Lag 100                    -0.21502402                  -0.2194216
## Lag 500                    -0.20000700                  -0.2023328
## Lag 1000                   -0.19364240                  -0.1958537
## Lag 5000                   -0.02836013                  -0.0258784
##          traittarsus.1:traittarsus.2.units traitbwt.1:traittarsus.2.units
## Lag 0                       -0.18569026                     -0.21461708
## Lag 100                     -0.19134621                     -0.21502402
## Lag 500                     -0.19158726                     -0.20000700
## Lag 1000                    -0.17346895                     -0.19364240
## Lag 5000                    -0.04965337                     -0.02836013
##          traittarsus.2:traittarsus.2.units traitbwt.2:traittarsus.2.units
## Lag 0                         1.0000000                      0.92685734
## Lag 100                       0.8892164                      0.83343965
## Lag 500                       0.7197831                      0.67640907
## Lag 1000                      0.5723349                      0.53670401
## Lag 5000                     -0.0393405                     -0.08858763
##          traittarsus.1:traitbwt.2.units traitbwt.1:traitbwt.2.units
## Lag 0                      -0.20065634                  -0.2187484
## Lag 100                    -0.20598290                  -0.2194216
## Lag 500                    -0.20439959                  -0.2023328
## Lag 1000                   -0.18874412                  -0.1958537
## Lag 5000                   -0.05447094                  -0.0258784
##          traittarsus.2:traitbwt.2.units traitbwt.2:traitbwt.2.units
## Lag 0                       0.92685734                  0.75421487
## Lag 100                     0.83343965                  0.68043059
## Lag 500                     0.67640907                  0.55259827
## Lag 1000                    0.53670401                  0.43176584
## Lag 5000                   -0.08858763                 -0.08998996
##
```

```
## , , traitbwt.2:traittarsus.2.units
##
##          traittarsus.1:traittarsus.1.animal traitbwt.1:traittarsus.1.animal
## Lag 0                           -0.09066377                     -0.12847847
## Lag 100                         -0.06791265                     -0.11660390
## Lag 500                         -0.02813480                     -0.08793510
## Lag 1000                        -0.02464042                     -0.10829057
## Lag 5000                         0.09059977                      0.04232726
##          traittarsus.2:traittarsus.1.animal traitbwt.2:traittarsus.1.animal
## Lag 0                            -0.5208193                      -0.6200400
## Lag 100                          -0.4814739                      -0.5760115
## Lag 500                          -0.4160646                      -0.4939845
## Lag 1000                         -0.3309504                      -0.3961937
## Lag 5000                          0.1719378                       0.1704323
##          traittarsus.1:traitbwt.1.animal traitbwt.1:traitbwt.1.animal
## Lag 0                        -0.12847847                  -0.16728073
## Lag 100                      -0.11660390                  -0.16431801
## Lag 500                      -0.08793510                  -0.14580635
## Lag 1000                     -0.10829057                  -0.17627597
## Lag 5000                      0.04232726                   0.02621324
##          traittarsus.2:traitbwt.1.animal traitbwt.2:traitbwt.1.animal
## Lag 0                         -0.4729141                  -0.49584021
## Lag 100                       -0.4400289                  -0.46178772
## Lag 500                       -0.3667218                  -0.38855190
## Lag 1000                      -0.3075053                  -0.32632756
## Lag 5000                       0.1176403                   0.08762877
##          traittarsus.1:traittarsus.2.animal traitbwt.1:traittarsus.2.animal
## Lag 0                            -0.5208193                      -0.4729141
## Lag 100                          -0.4814739                      -0.4400289
## Lag 500                          -0.4160646                      -0.3667218
## Lag 1000                         -0.3309504                      -0.3075053
## Lag 5000                          0.1719378                       0.1176403
##          traittarsus.2:traittarsus.2.animal traitbwt.2:traittarsus.2.animal
## Lag 0                           -0.84107771                     -0.93853010
## Lag 100                         -0.80537663                     -0.88900373
## Lag 500                         -0.70011206                     -0.74957513
## Lag 1000                        -0.58965340                     -0.62094832
## Lag 5000                        -0.01326034                      0.04348338
##          traittarsus.1:traitbwt.2.animal traitbwt.1:traitbwt.2.animal
## Lag 0                         -0.6200400                  -0.49584021
## Lag 100                       -0.5760115                  -0.46178772
## Lag 500                       -0.4939845                  -0.38855190
## Lag 1000                      -0.3961937                  -0.32632756
## Lag 5000                       0.1704323                   0.08762877
##          traittarsus.2:traitbwt.2.animal traitbwt.2:traitbwt.2.animal
## Lag 0                        -0.93853010                  -0.85484247
## Lag 100                      -0.88900373                  -0.80629890
```

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## Lag 500                    -0.74957513                 -0.66699739
## Lag 1000                   -0.62094832                 -0.53588327
## Lag 5000                    0.04348338                  0.06798066
##           traittarsus.1.byear traitbwt.1.byear traittarsus.2.byear
## Lag 0            -0.04533921     -0.001638125         -0.07410803
## Lag 100          -0.04526568      0.002752216         -0.05435921
## Lag 500          -0.02361959     -0.010266769         -0.04066778
## Lag 1000         -0.08661480     -0.055915794         -0.03404716
## Lag 5000          0.02028860     -0.015718402          0.05000555
##           traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother
## Lag 0         0.09224924          -0.08507034       0.117048388
## Lag 100       0.09712475          -0.09090158       0.119562799
## Lag 500       0.06704383          -0.06950074       0.093258667
## Lag 1000      0.06946025          -0.09719184       0.091569829
## Lag 5000     -0.05957284          -0.01506617      -0.004965446
##           traittarsus.2.mother traitbwt.2.mother
## Lag 0             0.11599294       -0.06384447
## Lag 100           0.12644815       -0.06061567
## Lag 500           0.12233108       -0.05933391
## Lag 1000          0.11302925       -0.05409993
## Lag 5000          0.02623229        0.01443371
##           traittarsus.1:traittarsus.1.units traitbwt.1:traittarsus.1.units
## Lag 0                            0.11602826                     0.13276682
## Lag 100                          0.08412251                     0.10350782
## Lag 500                          0.06419072                     0.10039070
## Lag 1000                         0.08359941                     0.11689682
## Lag 5000                        -0.10317497                    -0.07583069
##           traittarsus.2:traittarsus.1.units traitbwt.2:traittarsus.1.units
## Lag 0                            -0.1801544                     -0.2276707
## Lag 100                          -0.1866591                     -0.2347923
## Lag 500                          -0.1769783                     -0.2196866
## Lag 1000                         -0.1617965                     -0.1997778
## Lag 5000                         -0.0380065                     -0.0414611
##           traittarsus.1:traitbwt.1.units traitbwt.1:traitbwt.1.units
## Lag 0                         0.13276682                  0.13741353
## Lag 100                       0.10350782                  0.11641231
## Lag 500                       0.10039070                  0.12001620
## Lag 1000                      0.11689682                  0.15480317
## Lag 5000                     -0.07583069                 -0.03093518
##           traittarsus.2:traitbwt.1.units traitbwt.2:traitbwt.1.units
## Lag 0                        -0.21678569                  -0.2507033
## Lag 100                      -0.22198433                  -0.2562972
## Lag 500                      -0.20689452                  -0.2323026
## Lag 1000                     -0.19261030                  -0.2149386
## Lag 5000                     -0.02955808                  -0.0282441
##           traittarsus.1:traittarsus.2.units traitbwt.1:traittarsus.2.units
## Lag 0                            -0.1801544                    -0.21678569
```

```
## Lag 100                     -0.1866591                   -0.22198433
## Lag 500                     -0.1769783                   -0.20689452
## Lag 1000                    -0.1617965                   -0.19261030
## Lag 5000                    -0.0380065                   -0.02955808
##          traittarsus.2:traittarsus.2.units traitbwt.2:traittarsus.2.units
## Lag 0                        0.926857338                     1.00000000
## Lag 100                      0.838930228                     0.89252017
## Lag 500                      0.714319171                     0.73419722
## Lag 1000                     0.601447081                     0.60685285
## Lag 5000                    -0.005767447                    -0.05722557
##          traittarsus.1:traitbwt.2.units traitbwt.1:traitbwt.2.units
## Lag 0                        -0.2276707                  -0.2507033
## Lag 100                      -0.2347923                  -0.2562972
## Lag 500                      -0.2196866                  -0.2323026
## Lag 1000                     -0.1997778                  -0.2149386
## Lag 5000                     -0.0414611                  -0.0282441
##          traittarsus.2:traitbwt.2.units traitbwt.2:traitbwt.2.units
## Lag 0                        1.00000000                  0.92347712
## Lag 100                      0.89252017                  0.81767393
## Lag 500                      0.73419722                  0.65250913
## Lag 1000                     0.60685285                  0.52632018
## Lag 5000                    -0.05722557                 -0.07523754
##
## , , traittarsus.1:traitbwt.2.units
##
##          traittarsus.1:traittarsus.1.animal traitbwt.1:traittarsus.1.animal
## Lag 0                             0.1843936                      0.13991929
## Lag 100                           0.1916063                      0.14051238
## Lag 500                           0.1997384                      0.15350375
## Lag 1000                          0.1779242                      0.14333349
## Lag 5000                          0.1059309                      0.02408511
##          traittarsus.2:traittarsus.1.animal traitbwt.2:traittarsus.1.animal
## Lag 0                             0.2159001                      0.18941930
## Lag 100                           0.2292097                      0.19756460
## Lag 500                           0.2470830                      0.21294438
## Lag 1000                          0.2430281                      0.21181509
## Lag 5000                          0.1564420                      0.09549646
##          traittarsus.1:traitbwt.1.animal traitbwt.1:traitbwt.1.animal
## Lag 0                         0.13991929                   0.11864383
## Lag 100                       0.14051238                   0.11475981
## Lag 500                       0.15350375                   0.12191537
## Lag 1000                      0.14333349                   0.12719171
## Lag 5000                      0.02408511                  -0.00131242
##          traittarsus.2:traitbwt.1.animal traitbwt.2:traitbwt.1.animal
## Lag 0                          0.1778597                    0.1473359
## Lag 100                        0.1832967                    0.1558541
## Lag 500                        0.2035349                    0.1829320
```

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## Lag 1000                      0.2085231                      0.1947599
## Lag 5000                      0.1096782                      0.1076230
##          traittarsus.1:traittarsus.2.animal traitbwt.1:traittarsus.2.animal
## Lag 0                                0.2159001                       0.1778597
## Lag 100                              0.2292097                       0.1832967
## Lag 500                              0.2470830                       0.2035349
## Lag 1000                             0.2430281                       0.2085231
## Lag 5000                             0.1564420                       0.1096782
##          traittarsus.2:traittarsus.2.animal traitbwt.2:traittarsus.2.animal
## Lag 0                                0.2148002                       0.2380759
## Lag 100                              0.2260582                       0.2490150
## Lag 500                              0.2434250                       0.2659527
## Lag 1000                             0.2396319                       0.2621966
## Lag 5000                             0.2311987                       0.2321063
##          traittarsus.1:traitbwt.2.animal traitbwt.1:traitbwt.2.animal
## Lag 0                         0.18941930                    0.1473359
## Lag 100                       0.19756460                    0.1558541
## Lag 500                       0.21294438                    0.1829320
## Lag 1000                      0.21181509                    0.1947599
## Lag 5000                      0.09549646                    0.1076230
##          traittarsus.2:traitbwt.2.animal traitbwt.2:traitbwt.2.animal
## Lag 0                          0.2380759                    0.2116292
## Lag 100                        0.2490150                    0.2231338
## Lag 500                        0.2659527                    0.2429222
## Lag 1000                       0.2621966                    0.2441661
## Lag 5000                       0.2321063                    0.2236298
##          traittarsus.1.byear traitbwt.1.byear traittarsus.2.byear
## Lag 0           -0.032369970       0.05768879          0.06054337
## Lag 100         -0.031641858       0.05864059          0.06580478
## Lag 500         -0.001530924       0.04503326          0.07399288
## Lag 1000        -0.016005519       0.03161375          0.08585903
## Lag 5000         0.010619935       0.01730446         -0.02417570
##          traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother
## Lag 0        -0.032356483            0.1703875       0.012376673
## Lag 100      -0.034654911            0.1647608       0.013581085
## Lag 500      -0.052597308            0.1600416       0.005553001
## Lag 1000     -0.039591608            0.1872703      -0.009042770
## Lag 5000      0.004455343            0.1972374      -0.027185781
##          traittarsus.2.mother traitbwt.2.mother
## Lag 0             -0.03846399        0.07575889
## Lag 100           -0.03390447        0.06853459
## Lag 500           -0.02862102        0.06274714
## Lag 1000          -0.01799649        0.06065063
## Lag 5000          -0.05555704        0.02202828
##          traittarsus.1:traittarsus.1.units traitbwt.1:traittarsus.1.units
## Lag 0                               -0.2645685                     -0.18013988
## Lag 100                             -0.2616234                     -0.17607364
```

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## Lag 500                       -0.2652457                     -0.18034511
## Lag 1000                      -0.2671219                     -0.17702256
## Lag 5000                      -0.2093233                     -0.06028968
##          traittarsus.2:traittarsus.1.units traitbwt.2:traittarsus.1.units
## Lag 0                         0.9603400                       1.0000000
## Lag 100                       0.9432077                       0.9762869
## Lag 500                       0.9124477                       0.9252632
## Lag 1000                      0.8838890                       0.8792611
## Lag 5000                      0.6117319                       0.6007465
##          traittarsus.1:traitbwt.1.units traitbwt.1:traitbwt.1.units
## Lag 0                       -0.18013988                 -0.15026999
## Lag 100                     -0.17607364                 -0.14749648
## Lag 500                     -0.18034511                 -0.15145709
## Lag 1000                    -0.17702256                 -0.15538707
## Lag 5000                    -0.06028968                 -0.02621414
##          traittarsus.2:traitbwt.1.units traitbwt.2:traitbwt.1.units
## Lag 0                         0.9303986                   0.9527160
## Lag 100                       0.9147001                   0.9321247
## Lag 500                       0.8850543                   0.8884276
## Lag 1000                      0.8576398                   0.8431799
## Lag 5000                      0.5876791                   0.5807055
##          traittarsus.1:traittarsus.2.units traitbwt.1:traittarsus.2.units
## Lag 0                         0.9603400                       0.9303986
## Lag 100                       0.9432077                       0.9147001
## Lag 500                       0.9124477                       0.8850543
## Lag 1000                      0.8838890                       0.8576398
## Lag 5000                      0.6117319                       0.5876791
##          traittarsus.2:traittarsus.2.units traitbwt.2:traittarsus.2.units
## Lag 0                        -0.2006563                      -0.2276707
## Lag 100                      -0.2124295                      -0.2354203
## Lag 500                      -0.2379446                      -0.2556157
## Lag 1000                     -0.2389714                      -0.2561306
## Lag 5000                     -0.2130152                      -0.2137306
##          traittarsus.1:traitbwt.2.units traitbwt.1:traitbwt.2.units
## Lag 0                         1.0000000                   0.9527160
## Lag 100                       0.9762869                   0.9321247
## Lag 500                       0.9252632                   0.8884276
## Lag 1000                      0.8792611                   0.8431799
## Lag 5000                      0.6007465                   0.5807055
##          traittarsus.2:traitbwt.2.units traitbwt.2:traitbwt.2.units
## Lag 0                        -0.2276707                  -0.2128094
## Lag 100                      -0.2354203                  -0.2168142
## Lag 500                      -0.2556157                  -0.2324758
## Lag 1000                     -0.2561306                  -0.2373888
## Lag 5000                     -0.2137306                  -0.1974646
##
## , , traitbwt.1:traitbwt.2.units
```

```
##
##          traittarsus.1:traittarsus.1.animal traitbwt.1:traittarsus.1.animal
## Lag 0                             0.1045202                      0.10675486
## Lag 100                           0.1144301                      0.10909010
## Lag 500                           0.1244192                      0.13415361
## Lag 1000                          0.1101292                      0.11544191
## Lag 5000                          0.1331335                      0.04367713
##          traittarsus.2:traittarsus.1.animal traitbwt.2:traittarsus.1.animal
## Lag 0                             0.1751169                      0.18455878
## Lag 100                           0.1936998                      0.19497627
## Lag 500                           0.2199790                      0.20989089
## Lag 1000                          0.2292872                      0.21238609
## Lag 5000                          0.1693953                      0.06254965
##          traittarsus.1:traitbwt.1.animal traitbwt.1:traitbwt.1.animal
## Lag 0                         0.10675486                   0.15466547
## Lag 100                       0.10909010                   0.15753844
## Lag 500                       0.13415361                   0.17187977
## Lag 1000                      0.11544191                   0.14889411
## Lag 5000                      0.04367713                  -0.01393939
##          traittarsus.2:traitbwt.1.animal traitbwt.2:traitbwt.1.animal
## Lag 0                          0.1618783                   0.17860886
## Lag 100                        0.1807130                   0.20406604
## Lag 500                        0.2315550                   0.24587070
## Lag 1000                       0.2433453                   0.24000705
## Lag 5000                       0.1313066                   0.07959284
##          traittarsus.1:traittarsus.2.animal traitbwt.1:traittarsus.2.animal
## Lag 0                             0.1751169                       0.1618783
## Lag 100                           0.1936998                       0.1807130
## Lag 500                           0.2199790                       0.2315550
## Lag 1000                          0.2292872                       0.2433453
## Lag 5000                          0.1693953                       0.1313066
##          traittarsus.2:traittarsus.2.animal traitbwt.2:traittarsus.2.animal
## Lag 0                             0.2339355                       0.2581627
## Lag 100                           0.2476485                       0.2736295
## Lag 500                           0.2790724                       0.3078386
## Lag 1000                          0.2842308                       0.3166841
## Lag 5000                          0.2101542                       0.1923682
##          traittarsus.1:traitbwt.2.animal traitbwt.1:traitbwt.2.animal
## Lag 0                         0.18455878                   0.17860886
## Lag 100                       0.19497627                   0.20406604
## Lag 500                       0.20989089                   0.24587070
## Lag 1000                      0.21238609                   0.24000705
## Lag 5000                      0.06254965                   0.07959284
##          traittarsus.2:traitbwt.2.animal traitbwt.2:traitbwt.2.animal
## Lag 0                          0.2581627                    0.2416106
## Lag 100                        0.2736295                    0.2608676
## Lag 500                        0.3078386                    0.2963880
```

```
## Lag 1000                        0.3166841                        0.3068141
## Lag 5000                        0.1923682                        0.1712560
##          traittarsus.1.byear traitbwt.1.byear traittarsus.2.byear
## Lag 0           -0.023701193       0.04700881          0.05361674
## Lag 100         -0.021944414       0.05837761          0.06114321
## Lag 500         -0.004019018       0.04124133          0.05472308
## Lag 1000        -0.014592442       0.02897141          0.08299624
## Lag 5000        -0.001455363       0.01713092         -0.03330245
##          traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother
## Lag 0         -0.03458419            0.1501420      -0.030979909
## Lag 100       -0.02882752            0.1495980      -0.034573917
## Lag 500       -0.05044049            0.1542703      -0.037881298
## Lag 1000      -0.04326520            0.1753867      -0.049179995
## Lag 5000       0.01976572            0.1700994      -0.002621514
##          traittarsus.2.mother traitbwt.2.mother
## Lag 0             -0.05091781        0.08248472
## Lag 100           -0.04612708        0.07643625
## Lag 500           -0.04592155        0.07211789
## Lag 1000          -0.02428388        0.04810929
## Lag 5000          -0.05454058        0.02230047
##          traittarsus.1:traittarsus.1.units traitbwt.1:traittarsus.1.units
## Lag 0                           -0.1971901                    -0.17008659
## Lag 100                         -0.2006748                    -0.16466175
## Lag 500                         -0.2146434                    -0.17764629
## Lag 1000                        -0.2152829                    -0.15594317
## Lag 5000                        -0.2163189                    -0.07951097
##          traittarsus.2:traittarsus.1.units traitbwt.2:traittarsus.1.units
## Lag 0                            0.9034487                      0.9527160
## Lag 100                          0.8867034                      0.9318204
## Lag 500                          0.8558412                      0.8820862
## Lag 1000                         0.8281770                      0.8332104
## Lag 5000                         0.5777198                      0.5582022
##          traittarsus.1:traitbwt.1.units traitbwt.1:traitbwt.1.units
## Lag 0                       -0.17008659                  -0.1902055
## Lag 100                     -0.16466175                  -0.1881759
## Lag 500                     -0.17764629                  -0.1918480
## Lag 1000                    -0.15594317                  -0.1592987
## Lag 5000                    -0.07951097                  -0.0307547
##          traittarsus.2:traitbwt.1.units traitbwt.2:traitbwt.1.units
## Lag 0                         0.9457989                   1.0000000
## Lag 100                       0.9171312                   0.9591397
## Lag 500                       0.8650556                   0.8846934
## Lag 1000                      0.8286470                   0.8252821
## Lag 5000                      0.5520607                   0.5384118
##          traittarsus.1:traittarsus.2.units traitbwt.1:traittarsus.2.units
## Lag 0                            0.9034487                      0.9457989
## Lag 100                          0.8867034                      0.9171312
```

```
## Lag 500                          0.8558412                       0.8650556
## Lag 1000                         0.8281770                       0.8286470
## Lag 5000                         0.5777198                       0.5520607
##          traittarsus.2:traittarsus.2.units traitbwt.2:traittarsus.2.units
## Lag 0                           -0.2187484                      -0.2507033
## Lag 100                         -0.2283894                      -0.2593514
## Lag 500                         -0.2686154                      -0.2983604
## Lag 1000                        -0.2818961                      -0.3082824
## Lag 5000                        -0.1951997                      -0.1732268
##          traittarsus.1:traitbwt.2.units traitbwt.1:traitbwt.2.units
## Lag 0                         0.9527160                   1.0000000
## Lag 100                       0.9318204                   0.9591397
## Lag 500                       0.8820862                   0.8846934
## Lag 1000                      0.8332104                   0.8252821
## Lag 5000                      0.5582022                   0.5384118
##          traittarsus.2:traitbwt.2.units traitbwt.2:traitbwt.2.units
## Lag 0                        -0.2507033                  -0.2443613
## Lag 100                      -0.2593514                  -0.2551879
## Lag 500                      -0.2983604                  -0.2884325
## Lag 1000                     -0.3082824                  -0.2942164
## Lag 5000                     -0.1732268                  -0.1455134
##
## , , traittarsus.2:traitbwt.2.units
##
##          traittarsus.1:traittarsus.1.animal traitbwt.1:traittarsus.1.animal
## Lag 0                           -0.09066377                     -0.12847847
## Lag 100                         -0.06791265                     -0.11660390
## Lag 500                         -0.02813480                     -0.08793510
## Lag 1000                        -0.02464042                     -0.10829057
## Lag 5000                         0.09059977                      0.04232726
##          traittarsus.2:traittarsus.1.animal traitbwt.2:traittarsus.1.animal
## Lag 0                            -0.5208193                      -0.6200400
## Lag 100                          -0.4814739                      -0.5760115
## Lag 500                          -0.4160646                      -0.4939845
## Lag 1000                         -0.3309504                      -0.3961937
## Lag 5000                          0.1719378                       0.1704323
##          traittarsus.1:traitbwt.1.animal traitbwt.1:traitbwt.1.animal
## Lag 0                        -0.12847847                  -0.16728073
## Lag 100                      -0.11660390                  -0.16431801
## Lag 500                      -0.08793510                  -0.14580635
## Lag 1000                     -0.10829057                  -0.17627597
## Lag 5000                      0.04232726                   0.02621324
##          traittarsus.2:traitbwt.1.animal traitbwt.2:traitbwt.1.animal
## Lag 0                          -0.4729141                  -0.49584021
## Lag 100                        -0.4400289                  -0.46178772
## Lag 500                        -0.3667218                  -0.38855190
## Lag 1000                       -0.3075053                  -0.32632756
```

```
## Lag 5000                      0.1176403                  0.08762877
##          traittarsus.1:traittarsus.2.animal traitbwt.1:traittarsus.2.animal
## Lag 0                             -0.5208193                      -0.4729141
## Lag 100                           -0.4814739                      -0.4400289
## Lag 500                           -0.4160646                      -0.3667218
## Lag 1000                          -0.3309504                      -0.3075053
## Lag 5000                           0.1719378                       0.1176403
##          traittarsus.2:traittarsus.2.animal traitbwt.2:traittarsus.2.animal
## Lag 0                            -0.84107771                     -0.93853010
## Lag 100                          -0.80537663                     -0.88900373
## Lag 500                          -0.70011206                     -0.74957513
## Lag 1000                         -0.58965340                     -0.62094832
## Lag 5000                         -0.01326034                      0.04348338
##          traittarsus.1:traitbwt.2.animal traitbwt.1:traitbwt.2.animal
## Lag 0                          -0.6200400                  -0.49584021
## Lag 100                        -0.5760115                  -0.46178772
## Lag 500                        -0.4939845                  -0.38855190
## Lag 1000                       -0.3961937                  -0.32632756
## Lag 5000                        0.1704323                   0.08762877
##          traittarsus.2:traitbwt.2.animal traitbwt.2:traitbwt.2.animal
## Lag 0                         -0.93853010                  -0.85484247
## Lag 100                       -0.88900373                  -0.80629890
## Lag 500                       -0.74957513                  -0.66699739
## Lag 1000                      -0.62094832                  -0.53588327
## Lag 5000                       0.04348338                   0.06798066
##          traittarsus.1.byear traitbwt.1.byear traittarsus.2.byear
## Lag 0            -0.04533921     -0.001638125         -0.07410803
## Lag 100          -0.04526568      0.002752216         -0.05435921
## Lag 500          -0.02361959     -0.010266769         -0.04066778
## Lag 1000         -0.08661480     -0.055915794         -0.03404716
## Lag 5000          0.02028860     -0.015718402          0.05000555
##          traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother
## Lag 0          0.09224924          -0.08507034       0.117048388
## Lag 100        0.09712475          -0.09090158       0.119562799
## Lag 500        0.06704383          -0.06950074       0.093258667
## Lag 1000       0.06946025          -0.09719184       0.091569829
## Lag 5000      -0.05957284          -0.01506617      -0.004965446
##          traittarsus.2.mother traitbwt.2.mother
## Lag 0              0.11599294       -0.06384447
## Lag 100            0.12644815       -0.06061567
## Lag 500            0.12233108       -0.05933391
## Lag 1000           0.11302925       -0.05409993
## Lag 5000           0.02623229        0.01443371
##          traittarsus.1:traittarsus.1.units traitbwt.1:traittarsus.1.units
## Lag 0                           0.11602826                     0.13276682
## Lag 100                         0.08412251                     0.10350782
## Lag 500                         0.06419072                     0.10039070
```

```
## Lag 1000                     0.08359941                     0.11689682
## Lag 5000                    -0.10317497                    -0.07583069
##          traittarsus.2:traittarsus.1.units traitbwt.2:traittarsus.1.units
## Lag 0                           -0.1801544                     -0.2276707
## Lag 100                         -0.1866591                     -0.2347923
## Lag 500                         -0.1769783                     -0.2196866
## Lag 1000                        -0.1617965                     -0.1997778
## Lag 5000                        -0.0380065                     -0.0414611
##          traittarsus.1:traitbwt.1.units traitbwt.1:traitbwt.1.units
## Lag 0                        0.13276682                  0.13741353
## Lag 100                      0.10350782                  0.11641231
## Lag 500                      0.10039070                  0.12001620
## Lag 1000                     0.11689682                  0.15480317
## Lag 5000                    -0.07583069                 -0.03093518
##          traittarsus.2:traitbwt.1.units traitbwt.2:traitbwt.1.units
## Lag 0                       -0.21678569                  -0.2507033
## Lag 100                     -0.22198433                  -0.2562972
## Lag 500                     -0.20689452                  -0.2323026
## Lag 1000                    -0.19261030                  -0.2149386
## Lag 5000                    -0.02955808                  -0.0282441
##          traittarsus.1:traittarsus.2.units traitbwt.1:traittarsus.2.units
## Lag 0                           -0.1801544                    -0.21678569
## Lag 100                         -0.1866591                    -0.22198433
## Lag 500                         -0.1769783                    -0.20689452
## Lag 1000                        -0.1617965                    -0.19261030
## Lag 5000                        -0.0380065                    -0.02955808
##          traittarsus.2:traittarsus.2.units traitbwt.2:traittarsus.2.units
## Lag 0                          0.926857338                     1.00000000
## Lag 100                        0.838930228                     0.89252017
## Lag 500                        0.714319171                     0.73419722
## Lag 1000                       0.601447081                     0.60685285
## Lag 5000                      -0.005767447                    -0.05722557
##          traittarsus.1:traitbwt.2.units traitbwt.1:traitbwt.2.units
## Lag 0                        -0.2276707                  -0.2507033
## Lag 100                      -0.2347923                  -0.2562972
## Lag 500                      -0.2196866                  -0.2323026
## Lag 1000                     -0.1997778                  -0.2149386
## Lag 5000                     -0.0414611                  -0.0282441
##          traittarsus.2:traitbwt.2.units traitbwt.2:traitbwt.2.units
## Lag 0                        1.00000000                  0.92347712
## Lag 100                      0.89252017                  0.81767393
## Lag 500                      0.73419722                  0.65250913
## Lag 1000                     0.60685285                  0.52632018
## Lag 5000                    -0.05722557                 -0.07523754
##
## , , traitbwt.2:traitbwt.2.units
##
```

```
##           traittarsus.1:traittarsus.1.animal traitbwt.1:traittarsus.1.animal
## Lag 0                           -0.043059890                     -0.10947233
## Lag 100                         -0.021006970                     -0.08947374
## Lag 500                         -0.001331729                     -0.06046211
## Lag 1000                        -0.008677951                     -0.10284705
## Lag 5000                         0.111890868                      0.03101996
##           traittarsus.2:traittarsus.1.animal traitbwt.2:traittarsus.1.animal
## Lag 0                             -0.3939711                      -0.5649761
## Lag 100                           -0.3674489                      -0.5248935
## Lag 500                           -0.3564907                      -0.4716725
## Lag 1000                          -0.3026255                      -0.3959870
## Lag 5000                           0.1392553                       0.1506927
##           traittarsus.1:traitbwt.1.animal traitbwt.1:traitbwt.1.animal
## Lag 0                         -0.10947233                 -0.187811354
## Lag 100                       -0.08947374                 -0.167609258
## Lag 500                       -0.06046211                 -0.153207032
## Lag 1000                      -0.10284705                 -0.191376283
## Lag 5000                       0.03101996                 -0.009266993
##           traittarsus.2:traitbwt.1.animal traitbwt.2:traitbwt.1.animal
## Lag 0                         -0.43960419                  -0.56988609
## Lag 100                       -0.41008412                  -0.52185804
## Lag 500                       -0.34705550                  -0.43385778
## Lag 1000                      -0.31152313                  -0.36023626
## Lag 5000                       0.07052962                   0.07222864
##           traittarsus.1:traittarsus.2.animal traitbwt.1:traittarsus.2.animal
## Lag 0                             -0.3939711                     -0.43960419
## Lag 100                           -0.3674489                     -0.41008412
## Lag 500                           -0.3564907                     -0.34705550
## Lag 1000                          -0.3026255                     -0.31152313
## Lag 5000                           0.1392553                      0.07052962
##           traittarsus.2:traittarsus.2.animal traitbwt.2:traittarsus.2.animal
## Lag 0                            -0.67910852                     -0.85888343
## Lag 100                          -0.65466001                     -0.81238323
## Lag 500                          -0.60647885                     -0.70052835
## Lag 1000                         -0.54835587                     -0.61884830
## Lag 5000                         -0.02772098                      0.03373215
##           traittarsus.1:traitbwt.2.animal traitbwt.1:traitbwt.2.animal
## Lag 0                          -0.5649761                  -0.56988609
## Lag 100                        -0.5248935                  -0.52185804
## Lag 500                        -0.4716725                  -0.43385778
## Lag 1000                       -0.3959870                  -0.36023626
## Lag 5000                        0.1506927                   0.07222864
##           traittarsus.2:traitbwt.2.animal traitbwt.2:traitbwt.2.animal
## Lag 0                         -0.85888343                  -0.90703776
## Lag 100                       -0.81238323                  -0.83971454
## Lag 500                       -0.70052835                  -0.68420955
## Lag 1000                      -0.61884830                  -0.57020879
```

```
## Lag 5000                   0.03373215                    0.07361913
##           traittarsus.1.byear traitbwt.1.byear traittarsus.2.byear
## Lag 0            -0.044815839     -0.007601342         -0.09539294
## Lag 100          -0.046632422     -0.009618828         -0.07733270
## Lag 500          -0.039749429     -0.026455434         -0.05466463
## Lag 1000         -0.096232932     -0.063248471         -0.04859295
## Lag 5000         -0.007307801     -0.011838332          0.07303267
##           traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother
## Lag 0          0.07926090          -0.11755479      0.1533639724
## Lag 100        0.09525987          -0.11193096      0.1505628703
## Lag 500        0.05998165          -0.06092327      0.1143539752
## Lag 1000       0.06572238          -0.09798980      0.1117926423
## Lag 5000      -0.05632018          -0.00703712      0.0007242137
##           traittarsus.2.mother traitbwt.2.mother
## Lag 0               0.09798770       -0.07912857
## Lag 100             0.09530597       -0.05178227
## Lag 500             0.10285009       -0.03607903
## Lag 1000            0.08664286       -0.05475142
## Lag 5000            0.03594017        0.03608548
##           traittarsus.1:traittarsus.1.units traitbwt.1:traittarsus.1.units
## Lag 0                            0.10062986                     0.11344391
## Lag 100                          0.07039582                     0.08507484
## Lag 500                          0.04998573                     0.08084299
## Lag 1000                         0.07979248                     0.11040825
## Lag 5000                        -0.11441105                    -0.06475361
##           traittarsus.2:traittarsus.1.units traitbwt.2:traittarsus.1.units
## Lag 0                           -0.13454205                    -0.21280936
## Lag 100                         -0.14136050                    -0.21928247
## Lag 500                         -0.12646869                    -0.19382371
## Lag 1000                        -0.12162967                    -0.17751558
## Lag 5000                        -0.02590274                    -0.02880894
##           traittarsus.1:traitbwt.1.units traitbwt.1:traitbwt.1.units
## Lag 0                         0.11344391                 0.131450832
## Lag 100                       0.08507484                 0.105602349
## Lag 500                       0.08084299                 0.125553514
## Lag 1000                      0.11040825                 0.165398766
## Lag 5000                     -0.06475361                 0.003312387
##           traittarsus.2:traitbwt.1.units traitbwt.2:traitbwt.1.units
## Lag 0                        -0.18001725                 -0.24436125
## Lag 100                      -0.18862947                 -0.25750569
## Lag 500                      -0.17962012                 -0.23342183
## Lag 1000                     -0.16368716                 -0.20650410
## Lag 5000                     -0.02638416                 -0.02742457
##           traittarsus.1:traittarsus.2.units traitbwt.1:traittarsus.2.units
## Lag 0                           -0.13454205                    -0.18001725
## Lag 100                         -0.14136050                    -0.18862947
## Lag 500                         -0.12646869                    -0.17962012
```

```
## Lag 1000                      -0.12162967                    -0.16368716
## Lag 5000                      -0.02590274                    -0.02638416
##            traittarsus.2:traittarsus.2.units traitbwt.2:traittarsus.2.units
## Lag 0                          0.75421487                     0.92347712
## Lag 100                        0.68911416                     0.81697064
## Lag 500                        0.62438762                     0.68932883
## Lag 1000                       0.56071503                     0.60055861
## Lag 5000                       0.01204694                    -0.04603239
##            traittarsus.1:traitbwt.2.units traitbwt.1:traitbwt.2.units
## Lag 0                       -0.21280936                 -0.24436125
## Lag 100                     -0.21928247                 -0.25750569
## Lag 500                     -0.19382371                 -0.23342183
## Lag 1000                    -0.17751558                 -0.20650410
## Lag 5000                    -0.02880894                 -0.02742457
##            traittarsus.2:traitbwt.2.units traitbwt.2:traitbwt.2.units
## Lag 0                        0.92347712                  1.00000000
## Lag 100                      0.81697064                  0.84520133
## Lag 500                      0.68932883                  0.66116525
## Lag 1000                     0.60055861                  0.55204450
## Lag 5000                    -0.04603239                 -0.08094849
```

3.5 brms

First load brms:

```
library(brms)
Amat <- as.matrix(nadiv::makeA(gryphonped))
```

3.5.1 Fitting the model

Fitting a multivariate model in brms involves several new consideration above those for fitting univariate models. First, we need to create two models/objects with the function `bf` fitting the desired univariate model structure for each response variable (here `bwt` and `tarsus`). It is the equivalent of writing `mvbf(bwt, tarsus)`, but the advantage to create two distinct model is to specific different model structure (fixed or random effect) for each response variable.

Then, the two objects/models are added into a third model to quantify all the estimates in addition to their covariance. Contrary to MCMCglmm or asreml-R, brms directly estimate the covariance and the correlation in its outputs. Our most basic model can be specified as:

```
bf_bwt <- bf(bwt ~ 1 + (1 | a | gr(animal, cov = Amat)))
bf_tarsus <- bf(tarsus ~ 1 + (1 | a | gr(animal, cov = Amat)))
brms_m2.1 <- brm(
  bf_bwt + bf_tarsus + set_rescor(TRUE),
  data = gryphon,
```

```
  data2 = list(Amat = Amat),
  chains = 2, cores = 2, iter = 1000
)
save(brms_m2.1, file = "data/brms_m2_1.rda")
```

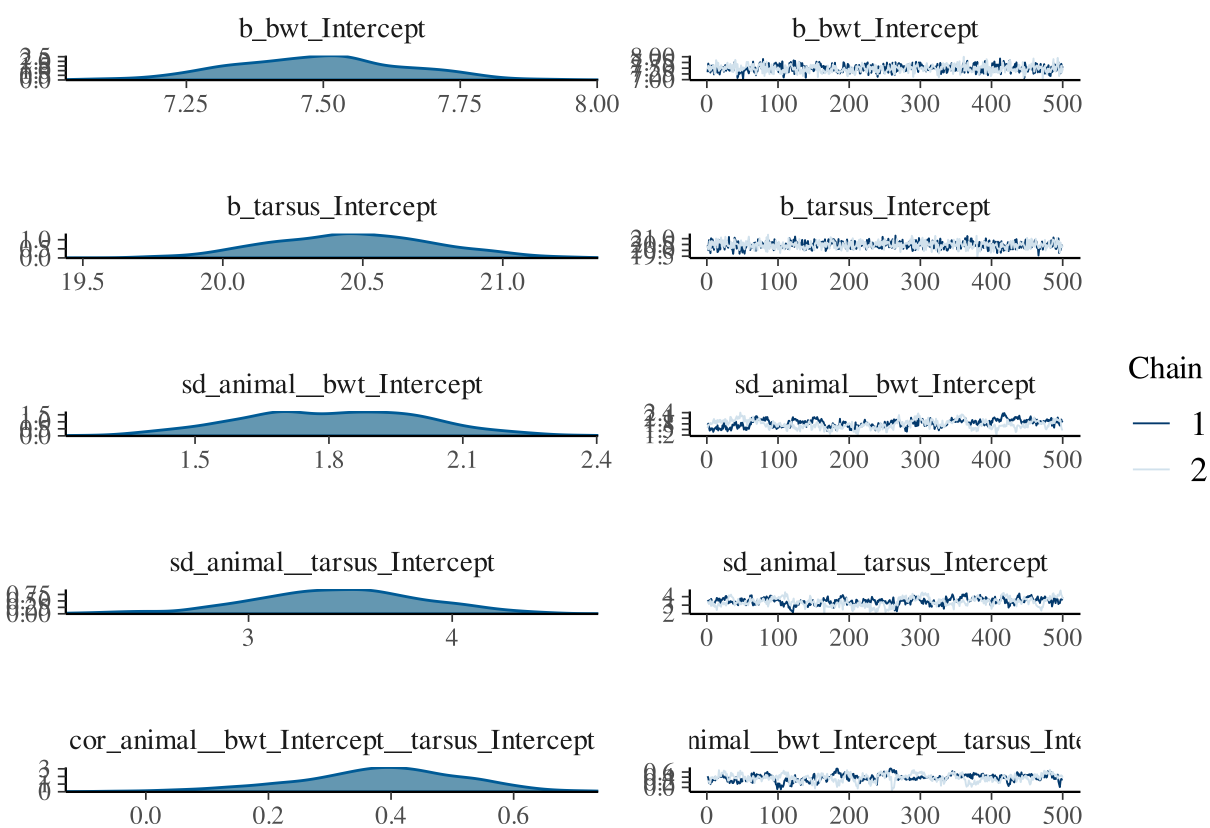
Again we have provided the data from one such run. It can be accessed using the code:

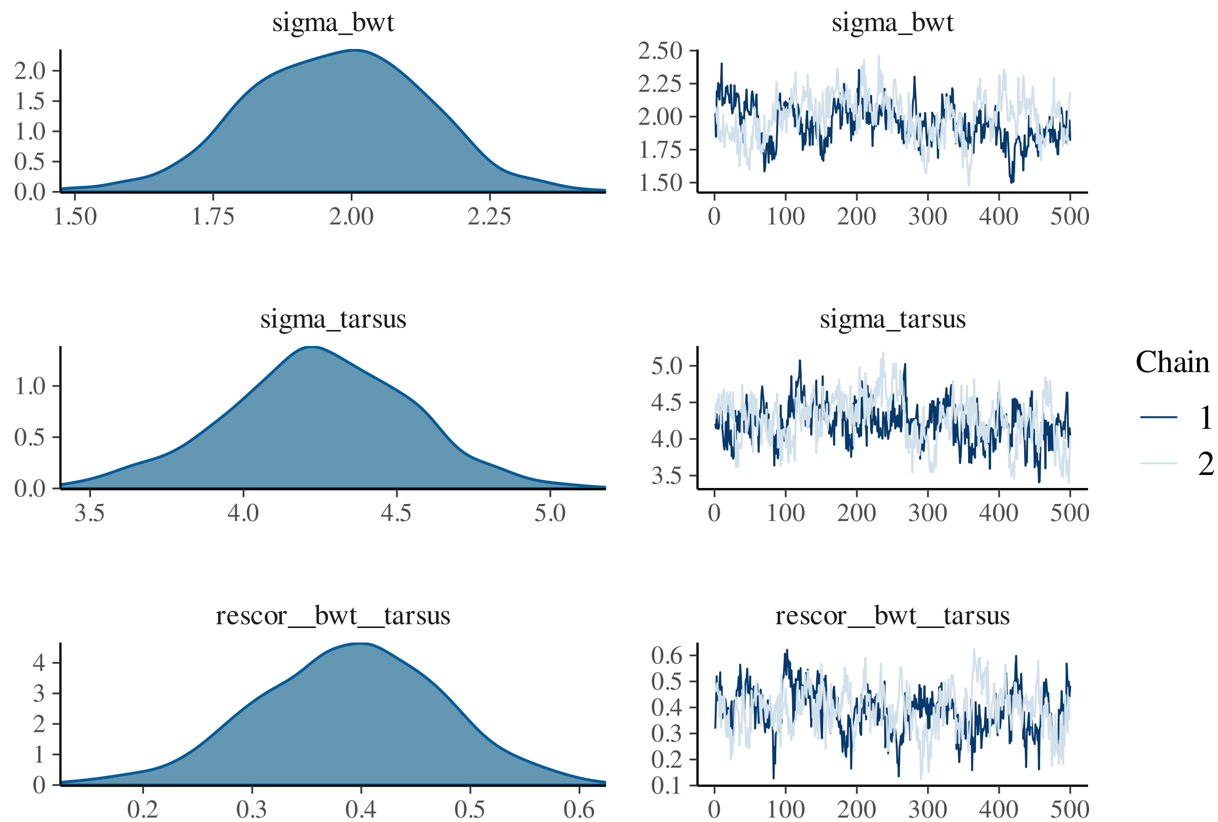
```
load("data/brms_m2_1.rda")
summary(brms_m2.1)
```

```
## Warning: Parts of the model have not converged (some Rhats are > 1.05). Be
## careful when analysing the results! We recommend running more iterations and/or
## setting stronger priors.

##  Family: MV(gaussian, gaussian)
##   Links: mu = identity; sigma = identity
##          mu = identity; sigma = identity
## Formula: bwt ~ 1 + (1 | p | gr(animal, cov = Amat))
##          tarsus ~ 1 + (1 | p | gr(animal, cov = Amat))
##    Data: gryphon (Number of observations: 683)
##   Draws: 2 chains, each with iter = 1000; warmup = 500; thin = 1;
##          total post-warmup draws = 1000
##
## Group-Level Effects:
## ~animal (Number of levels: 683)
##                                Estimate Est.Error l-95% CI u-95% CI Rhat
## sd(bwt_Intercept)                  1.81      0.21     1.41     2.20 1.06
## sd(tarsus_Intercept)               3.44      0.43     2.49     4.25 1.05
## cor(bwt_Intercept,tarsus_Intercept)     0.38      0.14     0.08     0.62 1.02
##                                Bulk_ESS Tail_ESS
## sd(bwt_Intercept)                    31      192
## sd(tarsus_Intercept)                 61      173
## cor(bwt_Intercept,tarsus_Intercept)      101      232
##
## Population-Level Effects:
##                  Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## bwt_Intercept        7.49      0.16     7.20     7.79 1.00      608      839
## tarsus_Intercept    20.47      0.30    19.92    21.03 1.00      868      803
##
## Family Specific Parameters:
##              Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## sigma_bwt        1.97      0.16     1.66     2.28 1.06       27      172
## sigma_tarsus     4.24      0.30     3.63     4.82 1.04       72      162
##
## Residual Correlations:
##                        Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
```

```
## rescor(bwt,tarsus)     0.39      0.09      0.21      0.55 1.02        95       179
##
## Draws were sampled using sampling(NUTS). For each parameter, Bulk_ESS
## and Tail_ESS are effective sample size measures, and Rhat is the potential
## scale reduction factor on split chains (at convergence, Rhat = 1).
```

```r
plot(brms_m2.1, ask = FALSE)
```






```
VarCorr(brms_m2.1)
```

```
## $animal
## $animal$sd
##                   Estimate Est.Error     Q2.5    Q97.5
## bwt_Intercept     1.808171 0.2050233 1.412824 2.204805
## tarsus_Intercept 3.438368 0.4283612 2.491218 4.245264
##
## $animal$cor
## , , bwt_Intercept
##
##                    Estimate Est.Error       Q2.5     Q97.5
## bwt_Intercept     1.0000000 0.0000000 1.00000000 1.0000000
## tarsus_Intercept 0.3814062 0.1380014 0.07581464 0.6209038
##
## , , tarsus_Intercept
##
##                    Estimate Est.Error       Q2.5     Q97.5
## bwt_Intercept     0.3814062 0.1380014 0.07581464 0.6209038
## tarsus_Intercept 1.0000000 0.0000000 1.00000000 1.0000000
##
##
## $animal$cov
```

```
## , , bwt_Intercept
##
##                   Estimate Est.Error      Q2.5    Q97.5
## bwt_Intercept    3.311473 0.7430185 1.9960721 4.861167
## tarsus_Intercept 2.440166 1.0901689 0.3870783 4.668720
##
## , , tarsus_Intercept
##
##                    Estimate Est.Error      Q2.5    Q97.5
## bwt_Intercept     2.440166  1.090169 0.3870783  4.66872
## tarsus_Intercept 12.005688  2.918741 6.2061701 18.02226
##
##
##
## $residual__
## $residual__$sd
##        Estimate Est.Error     Q2.5    Q97.5
## bwt    1.970532 0.1597581 1.658782 2.276074
## tarsus 4.244704 0.2984518 3.632824 4.820109
##
## $residual__$cor
## , , bwt
##
##         Estimate  Est.Error      Q2.5     Q97.5
## bwt    1.0000000 0.00000000 1.0000000 1.0000000
## tarsus 0.3888754 0.08510488 0.2127907 0.5526631
##
## , , tarsus
##
##         Estimate  Est.Error      Q2.5     Q97.5
## bwt    0.3888754 0.08510488 0.2127907 0.5526631
## tarsus 1.0000000 0.00000000 1.0000000 1.0000000
##
##
## $residual__$cov
## , , bwt
##
##        Estimate Est.Error     Q2.5    Q97.5
## bwt    3.908493 0.6282892 2.751557 5.180511
## tarsus 3.289995 0.9305960 1.572647 5.147133
##
## , , tarsus
##
##         Estimate Est.Error      Q2.5     Q97.5
## bwt     3.289995  0.930596  1.572647  5.147133
## tarsus 18.106495  2.530138 13.197409 23.233452
```

It is also possible to calculate the heritability for each trait using the function 'as.mcmc'

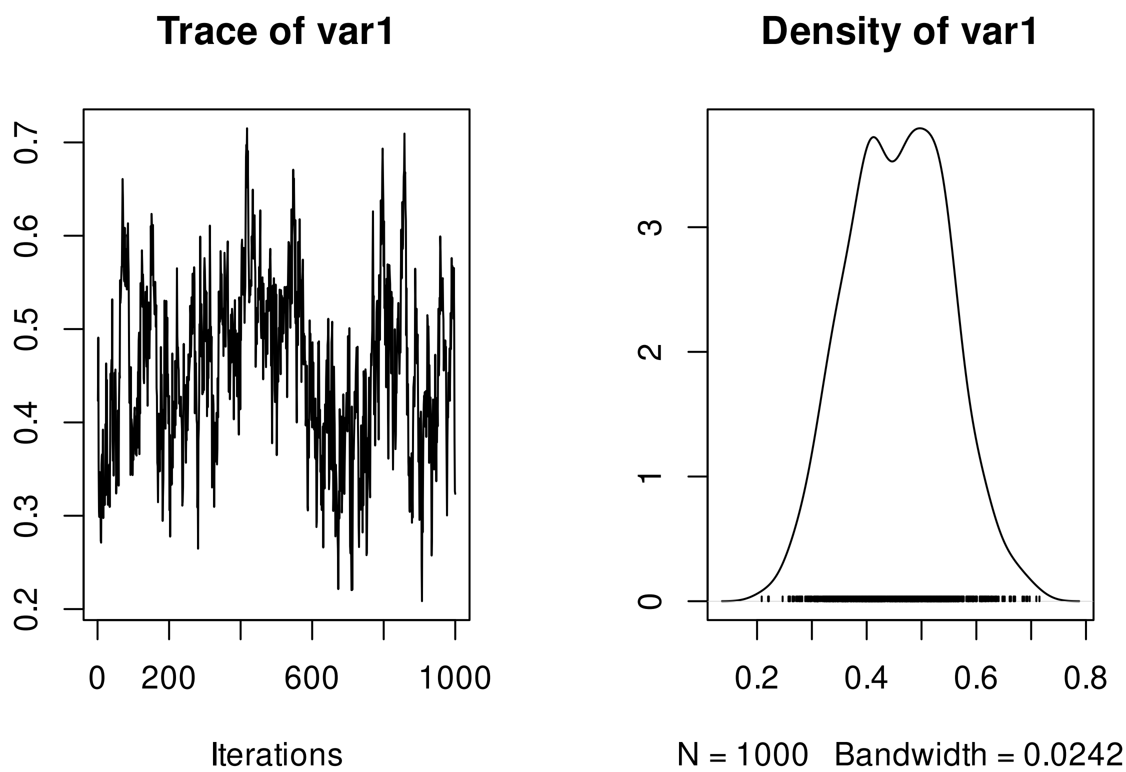
```
v_animal <- (VarCorr(brms_m2.1, summary = FALSE)$animal$sd)^2
v_r <- (VarCorr(brms_m2.1, summary = FALSE)$residual$sd)^2

h.bwt.2 <- as.mcmc(v_animal[, 1] / (v_animal[, 1] + v_r[, 1]))
h.tarsus.2 <- as.mcmc(v_animal[, 1] / (v_animal[, 1] + v_r[, 1]))

summary(h.bwt.2)
```

```
##
## Iterations = 1:1000
## Thinning interval = 1
## Number of chains = 1
## Sample size per chain = 1000
##
## 1. Empirical mean and standard deviation for each variable,
##    plus standard error of the mean:
##
##           Mean             SD       Naive SE Time-series SE
##       0.457051       0.090878       0.002874       0.011675
##
## 2. Quantiles for each variable:
##
##   2.5%    25%    50%    75%  97.5%
## 0.2878 0.3926 0.4596 0.5254 0.6297
```

```
summary(h.tarsus.2)
```

```
##
## Iterations = 1:1000
## Thinning interval = 1
## Number of chains = 1
## Sample size per chain = 1000
##
## 1. Empirical mean and standard deviation for each variable,
##    plus standard error of the mean:
##
##           Mean             SD       Naive SE Time-series SE
##       0.457051       0.090878       0.002874       0.011675
##
## 2. Quantiles for each variable:
##
##   2.5%    25%    50%    75%  97.5%
## 0.2878 0.3926 0.4596 0.5254 0.6297
```

```
plot(h.bwt.2)
plot(h.tarsus.2)
```



It is also possible to extract the correlation. Just to remember it is an example, the correlation distribution is skewed to 1 due to a weak prior and model parameters. Note, since

```
cor_g <- as.mcmc((VarCorr(brms_m2.1, summary = FALSE)$animal$cor[, 1, 2]))
cor_res <- as.mcmc((VarCorr(brms_m2.1, summary = FALSE)$residual$cor[, 1, 2]))

summary(cor_g)
```

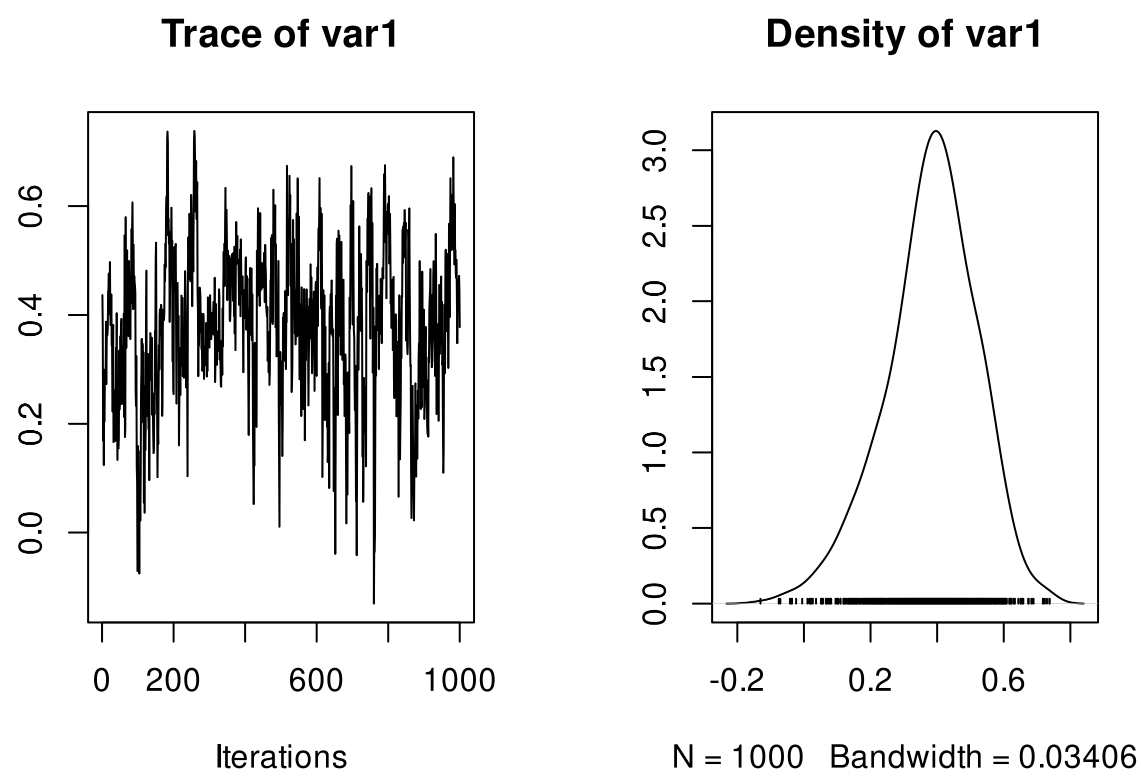
```
##
## Iterations = 1:1000
## Thinning interval = 1
## Number of chains = 1
## Sample size per chain = 1000
##
## 1. Empirical mean and standard deviation for each variable,
##    plus standard error of the mean:
##
##           Mean             SD       Naive SE Time-series SE
##       0.381406       0.138001       0.004364       0.014946
```

```
##
## 2. Quantiles for each variable:
##
##    2.5%     25%     50%     75%   97.5%
## 0.07581 0.30354 0.39041 0.47497 0.62090
```

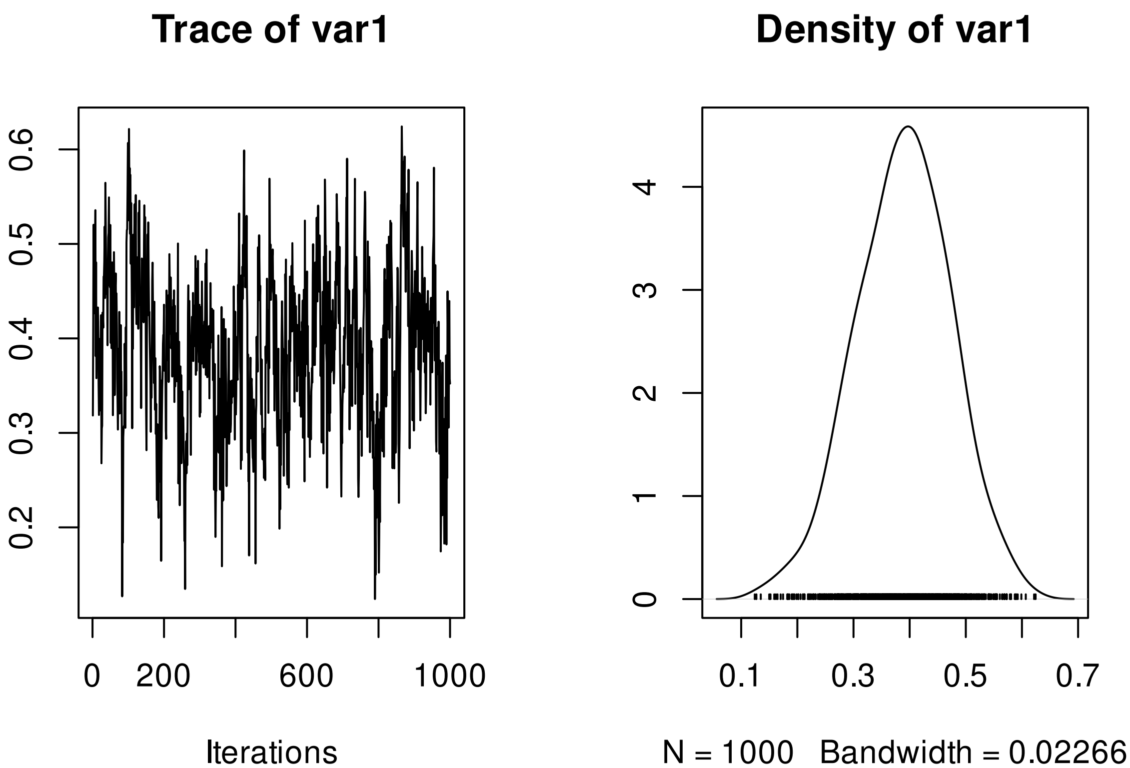
```r
summary(cor_res)
```

```
##
## Iterations = 1:1000
## Thinning interval = 1
## Number of chains = 1
## Sample size per chain = 1000
##
## 1. Empirical mean and standard deviation for each variable,
##    plus standard error of the mean:
##
##           Mean             SD       Naive SE Time-series SE
##       0.388875       0.085105       0.002691       0.009215
##
## 2. Quantiles for each variable:
##
##   2.5%    25%    50%    75%  97.5%
## 0.2128 0.3319 0.3913 0.4484 0.5527
```

```r
plot(cor_g)
```


Trace of var1
0.0
0.2
0.4
0.6
0
200
600
1000
Iterations
Density of var1
0.0
0.5
1.0
1.5
2.0
2.5
3.0
-0.2
0.2
0.6
N = 1000 Bandwidth = 0.03406

```
plot(cor_res)
```



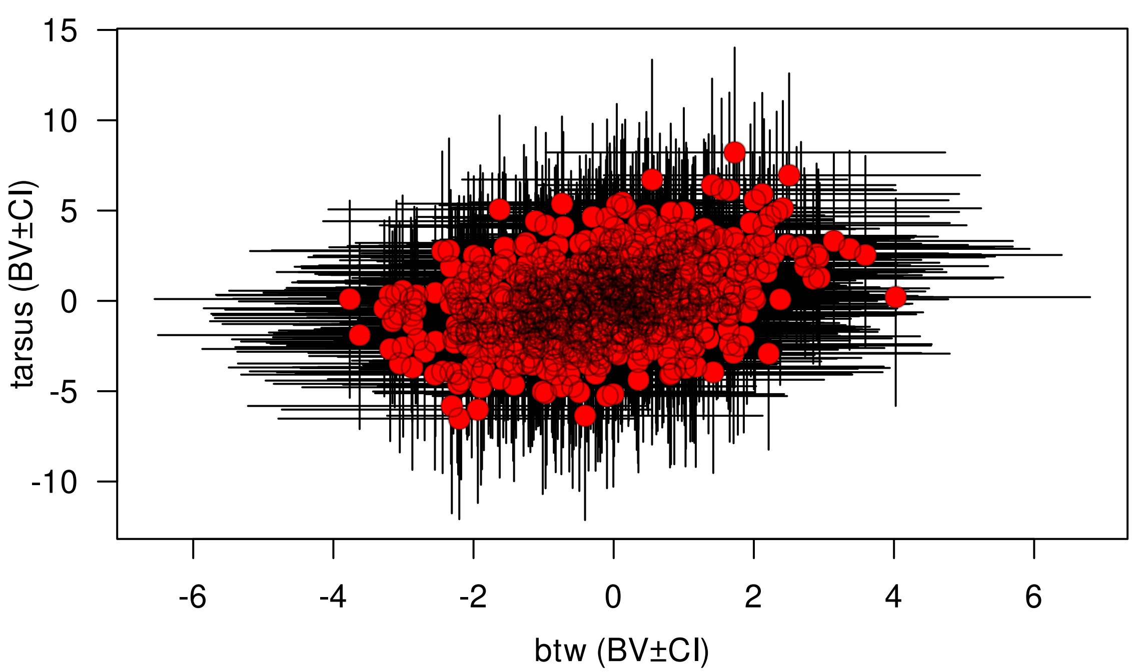
Here we can plot the genetic correlation by extraction the breeding values or BLUP.

```
bls_m2.1 <- ranef(brms_m2.1)$animal
bl_m2.1 <- as.data.frame(abind::abind(lapply(1:dim(bls_m2.1)[[3]], function(x) bls_m2.1[,
colnames(bl_m2.1) <- paste0(rep(dimnames(bls_m2.1)[[3]], each = 3), c("", "_lo", "_up"))
bl_m2.1$id <- rownames(bl_m2.1)
```

Here, some simple code to plot the genetic correlation.

```
plot(tarsus_Intercept ~ bwt_Intercept, bl_m2.1,
  xlab = "", ylab = "",
  xlim = c(min(bl_m2.1$bwt_Intercept_lo), max(bl_m2.1$bwt_Intercept_up)),
  ylim = c(min(bl_m2.1$tarsus_Intercept_lo), max(bl_m2.1$tarsus_Intercept_up)),
  las = 1.2, type = "n"
)
with(
  bl_m2.1,
  segments(
    x0 = bwt_Intercept, y0 = tarsus_Intercept_lo,
    x1 = bwt_Intercept, y1 = tarsus_Intercept_up,
    col = "black"
  )
```

```
)
with(bl_m2.1, segments(
  x0 = bwt_Intercept_lo, y0 = tarsus_Intercept,
  x1 = bwt_Intercept_up, y1 = tarsus_Intercept,
  col = "black"
))
points(tarsus_Intercept ~ bwt_Intercept, bl_m2.1, pch = 16, col = "red", cex = 1.5)
points(tarsus_Intercept ~ bwt_Intercept, bl_m2.1, pch = 1, col = rgb(0, 0, 0, 0.3), cex =
mtext("btw (BV±CI)", side = 1, line = 2.4)
mtext("tarsus (BV±CI)", side = 2, line = 2, las = 3)
```



3.5.2 Adding fixed and random effects

Fixed and random effects can be added just as for the univariate case. Given that our full model of bwt from tutorial 1 had sex as a fixed effect as well as random effects of byear and mother, we could specify a bivariate formulation of this using the following code (including a line to save the output):

```
bf_bwt_2 <- bf(bwt ~ 1 + sex + (1 | a | gr(animal, cov = Amat)) + (1 | b | byear) + (1 | c
bf_tarsus_2 <- bf(tarsus ~ 1 + sex + (1 | a | gr(animal, cov = Amat)) + (1 | b | byear) +
```

```
brms_m2.2 <- brm(
  bf_bwt_2 + bf_tarsus_2 + set_rescor(TRUE),
  data = gryphon,
  data2 = list(Amat = Amat),
  chains = 2, cores = 2, iter = 1000
)

save(brms_m2.2, file = "data/brms_m2_2.rda")
```

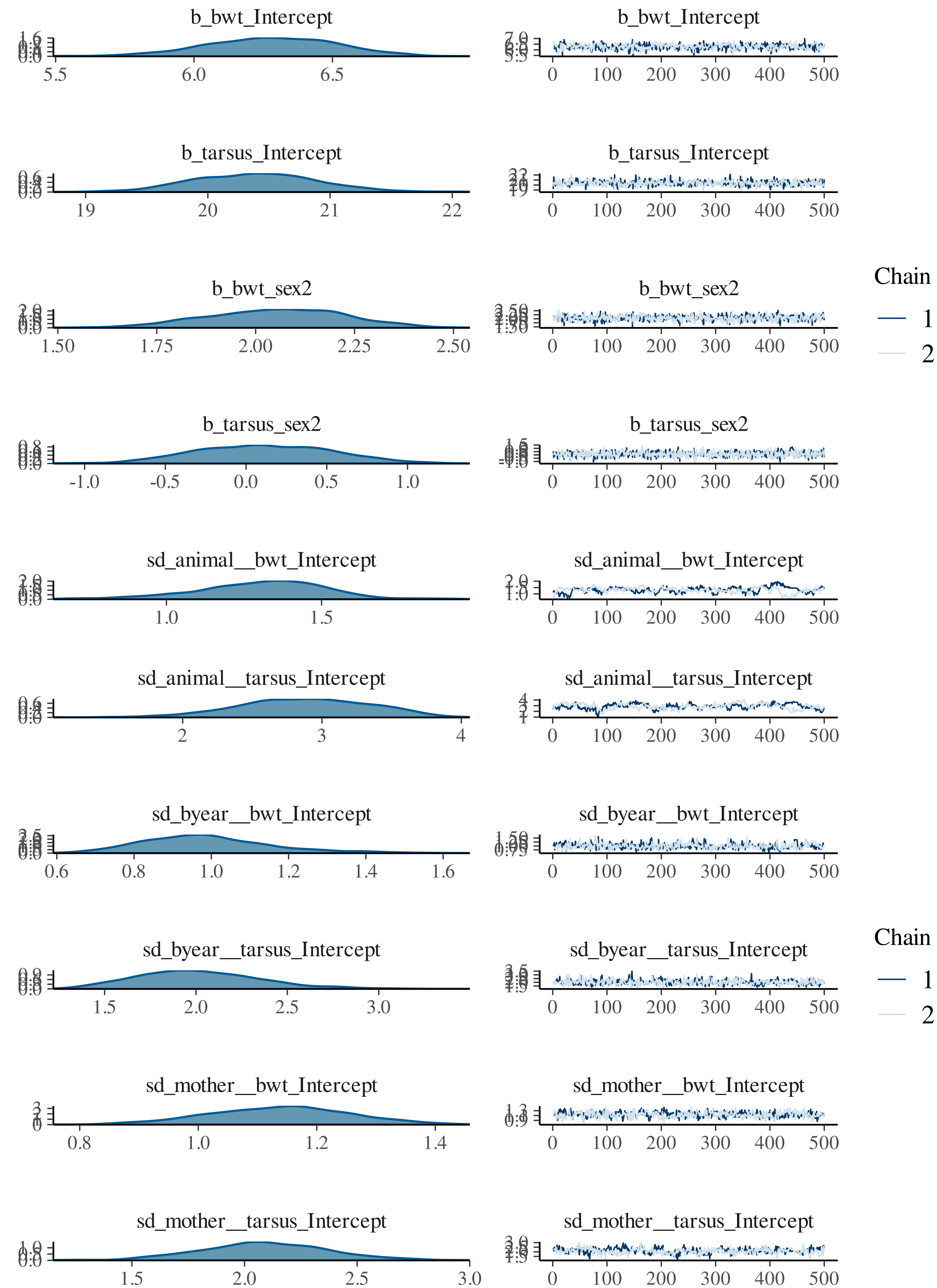
Again we have provided the data from one such run. It can be accessed using the code:

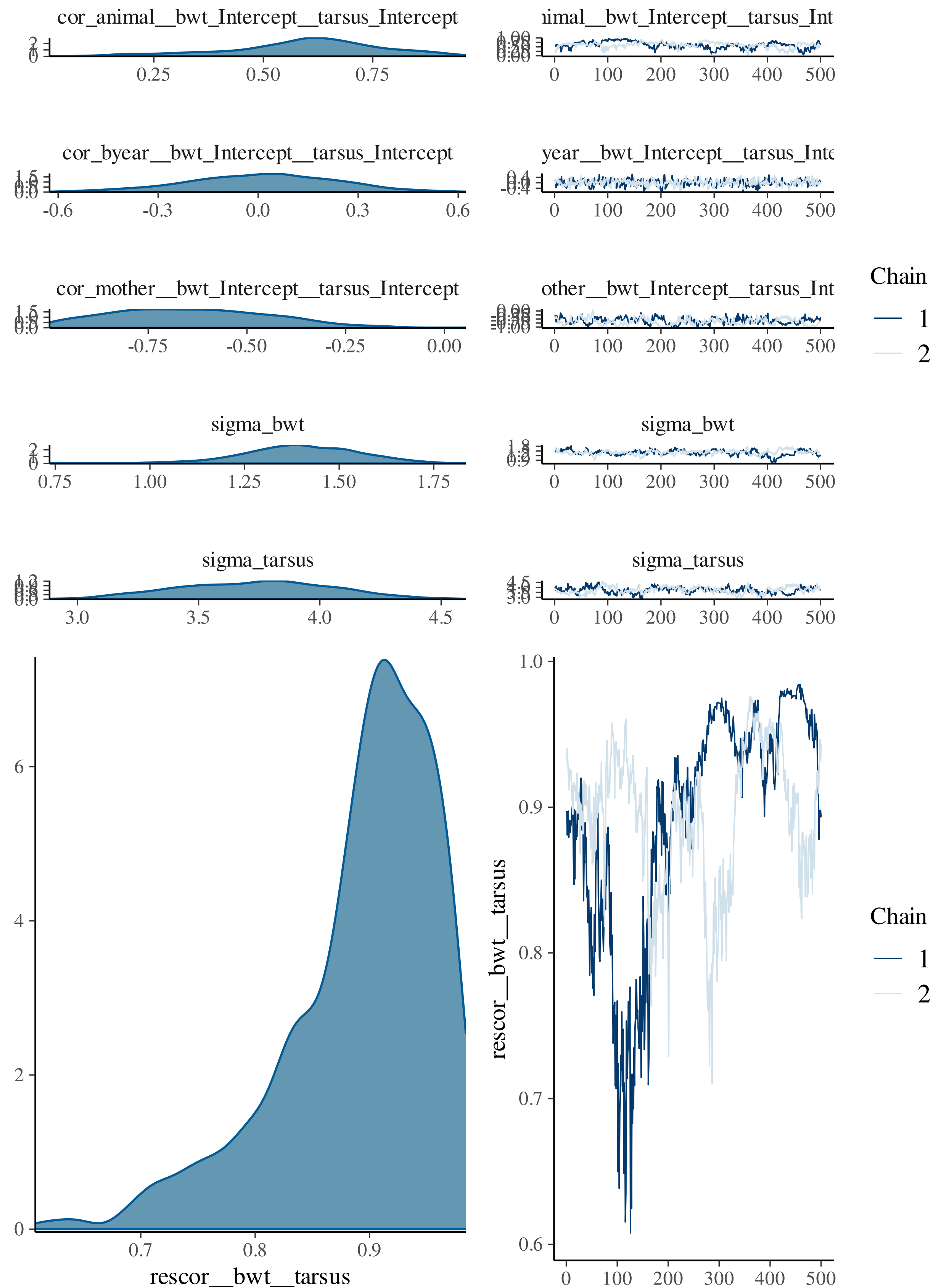
```
load("data/brms_m2_2.rda")
summary(brms_m2.2)
```

```
## Warning: Parts of the model have not converged (some Rhats are > 1.05). Be
## careful when analysing the results! We recommend running more iterations and/or
## setting stronger priors.

## Warning: There were 4 divergent transitions after warmup. Increasing adapt_delta
## above 0.8 may help. See http://mc-stan.org/misc/warnings.html#divergent-
## transitions-after-warmup

##  Family: MV(gaussian, gaussian)
##   Links: mu = identity; sigma = identity
##          mu = identity; sigma = identity
## Formula: bwt ~ 1 + sex + (1 | a | gr(animal, cov = Amat)) + (1 | b | byear) + (1 | c | 
##          tarsus ~ 1 + sex + (1 | a | gr(animal, cov = Amat)) + (1 | b | byear) + (1 | c
##    Data: gryphon (Number of observations: 683)
##   Draws: 2 chains, each with iter = 1000; warmup = 500; thin = 1;
##          total post-warmup draws = 1000
##
## Group-Level Effects:
## ~animal (Number of levels: 683)
##                                   Estimate Est.Error l-95% CI u-95% CI Rhat
## sd(bwt_Intercept)                     1.31      0.21     0.86     1.69 1.06
## sd(tarsus_Intercept)                  2.88      0.47     1.88     3.70 1.01
## cor(bwt_Intercept,tarsus_Intercept)   0.60      0.17     0.18     0.89 1.09
##                                   Bulk_ESS Tail_ESS
## sd(bwt_Intercept)                       54       58
## sd(tarsus_Intercept)                    52      162
## cor(bwt_Intercept,tarsus_Intercept)     25       30
##
## ~byear (Number of levels: 34)
##                                   Estimate Est.Error l-95% CI u-95% CI Rhat
## sd(bwt_Intercept)                     0.99      0.17     0.71     1.39 1.00
## sd(tarsus_Intercept)                  2.02      0.34     1.45     2.78 1.00
```

```
## cor(bwt_Intercept,tarsus_Intercept)     0.01      0.22    -0.44     0.44 1.01
##                                     Bulk_ESS Tail_ESS
## sd(bwt_Intercept)                        424      509
## sd(tarsus_Intercept)                     525      699
## cor(bwt_Intercept,tarsus_Intercept)      478      492
##
## ~mother (Number of levels: 352)
##                                     Estimate Est.Error l-95% CI u-95% CI Rhat
## sd(bwt_Intercept)                       1.14      0.12     0.90     1.36 1.01
## sd(tarsus_Intercept)                    2.09      0.29     1.54     2.67 1.01
## cor(bwt_Intercept,tarsus_Intercept)    -0.64      0.20    -0.97    -0.24 1.02
##                                     Bulk_ESS Tail_ESS
## sd(bwt_Intercept)                        370      764
## sd(tarsus_Intercept)                     134      420
## cor(bwt_Intercept,tarsus_Intercept)       84      147
##
## Population-Level Effects:
##                  Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## bwt_Intercept        6.28      0.24     5.80     6.73 1.00      453      703
## tarsus_Intercept    20.39      0.52    19.45    21.39 1.00      755      760
## bwt_sex2             2.05      0.17     1.71     2.37 1.00     1097      715
## tarsus_sex2          0.11      0.42    -0.67     0.90 1.00      780      578
##
## Family Specific Parameters:
##              Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## sigma_bwt        1.40      0.16     1.05     1.68 1.04       59       60
## sigma_tarsus     3.73      0.32     3.14     4.32 1.00       55      176
##
## Residual Correlations:
##                    Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## rescor(bwt,tarsus)     0.89      0.07     0.72     0.98 1.50        4       24
##
## Draws were sampled using sampling(NUTS). For each parameter, Bulk_ESS
## and Tail_ESS are effective sample size measures, and Rhat is the potential
## scale reduction factor on split chains (at convergence, Rhat = 1).
```

```r
plot(brms_m2.2, ask = FALSE)
```


b_bwt_Intercept
5.5 6.0 6.5
b_bwt_Intercept
0 100 200 300 400 500
b_tarsus_Intercept
19 20 21 22
b_tarsus_Intercept
0 100 200 300 400 500
b_bwt_sex2
1.50 1.75 2.00 2.25 2.50
b_bwt_sex2
0 100 200 300 400 500
b_tarsus_sex2
-1.0 -0.5 0.0 0.5 1.0
b_tarsus_sex2
0 100 200 300 400 500
sd_animal__bwt_Intercept
1.0 1.5
sd_animal__bwt_Intercept
0 100 200 300 400 500
sd_animal__tarsus_Intercept
2 3 4
sd_animal__tarsus_Intercept
0 100 200 300 400 500
sd_byear__bwt_Intercept
0.6 0.8 1.0 1.2 1.4 1.6
sd_byear__bwt_Intercept
0 100 200 300 400 500
sd_byear__tarsus_Intercept
1.5 2.0 2.5 3.0
sd_byear__tarsus_Intercept
0 100 200 300 400 500
sd_mother__bwt_Intercept
0.8 1.0 1.2 1.4
sd_mother__bwt_Intercept
0 100 200 300 400 500
sd_mother__tarsus_Intercept
1.5 2.0 2.5 3.0
sd_mother__tarsus_Intercept
0 100 200 300 400 500
Chain
1
2
Chain
1
2


cor_animal__bwt_Intercept__tarsus_Intercept
0.25
0.50
0.75
imal__bwt_Intercept__tarsus_Int
0
100
200
300
400
500
cor_byear__bwt_Intercept__tarsus_Intercept
-0.6
-0.3
0.0
0.3
0.6
year__bwt_Intercept__tarsus_Inte
cor_mother__bwt_Intercept__tarsus_Intercept
-0.75
-0.50
-0.25
0.00
other__bwt_Intercept__tarsus_Int
Chain
1
2
sigma_bwt
0.75
1.00
1.25
1.50
1.75
sigma_bwt
sigma_tarsus
3.0
3.5
4.0
4.5
sigma_tarsus
0
2
4
6
0.7
0.8
0.9
rescor__bwt__tarsus
1.0
0.9
0.8
0.7
0.6
rescor__bwt__tarsus
0
100
200
300
400
500
Chain
1
2

```r
VarCorr(brms_m2.2)
```

```
## $animal
## $animal$sd
##                   Estimate Est.Error      Q2.5    Q97.5
## bwt_Intercept    1.306921 0.2109780 0.8555702 1.687254
## tarsus_Intercept 2.876731 0.4718524 1.8827128 3.699873
## 
## $animal$cor
## , , bwt_Intercept
## 
##                    Estimate Est.Error      Q2.5     Q97.5
## bwt_Intercept    1.0000000 0.0000000 1.0000000 1.0000000
## tarsus_Intercept 0.5961514 0.1727943 0.1849725 0.8929607
## 
## , , tarsus_Intercept
## 
##                    Estimate Est.Error      Q2.5     Q97.5
## bwt_Intercept    0.5961514 0.1727943 0.1849725 0.8929607
## tarsus_Intercept 1.0000000 0.0000000 1.0000000 1.0000000
## 
## 
## $animal$cov
## , , bwt_Intercept
## 
##                   Estimate Est.Error      Q2.5    Q97.5
## bwt_Intercept    1.752510 0.5433004 0.7320013 2.846827
## tarsus_Intercept 2.357852 1.0462644 0.3960956 4.526731
## 
## , , tarsus_Intercept
## 
##                   Estimate Est.Error      Q2.5     Q97.5
## bwt_Intercept    2.357852  1.046264 0.3960956  4.526731
## tarsus_Intercept 8.498003  2.672465 3.5446115 13.689062
## 
## 
## 
## $byear
## $byear$sd
##                    Estimate Est.Error      Q2.5    Q97.5
## bwt_Intercept    0.9904858 0.1696752 0.7102391 1.390260
## tarsus_Intercept 2.0166804 0.3366954 1.4463862 2.777005
## 
## $byear$cor
## , , bwt_Intercept
```

```
##
##                    Estimate Est.Error       Q2.5     Q97.5
## bwt_Intercept    1.00000000 0.0000000  1.0000000 1.0000000
## tarsus_Intercept 0.01351405 0.2206186 -0.4367809 0.4412319
##
## , , tarsus_Intercept
##
##                    Estimate Est.Error       Q2.5     Q97.5
## bwt_Intercept    0.01351405 0.2206186 -0.4367809 0.4412319
## tarsus_Intercept 1.00000000 0.0000000  1.0000000 1.0000000
##
##
## $byear$cov
## , , bwt_Intercept
##
##                    Estimate Est.Error       Q2.5    Q97.5
## bwt_Intercept    1.00982294 0.3583697  0.5044397 1.932823
## tarsus_Intercept 0.06412895 0.4880116 -0.8559486 1.092317
##
## , , tarsus_Intercept
##
##                    Estimate Est.Error       Q2.5    Q97.5
## bwt_Intercept    0.06412895 0.4880116 -0.8559486 1.092317
## tarsus_Intercept 4.18025049 1.4249595  2.0920330 7.711755
##
##
##
## $mother
## $mother$sd
##                  Estimate Est.Error      Q2.5    Q97.5
## bwt_Intercept    1.137249 0.1175495 0.8968349 1.358078
## tarsus_Intercept 2.088602 0.2865291 1.5425683 2.673791
##
## $mother$cor
## , , bwt_Intercept
##
##                    Estimate Est.Error       Q2.5      Q97.5
## bwt_Intercept     1.0000000 0.0000000  1.0000000  1.0000000
## tarsus_Intercept -0.6413329 0.1968102 -0.9745925 -0.2367393
##
## , , tarsus_Intercept
##
##                    Estimate Est.Error       Q2.5      Q97.5
## bwt_Intercept    -0.6413329 0.1968102 -0.9745925 -0.2367393
## tarsus_Intercept  1.0000000 0.0000000  1.0000000  1.0000000
##
##
```

```
## $mother$cov
## , , bwt_Intercept
##
##                   Estimate Est.Error       Q2.5      Q97.5
## bwt_Intercept     1.307139 0.2669748  0.8043132  1.8443762
## tarsus_Intercept -1.467511 0.3650113 -2.1491979 -0.6718737
##
## , , tarsus_Intercept
##
##                   Estimate Est.Error      Q2.5      Q97.5
## bwt_Intercept    -1.467511 0.3650113 -2.149198 -0.6718737
## tarsus_Intercept  4.444274 1.2018090  2.379517  7.1491575
##
##
##
## $residual__
## $residual__$sd
##        Estimate Est.Error     Q2.5    Q97.5
## bwt    1.396815 0.1597393 1.052042 1.684810
## tarsus 3.733614 0.3170549 3.140204 4.319446
##
## $residual__$cor
## , , bwt
##
##         Estimate Est.Error      Q2.5     Q97.5
## bwt    1.0000000 0.0000000 1.0000000 1.0000000
## tarsus 0.8925119 0.0672286 0.7167862 0.9774545
##
## , , tarsus
##
##         Estimate Est.Error      Q2.5     Q97.5
## bwt    0.8925119 0.0672286 0.7167862 0.9774545
## tarsus 1.0000000 0.0000000 1.0000000 1.0000000
##
##
## $residual__$cov
## , , bwt
##
##        Estimate Est.Error     Q2.5    Q97.5
## bwt    1.976584 0.4347085 1.106793 2.838585
## tarsus 4.683451 0.9103808 2.846560 6.440550
##
## , , tarsus
##
##         Estimate Est.Error     Q2.5    Q97.5
## bwt     4.683451 0.9103808 2.846560  6.44055
## tarsus 14.040300 2.3674563 9.860883 18.65761
```

Evaluation of the statistical support for these genetic and maternal correlations is straightforward. Because we imposed no constraint on their estimation, we can evaluate the extent to which the posterior distributions overlap zero:

```
cor_g <- as.mcmc((VarCorr(brms_m2.2, summary = FALSE)$animal$cor[, 1, 2]))
cor_res <- as.mcmc((VarCorr(brms_m2.2, summary = FALSE)$residual$cor[, 1, 2]))
cor_mother <- as.mcmc((VarCorr(brms_m2.2, summary = FALSE)$mother$cor[, 1, 2]))
cor_byear <- as.mcmc((VarCorr(brms_m2.2, summary = FALSE)$byear$cor[, 1, 2]))

summary(cor_g)
```

```
##
## Iterations = 1:1000
## Thinning interval = 1
## Number of chains = 1
## Sample size per chain = 1000
##
## 1. Empirical mean and standard deviation for each variable,
##    plus standard error of the mean:
##
##           Mean             SD       Naive SE Time-series SE
##       0.596151       0.172794       0.005464       0.028178
##
## 2. Quantiles for each variable:
##
##   2.5%    25%    50%    75%  97.5%
## 0.1850 0.5065 0.6117 0.7064 0.8930
```

```
summary(cor_mother)
```

```
##
## Iterations = 1:1000
## Thinning interval = 1
## Number of chains = 1
## Sample size per chain = 1000
##
## 1. Empirical mean and standard deviation for each variable,
##    plus standard error of the mean:
##
##           Mean             SD       Naive SE Time-series SE
##      -0.641333       0.196810       0.006224       0.021355
##
## 2. Quantiles for each variable:
##
##    2.5%     25%     50%     75%   97.5%
## -0.9746 -0.7933 -0.6507 -0.5027 -0.2367
```

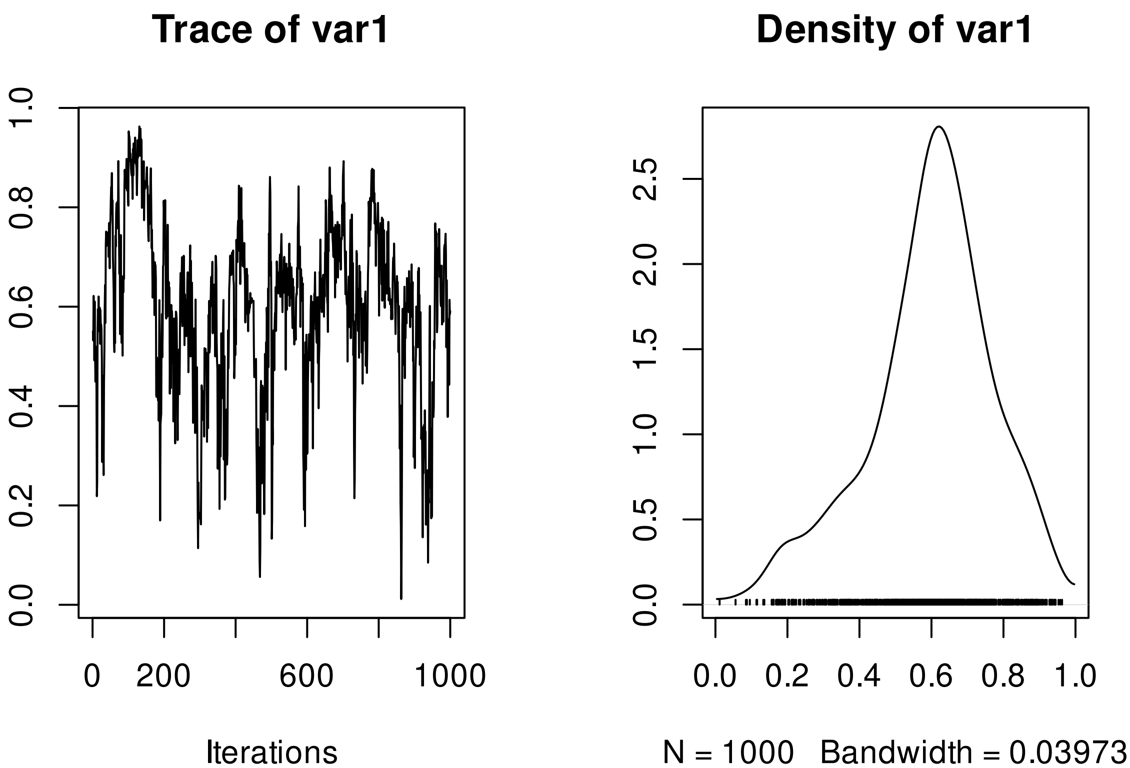
```r
summary(cor_byear)
```

```
##
## Iterations = 1:1000
## Thinning interval = 1
## Number of chains = 1
## Sample size per chain = 1000
##
## 1. Empirical mean and standard deviation for each variable,
##    plus standard error of the mean:
##
##           Mean             SD       Naive SE Time-series SE
##       0.013514       0.220619       0.006977       0.009633
##
## 2. Quantiles for each variable:
##
##     2.5%      25%      50%      75%    97.5%
## -0.43678 -0.13505  0.02408  0.16947  0.44123
```

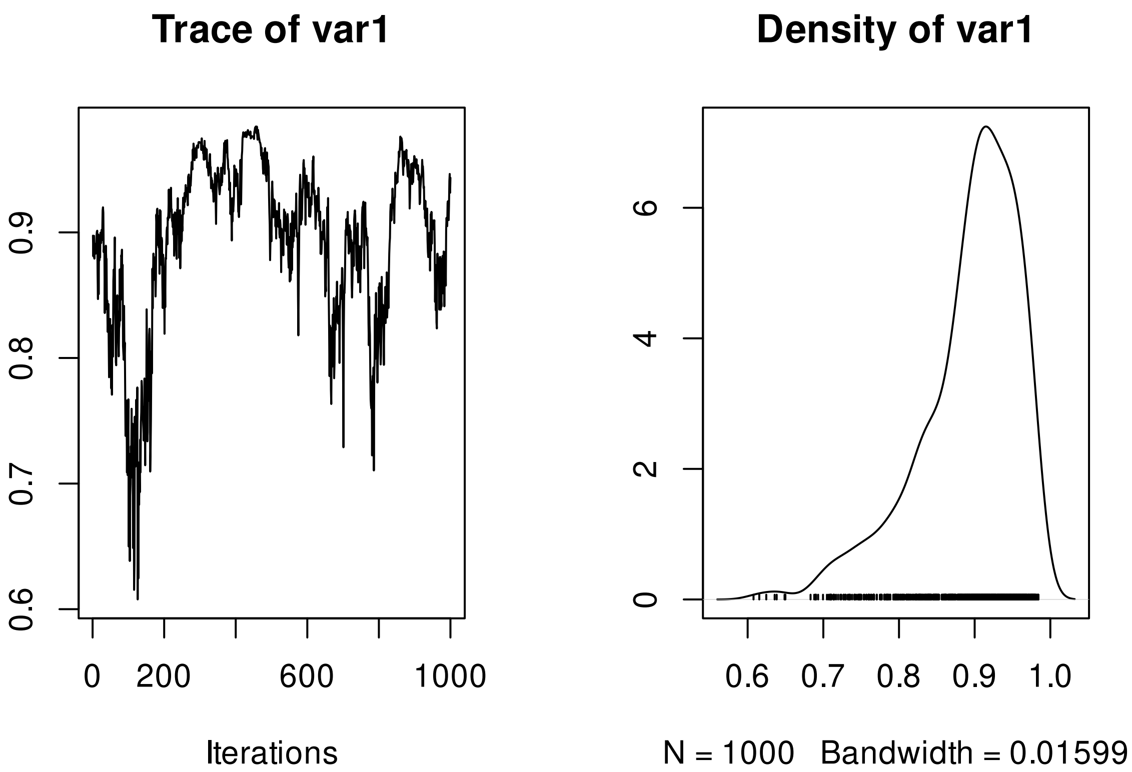
```r
summary(cor_res)
```

```
##
## Iterations = 1:1000
## Thinning interval = 1
## Number of chains = 1
## Sample size per chain = 1000
##
## 1. Empirical mean and standard deviation for each variable,
##    plus standard error of the mean:
##
##           Mean             SD       Naive SE Time-series SE
##       0.892512       0.067229       0.002126       0.026496
##
## 2. Quantiles for each variable:
##
##   2.5%    25%    50%    75%  97.5%
## 0.7168 0.8620 0.9069 0.9425 0.9775
```

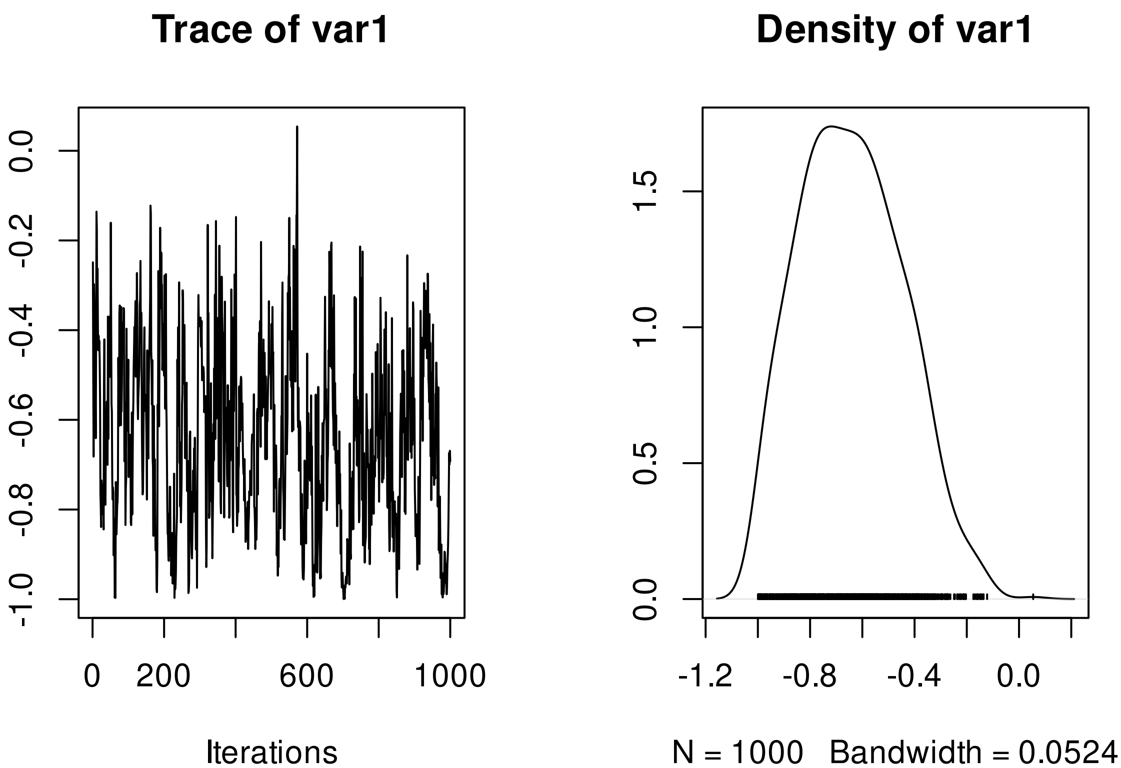
```r
plot(cor_g)
```


Trace of var1
1.0
0.8
0.6
0.4
0.2
0.0
0
200
600
1000
Iterations
Density of var1
2.5
2.0
1.5
1.0
0.5
0.0
0.0
0.2
0.4
0.6
0.8
1.0
N = 1000 Bandwidth = 0.03973

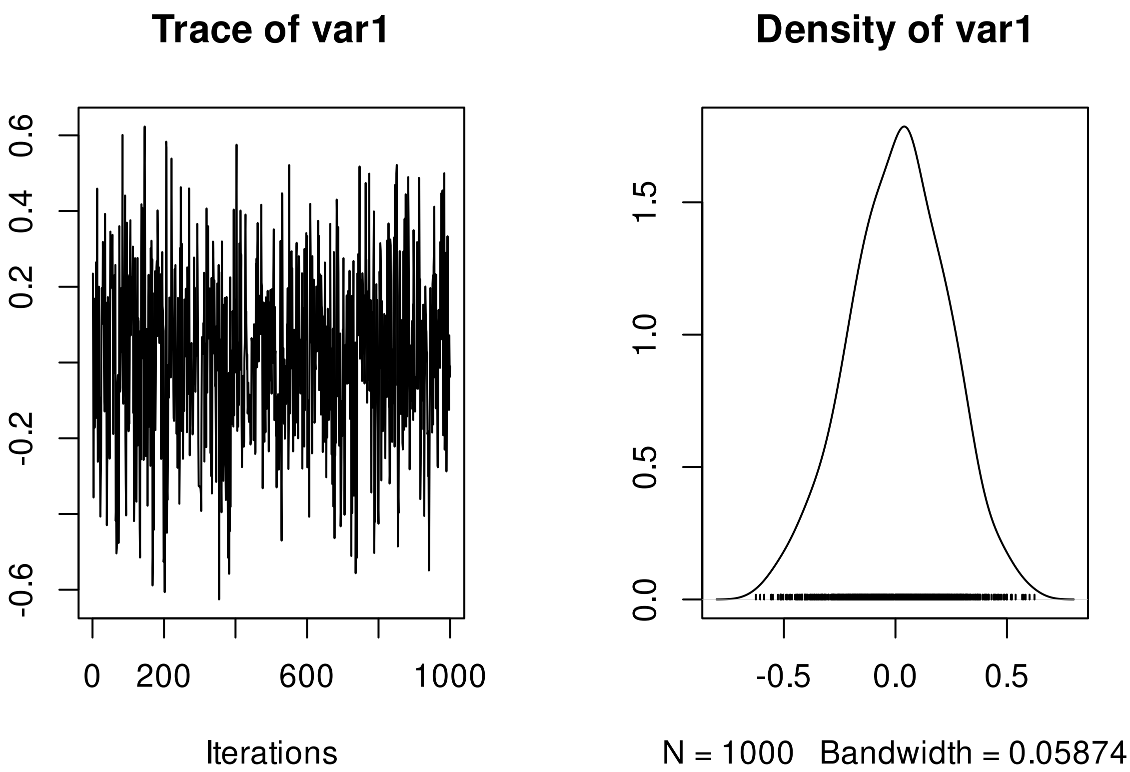
```
plot(cor_res)
```




```
plot(cor_mother)
```

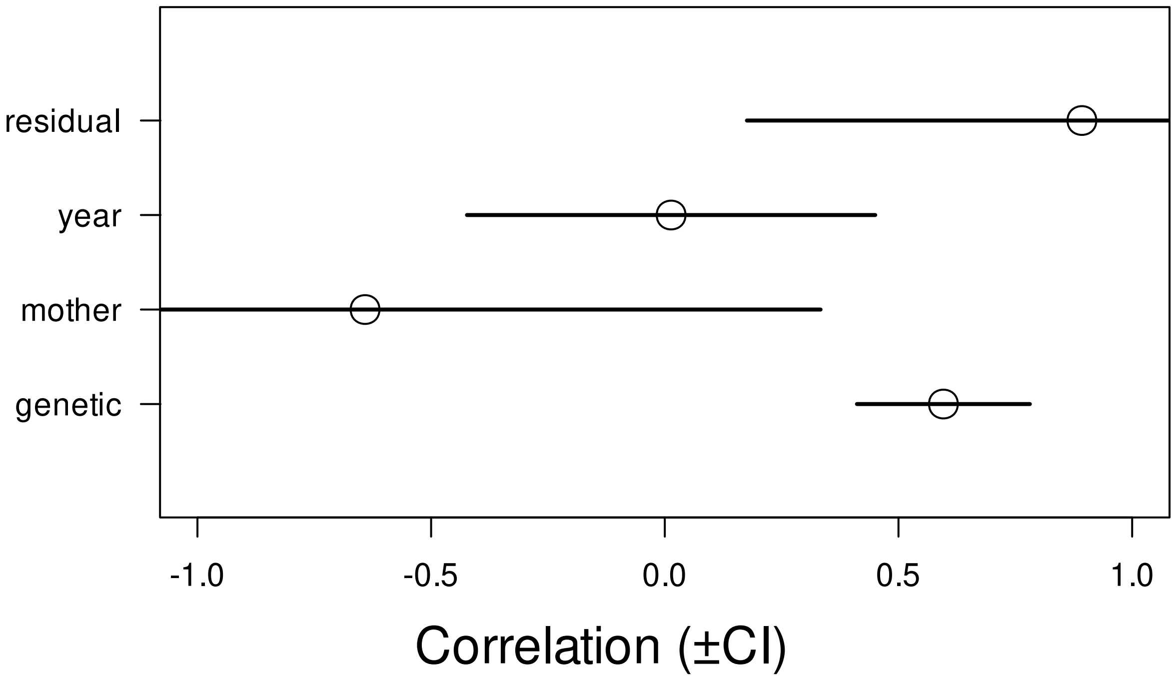



```r
plot(cor_byear)
```



Neither or these posterior distributions overlaps zero, so we can consider them both statistically supported.

```
cor.est <- rbind(
  cbind(summary(cor_g)$statistics[1], summary(cor_g)$quantiles[1], summary(cor_g)$quantile
  cbind(summary(cor_mother)$statistics[1], summary(cor_mother)$quantiles[1], summary(cor_m
  cbind(summary(cor_byear)$statistics[1], summary(cor_byear)$quantiles[1], summary(cor_bye
  cbind(summary(cor_res)$statistics[1], summary(cor_res)$quantiles[1], summary(cor_res)$qu
)


plot(c(1, 2, 3, 4) ~ cor.est[, 1], xlim = c(-1, 1), ylim = c(0, 5), xlab = "", ylab = "",
segments(y0 = 1, x0 = cor.est[1, 1] - cor.est[1, 2], y1 = 1, x1 = cor.est[1, 1] + cor.est[
segments(y0 = 2, x0 = cor.est[2, 1] - cor.est[2, 2], y1 = 2, x1 = cor.est[2, 1] + cor.est[
segments(y0 = 3, x0 = cor.est[3, 1] - cor.est[3, 2], y1 = 3, x1 = cor.est[3, 1] + cor.est[
segments(y0 = 4, x0 = cor.est[4, 1] - cor.est[4, 2], y1 = 4, x1 = cor.est[4, 1] + cor.est[
mtext("Correlation (±CI)", side = 1, las = 1, adj = 0.4, line = 3, cex = 1.6)
axis(2, at = 1, labels = c("genetic"), las = 2, cex.axis = 1)
axis(2, at = 2, labels = c("mother"), las = 2, cex.axis = 1)
axis(2, at = 3, labels = c("year"), las = 2, cex.axis = 1)
axis(2, at = 4, labels = c("residual"), las = 2, cex.axis = 1)
```



Note, brms estimates the correlation and also the covariance. We can also recalculate the correlation directly from the covariance.To facilitate the extraction of the different parameter, we can the fucntion `as_draws_df`

```
cov_g <- (VarCorr(brms_m2.2, summary = FALSE)$animal$cov)[, 1, 2]
cov_res <- (VarCorr(brms_m2.2, summary = FALSE)$residual$cov)[, 1, 2]
cov_mother <- (VarCorr(brms_m2.2, summary = FALSE)$mother$cov)[, 1, 2]
cov_byear <- (VarCorr(brms_m2.2, summary = FALSE)$byear$cov)[, 1, 2]

var.est <- as_draws_df(brms_m2.2, variable = c("sd", "sigma"), regex = TRUE)
var.est <- var.est^2

cor_g_2 <- as.mcmc(cov_g / sqrt(var.est[1] * var.est[2]))
cor_byear_2 <- as.mcmc(cov_byear / sqrt(var.est[3] * var.est[4]))
cor_mother_2 <- as.mcmc(cov_g / sqrt(var.est[5] * var.est[6]))
cor_res_2 <- as.mcmc(cov_res / sqrt(var.est[7] * var.est[8]))

summary(cor_g_2)
```

```
##
## Iterations = 1:1000
## Thinning interval = 1
## Number of chains = 1
```

```
## Sample size per chain = 1000
##
## 1. Empirical mean and standard deviation for each variable,
##    plus standard error of the mean:
##
##           Mean             SD       Naive SE Time-series SE
##       0.596151       0.172794       0.005464       0.028178
##
## 2. Quantiles for each variable:
##
##   2.5%    25%    50%    75%  97.5%
## 0.1850 0.5065 0.6117 0.7064 0.8930
```

```
summary(cor_byear_2)
```

```
##
## Iterations = 1:1000
## Thinning interval = 1
## Number of chains = 1
## Sample size per chain = 1000
##
## 1. Empirical mean and standard deviation for each variable,
##    plus standard error of the mean:
##
##           Mean             SD       Naive SE Time-series SE
##       0.013514       0.220619       0.006977       0.009633
##
## 2. Quantiles for each variable:
##
##     2.5%      25%      50%      75%    97.5%
## -0.43678 -0.13505  0.02408  0.16947  0.44123
```

```
summary(cor_mother_2)
```

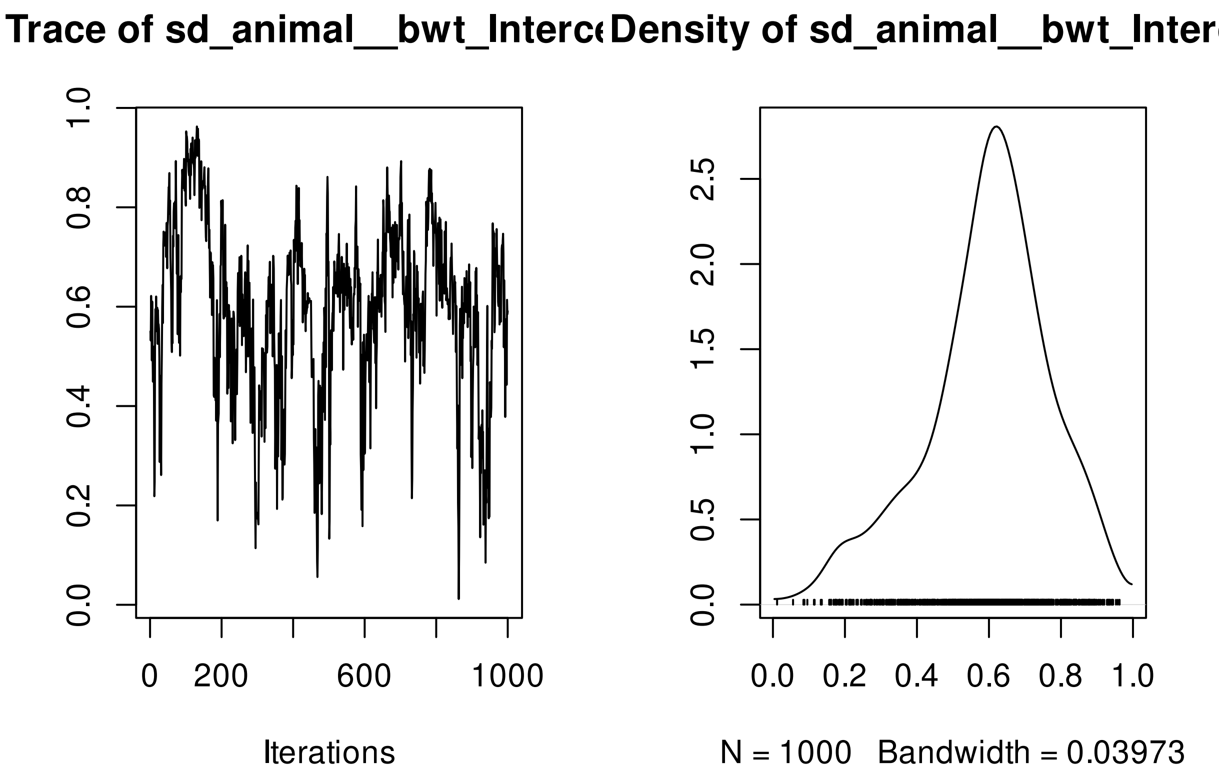
```
##
## Iterations = 1:1000
## Thinning interval = 1
## Number of chains = 1
## Sample size per chain = 1000
##
## 1. Empirical mean and standard deviation for each variable,
##    plus standard error of the mean:
##
##           Mean             SD       Naive SE Time-series SE
##        1.01862        0.46337        0.01465        0.06126
##
```

```
## 2. Quantiles for each variable:
##
##   2.5%    25%    50%    75%  97.5%
## 0.1514 0.6969 1.0310 1.3241 2.0032
```

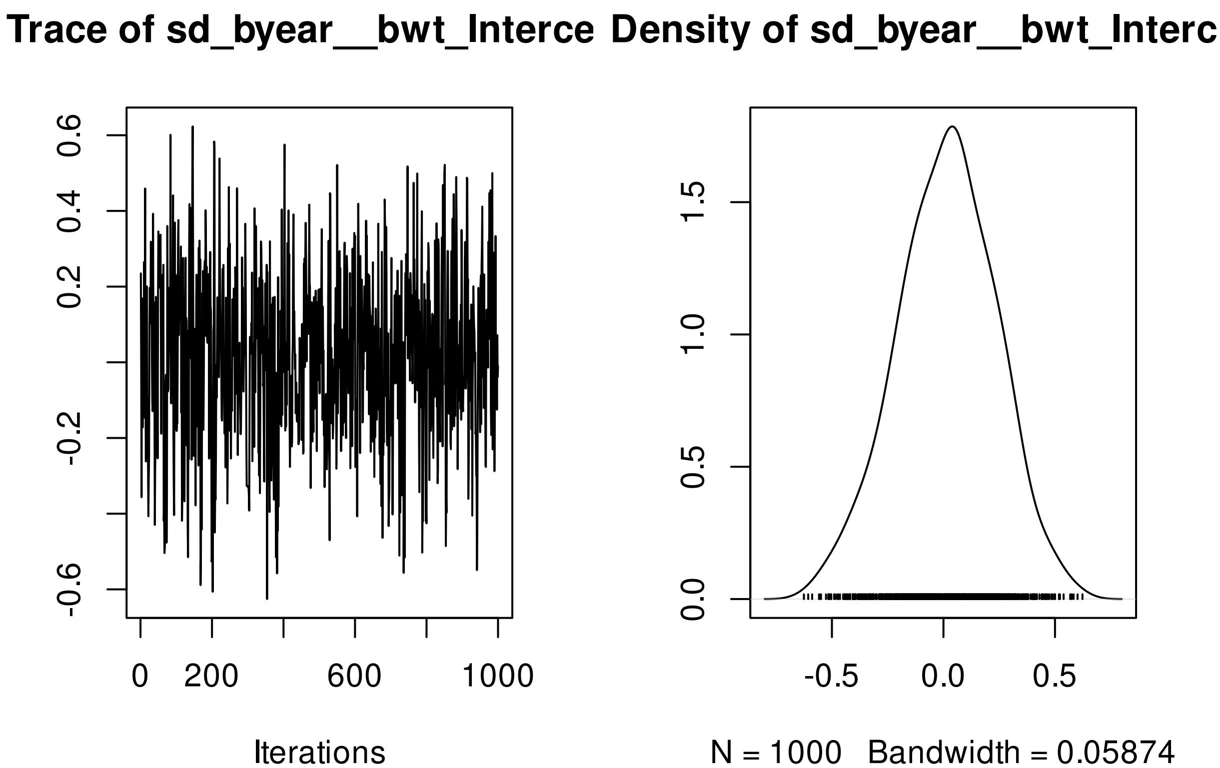
```r
summary(cor_res_2)
```

```
##
## Iterations = 1:1000
## Thinning interval = 1
## Number of chains = 1
## Sample size per chain = 1000
##
## 1. Empirical mean and standard deviation for each variable,
##    plus standard error of the mean:
##
##           Mean             SD       Naive SE Time-series SE
##       0.892512       0.067229       0.002126       0.026496
##
## 2. Quantiles for each variable:
##
##   2.5%    25%    50%    75%  97.5%
## 0.7168 0.8620 0.9069 0.9425 0.9775
```

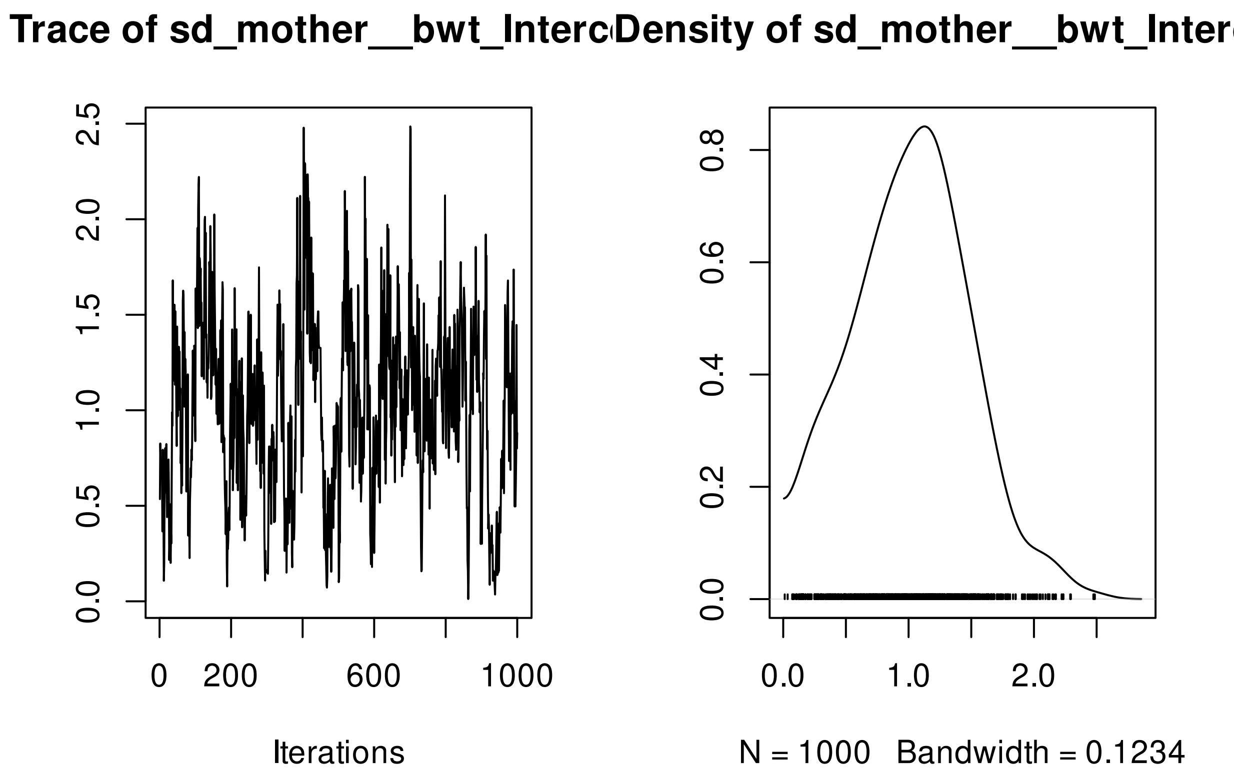
```r
plot(cor_g_2)
```



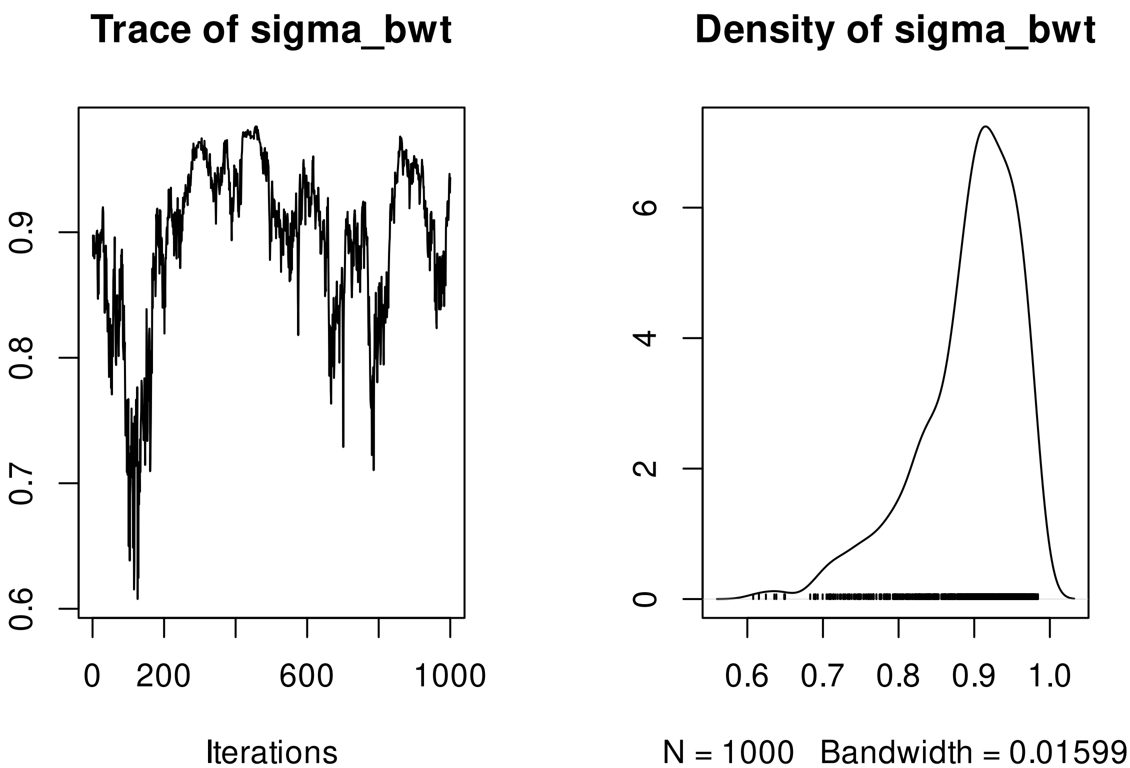

```r
plot(cor_byear_2)
```




```r
plot(cor_mother_2)
```




```r
plot(cor_res_2)
```



3.5.3 Partitioning (co)variances

As in the tutorial 1, it is possible to partition the variance-covariance matrix between groups (here sex)

```
bf_bwt_3 <- bf(bwt ~ 1 + sex + ((1 | a | gr(animal, cov = Amat, by = sex))) + (1 | b | bye
bf_tarsus_3 <- bf(tarsus ~ 1 + sex + (1 | a | gr(animal, cov = Amat, by = sex)) + (1 | b |

brms_m2.3 <- brm(
  bf_bwt_3 + bf_tarsus_3 + set_rescor(TRUE),
  data = gryphon,
  data2 = list(Amat = Amat),
  chains = 2, cores = 2, iter = 1000
)

save(brms_m2.3, file = "data/brms_m2_3.rda")
```

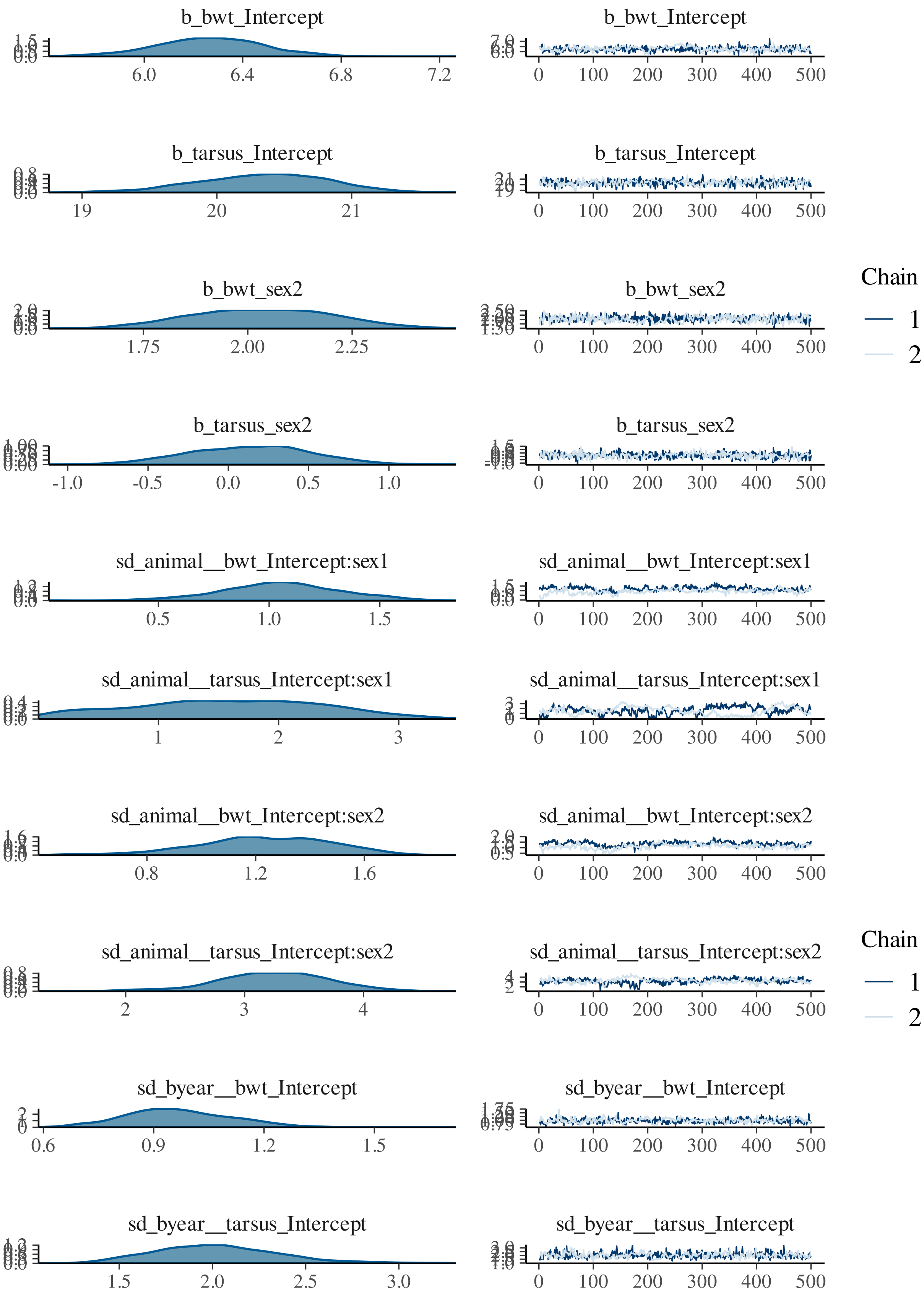
Again we have provided the data from one such run. It can be accessed using the code:

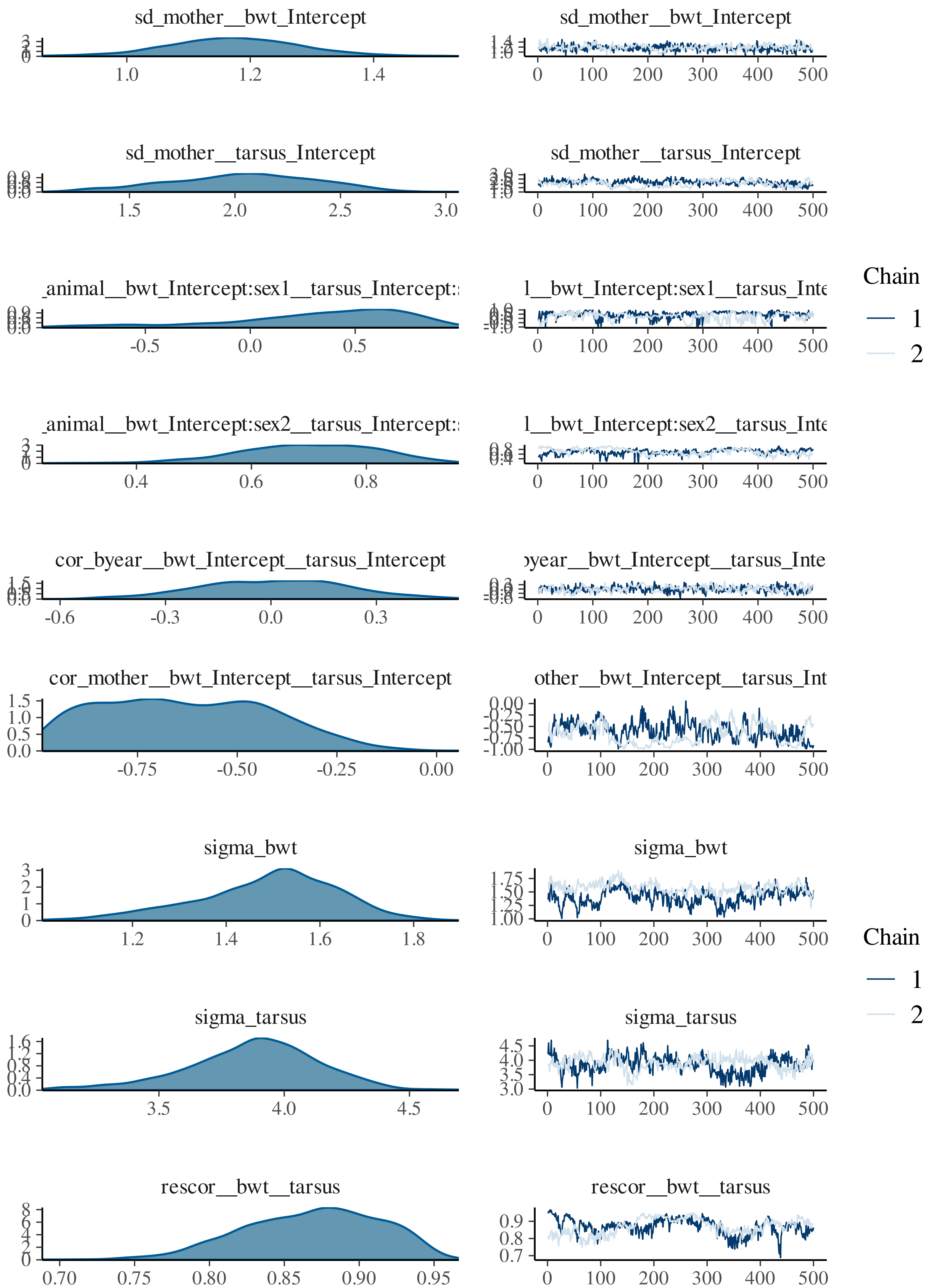
```
load("data/brms_m2_3.rda")
summary(brms_m2.3)
```

```
## Warning: Parts of the model have not converged (some Rhats are > 1.05). Be
## careful when analysing the results! We recommend running more iterations and/or
## setting stronger priors.

## Warning: There were 6 divergent transitions after warmup. Increasing adapt_delta
## above 0.8 may help. See http://mc-stan.org/misc/warnings.html#divergent-
## transitions-after-warmup

##  Family: MV(gaussian, gaussian)
##   Links: mu = identity; sigma = identity
##          mu = identity; sigma = identity
## Formula: bwt ~ 1 + sex + ((1 | a | gr(animal, cov = Amat, by = sex))) + (1 | b | byear)
##          tarsus ~ 1 + sex + (1 | a | gr(animal, cov = Amat, by = sex)) + (1 | b | byear
##    Data: gryphon (Number of observations: 683)
##   Draws: 2 chains, each with iter = 1000; warmup = 500; thin = 1;
##          total post-warmup draws = 1000
##
## Group-Level Effects:
## ~animal (Number of levels: 683)
##                                                 Estimate Est.Error l-95% CI
## sd(bwt_Intercept:sex1)                              1.05      0.28     0.48
## sd(tarsus_Intercept:sex1)                           1.57      0.78     0.14
## sd(bwt_Intercept:sex2)                              1.23      0.24     0.71
## sd(tarsus_Intercept:sex2)                           3.24      0.48     2.17
## cor(bwt_Intercept:sex1,tarsus_Intercept:sex1)     0.32      0.43    -0.78
## cor(bwt_Intercept:sex2,tarsus_Intercept:sex2)     0.70      0.12     0.45
##                                                 u-95% CI Rhat Bulk_ESS Tail_ESS
## sd(bwt_Intercept:sex1)                              1.58 1.27        6       39
## sd(tarsus_Intercept:sex1)                           3.03 1.08       24      117
## sd(bwt_Intercept:sex2)                              1.65 1.24        7       46
## sd(tarsus_Intercept:sex2)                           4.13 1.05       37       79
## cor(bwt_Intercept:sex1,tarsus_Intercept:sex1)     0.90 1.07       25      202
## cor(bwt_Intercept:sex2,tarsus_Intercept:sex2)     0.90 1.09       28       44
##
## ~byear (Number of levels: 34)
##                                   Estimate Est.Error l-95% CI u-95% CI Rhat
## sd(bwt_Intercept)                     0.97      0.14     0.70     1.26 1.01
## sd(tarsus_Intercept)                  2.03      0.34     1.47     2.80 1.00
## cor(bwt_Intercept,tarsus_Intercept)   0.01      0.21    -0.41     0.41 1.01
##                                   Bulk_ESS Tail_ESS
## sd(bwt_Intercept)                      282      292
## sd(tarsus_Intercept)                   324      361
## cor(bwt_Intercept,tarsus_Intercept)    183      393
##
## ~mother (Number of levels: 352)
##                                   Estimate Est.Error l-95% CI u-95% CI Rhat
## sd(bwt_Intercept)                     1.18      0.11     0.96     1.39 1.02
## sd(tarsus_Intercept)                  2.04      0.34     1.33     2.65 1.09
```

```
## cor(bwt_Intercept,tarsus_Intercept)    -0.63      0.21    -0.97    -0.23 1.08
##                                    Bulk_ESS Tail_ESS
## sd(bwt_Intercept)                       170      352
## sd(tarsus_Intercept)                     24       60
## cor(bwt_Intercept,tarsus_Intercept)      22      100
##
## Population-Level Effects:
##                  Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## bwt_Intercept        6.27      0.22     5.82     6.68 1.00      195      123
## tarsus_Intercept    20.35      0.48    19.35    21.21 1.00      494      578
## bwt_sex2             2.04      0.17     1.71     2.36 1.01      265      384
## tarsus_sex2          0.14      0.39    -0.60     0.88 1.00      691      621
##
## Family Specific Parameters:
##              Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## sigma_bwt        1.49      0.15     1.16     1.74 1.33        5       81
## sigma_tarsus     3.88      0.27     3.27     4.35 1.04       42       85
##
## Residual Correlations:
##                    Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## rescor(bwt,tarsus)     0.87      0.05     0.78     0.94 1.04       22       94
##
## Draws were sampled using sampling(NUTS). For each parameter, Bulk_ESS
## and Tail_ESS are effective sample size measures, and Rhat is the potential
## scale reduction factor on split chains (at convergence, Rhat = 1).
```

```
plot(brms_m2.3, ask = FALSE)
```


b_bwt_Intercept
b_bwt_Intercept
b_tarsus_Intercept
b_tarsus_Intercept
b_bwt_sex2
b_bwt_sex2
b_tarsus_sex2
b_tarsus_sex2
sd_animal__bwt_Intercept:sex1
sd_animal__bwt_Intercept:sex1
sd_animal__tarsus_Intercept:sex1
sd_animal__tarsus_Intercept:sex1
sd_animal__bwt_Intercept:sex2
sd_animal__bwt_Intercept:sex2
sd_animal__tarsus_Intercept:sex2
sd_animal__tarsus_Intercept:sex2
sd_byear__bwt_Intercept
sd_byear__bwt_Intercept
sd_byear__tarsus_Intercept
sd_byear__tarsus_Intercept
Chain
1
2
Chain
1
2


sd_mother__bwt_Intercept
sd_mother__bwt_Intercept
sd_mother__tarsus_Intercept
sd_mother__tarsus_Intercept
_animal__bwt_Intercept:sex1__tarsus_Intercept:
l__bwt_Intercept:sex1__tarsus_Inte
_animal__bwt_Intercept:sex2__tarsus_Intercept:
l__bwt_Intercept:sex2__tarsus_Inte
cor_byear__bwt_Intercept__tarsus_Intercept
byear__bwt_Intercept__tarsus_Inte
cor_mother__bwt_Intercept__tarsus_Intercept
other__bwt_Intercept__tarsus_Int
sigma_bwt
sigma_bwt
sigma_tarsus
sigma_tarsus
rescor__bwt__tarsus
rescor__bwt__tarsus
Chain
1
2
Chain
1
2

```r
VarCorr(brms_m2.3)
```

```
## $animal
## $animal$sd
##                       Estimate Est.Error      Q2.5    Q97.5
## bwt_Intercept:sex1    1.051791 0.2757021 0.4836926 1.575837
## tarsus_Intercept:sex1 1.573820 0.7777373 0.1389929 3.025426
## bwt_Intercept:sex2    1.232722 0.2436415 0.7075357 1.650628
## tarsus_Intercept:sex2 3.237363 0.4773725 2.1667846 4.126560
##
## $animal$cor
## , , bwt_Intercept:sex1
##
##                        Estimate Est.Error       Q2.5     Q97.5
## bwt_Intercept:sex1    1.0000000 0.0000000  1.0000000 1.0000000
## tarsus_Intercept:sex1 0.3232502 0.4324034 -0.7811983 0.9007145
## bwt_Intercept:sex2    0.0000000 0.0000000  0.0000000 0.0000000
## tarsus_Intercept:sex2 0.0000000 0.0000000  0.0000000 0.0000000
##
## , , tarsus_Intercept:sex1
##
##                        Estimate Est.Error       Q2.5     Q97.5
## bwt_Intercept:sex1    0.3232502 0.4324034 -0.7811983 0.9007145
## tarsus_Intercept:sex1 1.0000000 0.0000000  1.0000000 1.0000000
## bwt_Intercept:sex2    0.0000000 0.0000000  0.0000000 0.0000000
## tarsus_Intercept:sex2 0.0000000 0.0000000  0.0000000 0.0000000
##
## , , bwt_Intercept:sex2
##
##                        Estimate Est.Error      Q2.5     Q97.5
## bwt_Intercept:sex1    0.0000000 0.0000000 0.0000000 0.0000000
## tarsus_Intercept:sex1 0.0000000 0.0000000 0.0000000 0.0000000
## bwt_Intercept:sex2    1.0000000 0.0000000 1.0000000 1.0000000
## tarsus_Intercept:sex2 0.6975925 0.1213692 0.4474181 0.9047623
##
## , , tarsus_Intercept:sex2
##
##                        Estimate Est.Error      Q2.5     Q97.5
## bwt_Intercept:sex1    0.0000000 0.0000000 0.0000000 0.0000000
## tarsus_Intercept:sex1 0.0000000 0.0000000 0.0000000 0.0000000
## bwt_Intercept:sex2    0.6975925 0.1213692 0.4474181 0.9047623
## tarsus_Intercept:sex2 1.0000000 0.0000000 1.0000000 1.0000000
##
##
## $animal$cov
```

```
## , , bwt_Intercept:sex1
##
##                       Estimate Est.Error       Q2.5    Q97.5
## bwt_Intercept:sex1    1.1821990 0.5768155  0.2339592 2.483263
## tarsus_Intercept:sex1 0.7957577 0.9482719 -0.4879668 3.035395
## bwt_Intercept:sex2    0.0000000 0.0000000  0.0000000 0.000000
## tarsus_Intercept:sex2 0.0000000 0.0000000  0.0000000 0.000000
##
## , , tarsus_Intercept:sex1
##
##                       Estimate Est.Error        Q2.5    Q97.5
## bwt_Intercept:sex1    0.7957577 0.9482719 -0.48796685 3.035395
## tarsus_Intercept:sex1 3.0811806 2.5183190  0.01931907 9.153208
## bwt_Intercept:sex2    0.0000000 0.0000000  0.00000000 0.000000
## tarsus_Intercept:sex2 0.0000000 0.0000000  0.00000000 0.000000
##
## , , bwt_Intercept:sex2
##
##                       Estimate Est.Error      Q2.5    Q97.5
## bwt_Intercept:sex1    0.000000 0.0000000 0.0000000 0.000000
## tarsus_Intercept:sex1 0.000000 0.0000000 0.0000000 0.000000
## bwt_Intercept:sex2    1.578907 0.5865683 0.5006069 2.724572
## tarsus_Intercept:sex2 2.842372 1.0153859 1.1593760 5.086448
##
## , , tarsus_Intercept:sex2
##
##                        Estimate Est.Error     Q2.5     Q97.5
## bwt_Intercept:sex1     0.000000  0.000000 0.000000  0.000000
## tarsus_Intercept:sex1  0.000000  0.000000 0.000000  0.000000
## bwt_Intercept:sex2     2.842372  1.015386 1.159376  5.086448
## tarsus_Intercept:sex2 10.708178  3.017245 4.694964 17.028497
##
##
##
## $byear
## $byear$sd
##                   Estimate Est.Error      Q2.5    Q97.5
## bwt_Intercept    0.9676965 0.1434955 0.7018779 1.258518
## tarsus_Intercept 2.0290144 0.3382466 1.4650518 2.801932
##
## $byear$cor
## , , bwt_Intercept
##
##                     Estimate Est.Error       Q2.5    Q97.5
## bwt_Intercept    1.000000000 0.0000000  1.0000000 1.000000
## tarsus_Intercept 0.009103073 0.2077977 -0.4096021 0.410902
##
```

```
## , , tarsus_Intercept
##
##                     Estimate Est.Error       Q2.5    Q97.5
## bwt_Intercept    0.009103073 0.2077977 -0.4096021 0.410902
## tarsus_Intercept 1.000000000 0.0000000  1.0000000 1.000000
##
##
## $byear$cov
## , , bwt_Intercept
##
##                    Estimate Est.Error       Q2.5    Q97.5
## bwt_Intercept    0.95700691 0.2875804  0.4926327 1.583869
## tarsus_Intercept 0.04233908 0.4457863 -0.8475401 1.014920
##
## , , tarsus_Intercept
##
##                    Estimate Est.Error       Q2.5    Q97.5
## bwt_Intercept    0.04233908 0.4457863 -0.8475401 1.014920
## tarsus_Intercept 4.23119588 1.4453420  2.1463767 7.850826
##
##
##
## $mother
## $mother$sd
##                  Estimate Est.Error     Q2.5    Q97.5
## bwt_Intercept    1.175168 0.1083817 0.958963 1.388926
## tarsus_Intercept 2.038471 0.3445355 1.327549 2.648997
##
## $mother$cor
## , , bwt_Intercept
##
##                    Estimate Est.Error       Q2.5      Q97.5
## bwt_Intercept     1.0000000 0.0000000  1.0000000  1.0000000
## tarsus_Intercept -0.6301934 0.2113836 -0.9652044 -0.2283133
##
## , , tarsus_Intercept
##
##                    Estimate Est.Error       Q2.5      Q97.5
## bwt_Intercept    -0.6301934 0.2113836 -0.9652044 -0.2283133
## tarsus_Intercept  1.0000000 0.0000000  1.0000000  1.0000000
##
##
## $mother$cov
## , , bwt_Intercept
##
##                   Estimate Est.Error       Q2.5     Q97.5
## bwt_Intercept     1.392755 0.2562907  0.9196105  1.929117
```

```
## tarsus_Intercept -1.434727 0.3664843 -2.0769067 -0.674943
##
## , , tarsus_Intercept
##
##                   Estimate Est.Error      Q2.5     Q97.5
## bwt_Intercept    -1.434727 0.3664843 -2.076907 -0.674943
## tarsus_Intercept  4.273951 1.3914013  1.762387  7.017188
##
##
##
## $residual__
## $residual__$sd
##        Estimate Est.Error     Q2.5    Q97.5
## bwt    1.489342 0.1489641 1.162192 1.741559
## tarsus 3.875633 0.2650604 3.268802 4.345400
##
## $residual__$cor
## , , bwt
##
##         Estimate  Est.Error      Q2.5     Q97.5
## bwt    1.0000000 0.00000000 1.0000000 1.0000000
## tarsus 0.8685184 0.04534008 0.7772864 0.9414488
##
## , , tarsus
##
##         Estimate  Est.Error      Q2.5     Q97.5
## bwt    0.8685184 0.04534008 0.7772864 0.9414488
## tarsus 1.0000000 0.00000000 1.0000000 1.0000000
##
##
## $residual__$cov
## , , bwt
##
##        Estimate Est.Error     Q2.5    Q97.5
## bwt    2.240307 0.4341334 1.350691 3.033029
## tarsus 5.034739 0.7852137 3.272088 6.400539
##
## , , tarsus
##
##         Estimate Est.Error      Q2.5     Q97.5
## bwt     5.034739 0.7852137  3.272088  6.400539
## tarsus 15.090721 2.0309529 10.685067 18.882505
```

However, this model is lacking an important and essentiel group-specific partitionning (we do with the asreml-R and MCMCglmm). We need to partition the residual variance (or sigma) as well. Doing so, we will use the argument 'sigma“ to parititon the model by sex. To avoid an estimation of the difference between sexes, we need to remove the estimate of the intercept at the sigma level.

```r
bf_bwt_4 <- bf(bwt ~ 1 + sex + ((1 | a | gr(animal, cov = Amat, by = sex))) + (1 | b | bye
bf_tarsus_4 <- bf(tarsus ~ 1 + sex + (1 | a | gr(animal, cov = Amat, by = sex)) + (1 | b |

brms_m2.4 <- brm(
  bf_bwt_4 + bf_tarsus_4 + set_rescor(TRUE),
  data = gryphon,
  data2 = list(Amat = Amat),
  chains = 2, cores = 2, iter = 1000
)
save(brms_m2.4, file = "data/brms_m2_4.rda")
```

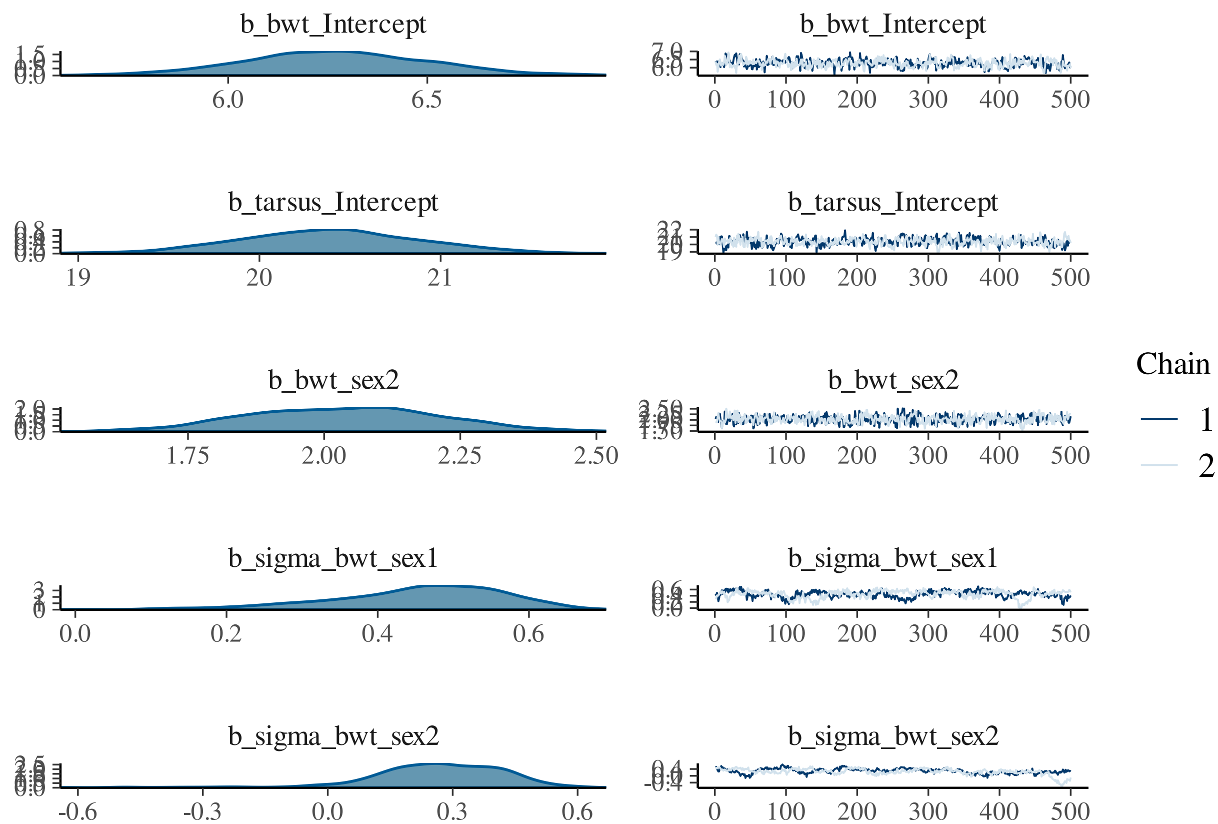
Again we have provided the data from one such run. It can be accessed using the code:

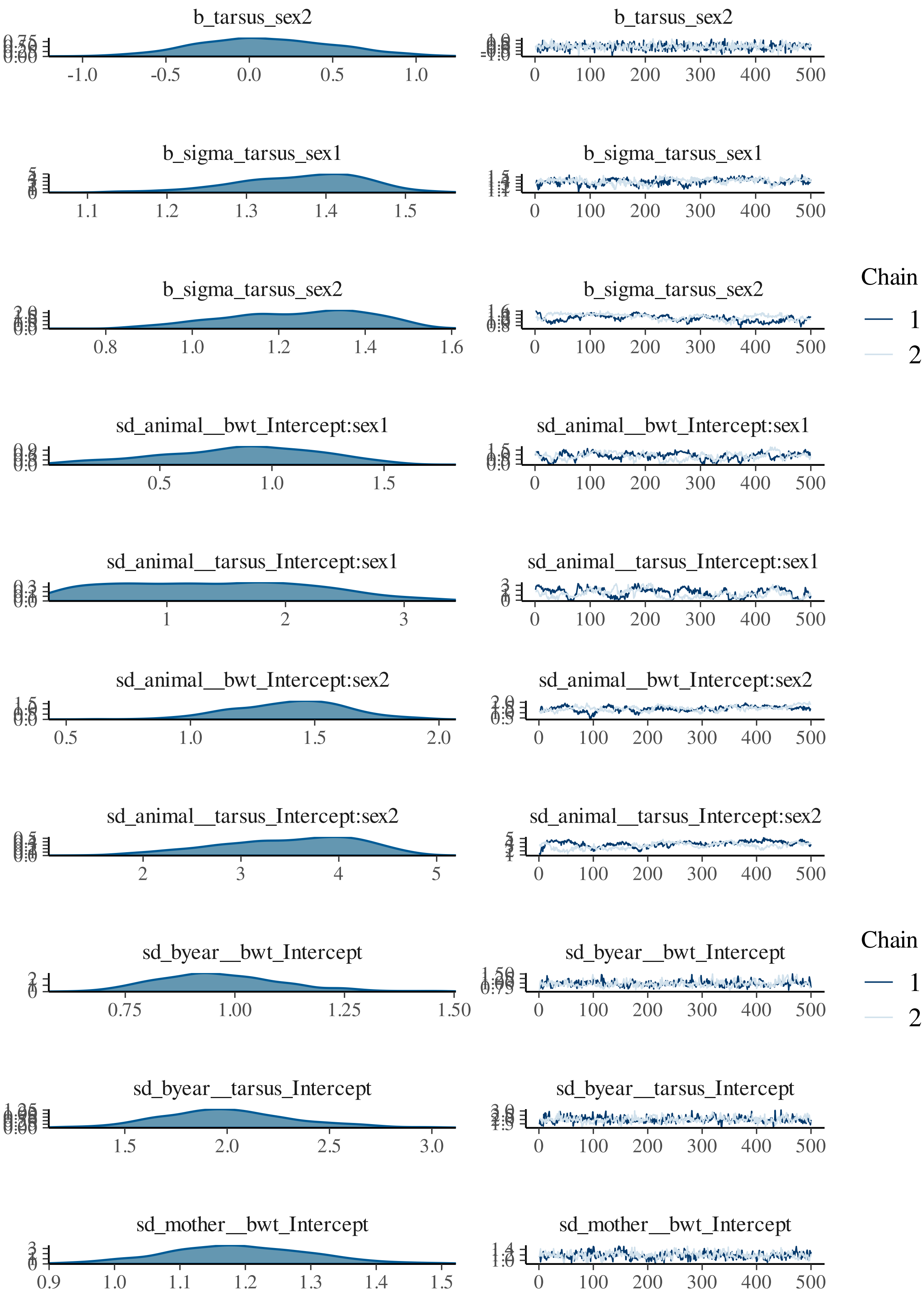
```r
load("data/brms_m2_4.rda")
summary(brms_m2.4)
```

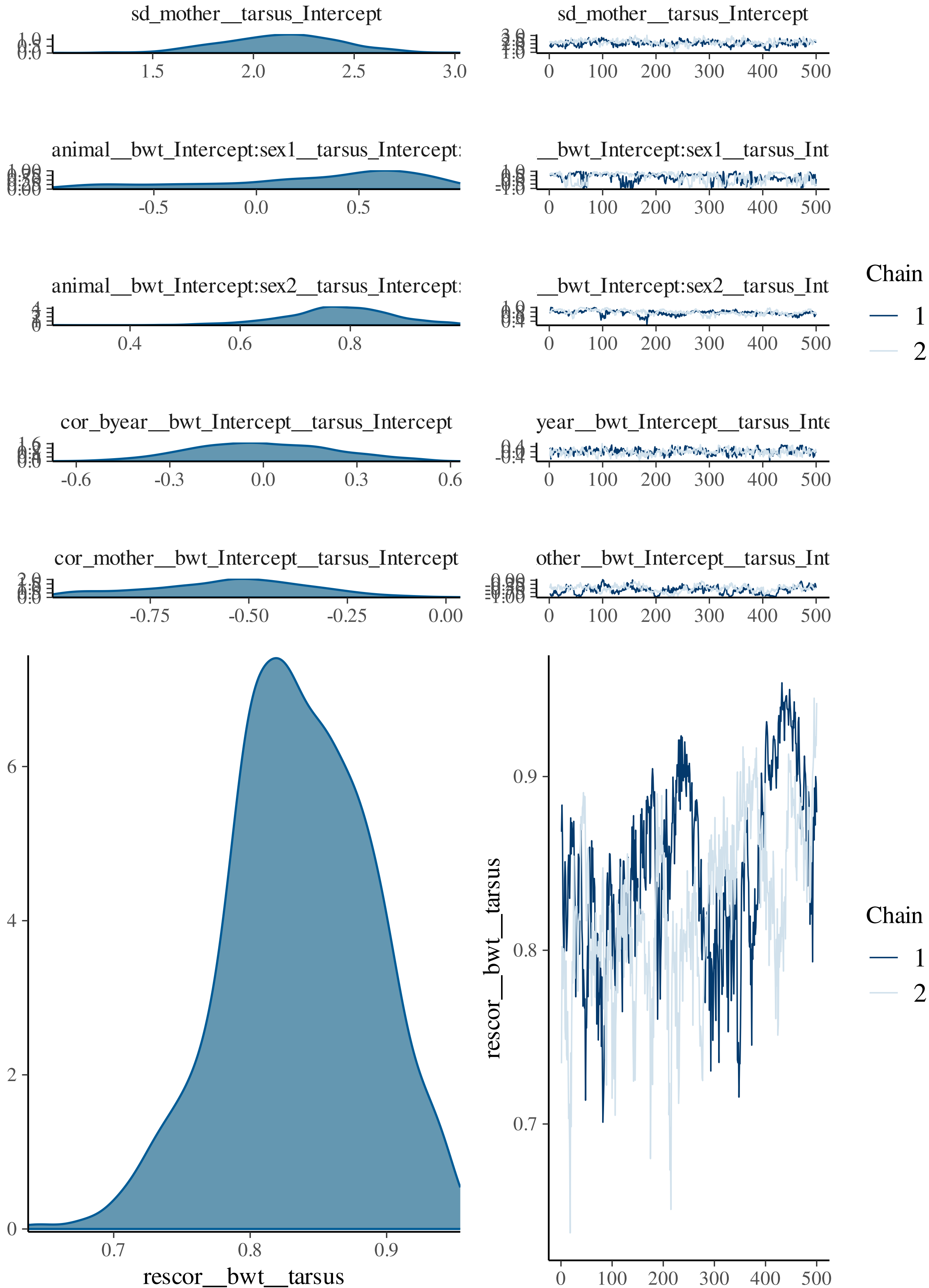
```
## Warning: Parts of the model have not converged (some Rhats are > 1.05). Be
## careful when analysing the results! We recommend running more iterations and/or
## setting stronger priors.

## Warning: There were 6 divergent transitions after warmup. Increasing adapt_delta
## above 0.8 may help. See http://mc-stan.org/misc/warnings.html#divergent-
## transitions-after-warmup

##  Family: MV(gaussian, gaussian)
##   Links: mu = identity; sigma = log
##          mu = identity; sigma = log
## Formula: bwt ~ 1 + sex + ((1 | a | gr(animal, cov = Amat, by = sex))) + (1 | b | byear)
##          sigma ~ sex - 1
##          tarsus ~ 1 + sex + (1 | a | gr(animal, cov = Amat, by = sex)) + (1 | b | byear
##          sigma ~ sex - 1
##    Data: gryphon (Number of observations: 683)
##   Draws: 2 chains, each with iter = 1000; warmup = 500; thin = 1;
##          total post-warmup draws = 1000
##
## Group-Level Effects:
## ~animal (Number of levels: 683)
##                                                 Estimate Est.Error l-95% CI
## sd(bwt_Intercept:sex1)                              0.86      0.35     0.14
## sd(tarsus_Intercept:sex1)                           1.40      0.82     0.10
## sd(bwt_Intercept:sex2)                              1.40      0.23     0.94
## sd(tarsus_Intercept:sex2)                           3.49      0.72     1.96
## cor(bwt_Intercept:sex1,tarsus_Intercept:sex1)      0.28      0.51    -0.85
## cor(bwt_Intercept:sex2,tarsus_Intercept:sex2)      0.78      0.10     0.56
##                                                 u-95% CI Rhat Bulk_ESS Tail_ESS
## sd(bwt_Intercept:sex1)                              1.48 1.00       59      101
```

```
## sd(tarsus_Intercept:sex1)                          3.00 1.07       45      111
## sd(bwt_Intercept:sex2)                             1.83 1.04       42       40
## sd(tarsus_Intercept:sex2)                          4.62 1.22        8       50
## cor(bwt_Intercept:sex1,tarsus_Intercept:sex1)     0.94 1.05       60      287
## cor(bwt_Intercept:sex2,tarsus_Intercept:sex2)     0.97 1.09       30       94
##
## ~byear (Number of levels: 34)
##                                     Estimate Est.Error l-95% CI u-95% CI Rhat
## sd(bwt_Intercept)                       0.97      0.15     0.73     1.30 1.01
## sd(tarsus_Intercept)                    2.01      0.33     1.41     2.70 1.00
## cor(bwt_Intercept,tarsus_Intercept)    -0.00      0.22    -0.42     0.45 1.02
##                                     Bulk_ESS Tail_ESS
## sd(bwt_Intercept)                        283      412
## sd(tarsus_Intercept)                     349      554
## cor(bwt_Intercept,tarsus_Intercept)      225      256
##
## ~mother (Number of levels: 352)
##                                     Estimate Est.Error l-95% CI u-95% CI Rhat
## sd(bwt_Intercept)                       1.19      0.11     0.98     1.42 1.00
## sd(tarsus_Intercept)                    2.14      0.30     1.57     2.71 1.05
## cor(bwt_Intercept,tarsus_Intercept)    -0.55      0.21    -0.96    -0.16 1.04
##                                     Bulk_ESS Tail_ESS
## sd(bwt_Intercept)                        279      434
## sd(tarsus_Intercept)                      46      227
## cor(bwt_Intercept,tarsus_Intercept)       46      122
##
## Population-Level Effects:
##                   Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## bwt_Intercept         6.27      0.23     5.82     6.73 1.01      336      556
## tarsus_Intercept     20.39      0.49    19.42    21.37 1.00      384      509
## bwt_sex2              2.04      0.17     1.70     2.38 1.00      483      507
## sigma_bwt_sex1        0.45      0.12     0.18     0.63 1.00       68      128
## sigma_bwt_sex2        0.26      0.17    -0.17     0.52 1.06       38       33
## tarsus_sex2           0.10      0.41    -0.69     0.92 1.00      658      659
## sigma_tarsus_sex1     1.37      0.08     1.19     1.50 1.04       65      215
## sigma_tarsus_sex2     1.24      0.16     0.91     1.50 1.22        7       67
##
## Residual Correlations:
##                    Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## rescor(bwt,tarsus)     0.84      0.05     0.73     0.93 1.15       11       29
##
## Draws were sampled using sampling(NUTS). For each parameter, Bulk_ESS
## and Tail_ESS are effective sample size measures, and Rhat is the potential
## scale reduction factor on split chains (at convergence, Rhat = 1).
```

```
plot(brms_m2.4, ask = FALSE)
```




b_tarsus_sex2
-1.0 -0.5 0.0 0.5 1.0
b_tarsus_sex2
0 100 200 300 400 500
b_sigma_tarsus_sex1
1.1 1.2 1.3 1.4 1.5
b_sigma_tarsus_sex1
0 100 200 300 400 500
b_sigma_tarsus_sex2
0.8 1.0 1.2 1.4 1.6
b_sigma_tarsus_sex2
0 100 200 300 400 500
Chain
1
2
sd_animal__bwt_Intercept:sex1
0.5 1.0 1.5
sd_animal__bwt_Intercept:sex1
0 100 200 300 400 500
sd_animal__tarsus_Intercept:sex1
1 2 3
sd_animal__tarsus_Intercept:sex1
0 100 200 300 400 500
sd_animal__bwt_Intercept:sex2
0.5 1.0 1.5 2.0
sd_animal__bwt_Intercept:sex2
0 100 200 300 400 500
sd_animal__tarsus_Intercept:sex2
2 3 4 5
sd_animal__tarsus_Intercept:sex2
0 100 200 300 400 500
sd_byear__bwt_Intercept
0.75 1.00 1.25 1.50
sd_byear__bwt_Intercept
0 100 200 300 400 500
Chain
1
2
sd_byear__tarsus_Intercept
1.5 2.0 2.5 3.0
sd_byear__tarsus_Intercept
0 100 200 300 400 500
sd_mother__bwt_Intercept
0.9 1.0 1.1 1.2 1.3 1.4 1.5
sd_mother__bwt_Intercept
0 100 200 300 400 500


sd_mother__tarsus_Intercept
sd_mother__tarsus_Intercept
animal__bwt_Intercept:sex1__tarsus_Intercept:
__bwt_Intercept:sex1__tarsus_Int
animal__bwt_Intercept:sex2__tarsus_Intercept:
__bwt_Intercept:sex2__tarsus_Int
cor_byear__bwt_Intercept__tarsus_Intercept
year__bwt_Intercept__tarsus_Inte
cor_mother__bwt_Intercept__tarsus_Intercept
other__bwt_Intercept__tarsus_Int
Chain
1
2
rescor__bwt__tarsus
rescor__bwt__tarsus
Chain
1
2

```r
VarCorr(brms_m2.4)
```

```
## $animal
## $animal$sd
##                        Estimate Est.Error       Q2.5    Q97.5
## bwt_Intercept:sex1    0.8628389 0.3531696 0.14360929 1.481121
## tarsus_Intercept:sex1 1.3985239 0.8163731 0.09977045 3.002609
## bwt_Intercept:sex2    1.4023202 0.2325863 0.93896619 1.833688
## tarsus_Intercept:sex2 3.4858243 0.7167230 1.96177030 4.620105
##
## $animal$cor
## , , bwt_Intercept:sex1
##
##                       Estimate Est.Error       Q2.5     Q97.5
## bwt_Intercept:sex1    1.000000 0.0000000  1.0000000 1.0000000
## tarsus_Intercept:sex1 0.277338 0.5119501 -0.8479996 0.9398158
## bwt_Intercept:sex2    0.000000 0.0000000  0.0000000 0.0000000
## tarsus_Intercept:sex2 0.000000 0.0000000  0.0000000 0.0000000
##
## , , tarsus_Intercept:sex1
##
##                       Estimate Est.Error       Q2.5     Q97.5
## bwt_Intercept:sex1    0.277338 0.5119501 -0.8479996 0.9398158
## tarsus_Intercept:sex1 1.000000 0.0000000  1.0000000 1.0000000
## bwt_Intercept:sex2    0.000000 0.0000000  0.0000000 0.0000000
## tarsus_Intercept:sex2 0.000000 0.0000000  0.0000000 0.0000000
##
## , , bwt_Intercept:sex2
##
##                        Estimate  Est.Error     Q2.5     Q97.5
## bwt_Intercept:sex1    0.0000000 0.00000000 0.000000 0.0000000
## tarsus_Intercept:sex1 0.0000000 0.00000000 0.000000 0.0000000
## bwt_Intercept:sex2    1.0000000 0.00000000 1.000000 1.0000000
## tarsus_Intercept:sex2 0.7781659 0.09850178 0.564036 0.9699765
##
## , , tarsus_Intercept:sex2
##
##                        Estimate  Est.Error     Q2.5     Q97.5
## bwt_Intercept:sex1    0.0000000 0.00000000 0.000000 0.0000000
## tarsus_Intercept:sex1 0.0000000 0.00000000 0.000000 0.0000000
## bwt_Intercept:sex2    0.7781659 0.09850178 0.564036 0.9699765
## tarsus_Intercept:sex2 1.0000000 0.00000000 1.000000 1.0000000
##
##
## $animal$cov
```

```
## , , bwt_Intercept:sex1
##
##                       Estimate Est.Error       Q2.5    Q97.5
## bwt_Intercept:sex1    0.8690949 0.6002446  0.0206250 2.193721
## tarsus_Intercept:sex1 0.6483841 0.9143700 -0.4481203 2.989048
## bwt_Intercept:sex2    0.0000000 0.0000000  0.0000000 0.000000
## tarsus_Intercept:sex2 0.0000000 0.0000000  0.0000000 0.000000
##
## , , tarsus_Intercept:sex1
##
##                       Estimate Est.Error         Q2.5    Q97.5
## bwt_Intercept:sex1    0.6483841  0.914370 -0.448120294 2.989048
## tarsus_Intercept:sex1 2.6216677  2.500989  0.009954235 9.015666
## bwt_Intercept:sex2    0.0000000  0.000000  0.000000000 0.000000
## tarsus_Intercept:sex2 0.0000000  0.000000  0.000000000 0.000000
##
## , , bwt_Intercept:sex2
##
##                       Estimate Est.Error      Q2.5    Q97.5
## bwt_Intercept:sex1    0.000000  0.000000 0.0000000 0.000000
## tarsus_Intercept:sex1 0.000000  0.000000 0.0000000 0.000000
## bwt_Intercept:sex2    2.020544  0.639550 0.8816577 3.362416
## tarsus_Intercept:sex2 3.875299  1.298562 1.4247624 6.415724
##
## , , tarsus_Intercept:sex2
##
##                        Estimate Est.Error     Q2.5     Q97.5
## bwt_Intercept:sex1     0.000000  0.000000 0.000000  0.000000
## tarsus_Intercept:sex1  0.000000  0.000000 0.000000  0.000000
## bwt_Intercept:sex2     3.875299  1.298562 1.424762  6.415724
## tarsus_Intercept:sex2 12.664149  4.814957 3.848544 21.345370
##
##
##
## $byear
## $byear$sd
##                  Estimate Est.Error      Q2.5    Q97.5
## bwt_Intercept    0.9707654 0.1478361 0.7256973 1.298668
## tarsus_Intercept 2.0073203 0.3290043 1.4102530 2.699770
##
## $byear$cor
## , , bwt_Intercept
##
##                      Estimate Est.Error       Q2.5     Q97.5
## bwt_Intercept     1.000000000 0.0000000  1.0000000 1.0000000
## tarsus_Intercept -0.001551923 0.2236193 -0.4237849 0.4526618
##
```

```
## , , tarsus_Intercept
##
##                       Estimate Est.Error       Q2.5     Q97.5
## bwt_Intercept    -0.001551923 0.2236193 -0.4237849 0.4526618
## tarsus_Intercept  1.000000000 0.0000000  1.0000000 1.0000000
##
##
## $byear$cov
## , , bwt_Intercept
##
##                   Estimate Est.Error       Q2.5    Q97.5
## bwt_Intercept    0.9642191 0.3021042  0.5266366 1.686538
## tarsus_Intercept 0.0252866 0.4713288 -0.8080314 1.069567
##
## , , tarsus_Intercept
##
##                   Estimate Est.Error       Q2.5    Q97.5
## bwt_Intercept    0.0252866 0.4713288 -0.8080314 1.069567
## tarsus_Intercept 4.1374703 1.3676889  1.9888135 7.288761
##
##
##
## $mother
## $mother$sd
##                  Estimate Est.Error      Q2.5    Q97.5
## bwt_Intercept    1.189902 0.1113270 0.9791374 1.423333
## tarsus_Intercept 2.139290 0.2985875 1.5714814 2.708199
##
## $mother$cor
## , , bwt_Intercept
##
##                    Estimate Est.Error       Q2.5      Q97.5
## bwt_Intercept     1.0000000 0.0000000  1.0000000  1.0000000
## tarsus_Intercept -0.5501934 0.2066985 -0.9589938 -0.1591737
##
## , , tarsus_Intercept
##
##                    Estimate Est.Error       Q2.5      Q97.5
## bwt_Intercept    -0.5501934 0.2066985 -0.9589938 -0.1591737
## tarsus_Intercept  1.0000000 0.0000000  1.0000000  1.0000000
##
##
## $mother$cov
## , , bwt_Intercept
##
##                   Estimate Est.Error      Q2.5      Q97.5
## bwt_Intercept     1.428247 0.2672833  0.958710  2.0258758
```

```
## tarsus_Intercept -1.335450 0.3932707 -2.051866 -0.5146954
##
## , , tarsus_Intercept
##
##                    Estimate Est.Error      Q2.5      Q97.5
## bwt_Intercept     -1.335450 0.3932707 -2.051866 -0.5146954
## tarsus_Intercept   4.665626 1.2688941  2.469554  7.3343400
```

Evaluation of the statistical support for these sex-specific correlations is straightforward. Because we imposed no constraint on their estimation, we can evaluate the extent to which the posterior distributions overlap zero or overlap each other:

```
cor_g_F <- as.mcmc((VarCorr(brms_m2.4, summary = FALSE)$animal$cor[, 1, 2]))
cor_g_M <- as.mcmc((VarCorr(brms_m2.4, summary = FALSE)$animal$cor[, 3, 4]))

summary(cor_g_F)
```

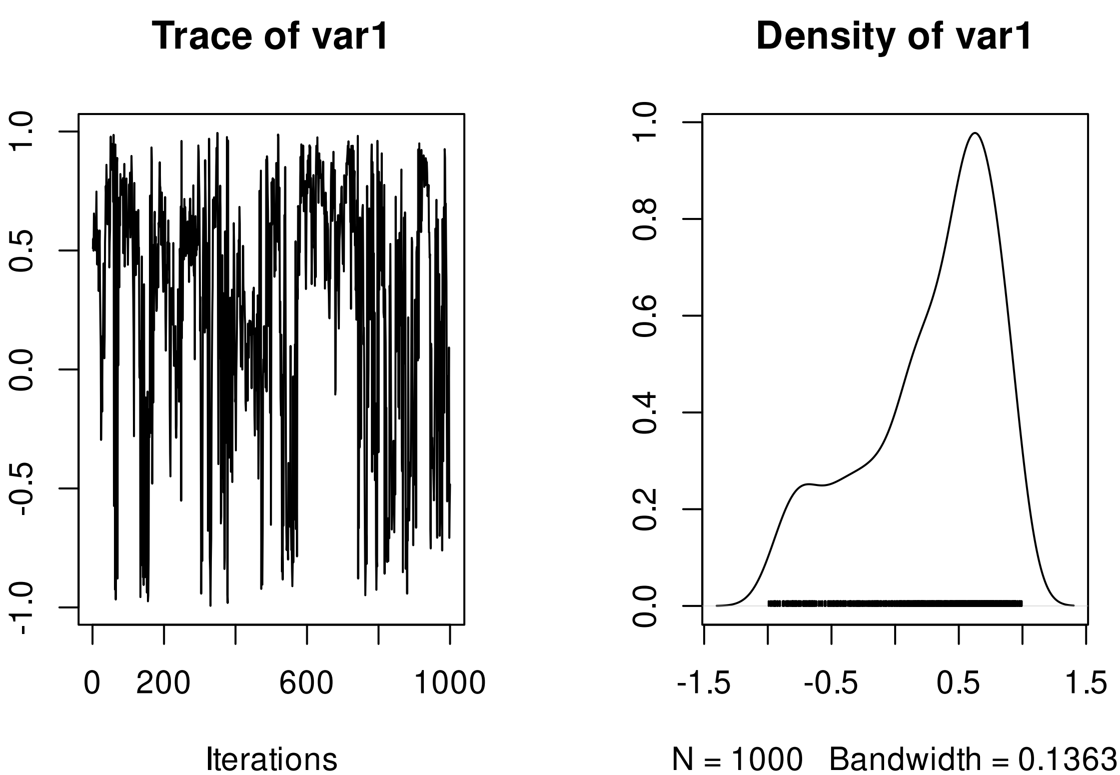
```
##
## Iterations = 1:1000
## Thinning interval = 1
## Number of chains = 1
## Sample size per chain = 1000
##
## 1. Empirical mean and standard deviation for each variable,
##    plus standard error of the mean:
##
##           Mean             SD       Naive SE Time-series SE
##        0.27734        0.51195        0.01619        0.05981
##
## 2. Quantiles for each variable:
##
##     2.5%      25%      50%      75%    97.5%
## -0.84800 -0.02476  0.43226  0.67124  0.93982
```

```
summary(cor_g_M)
```

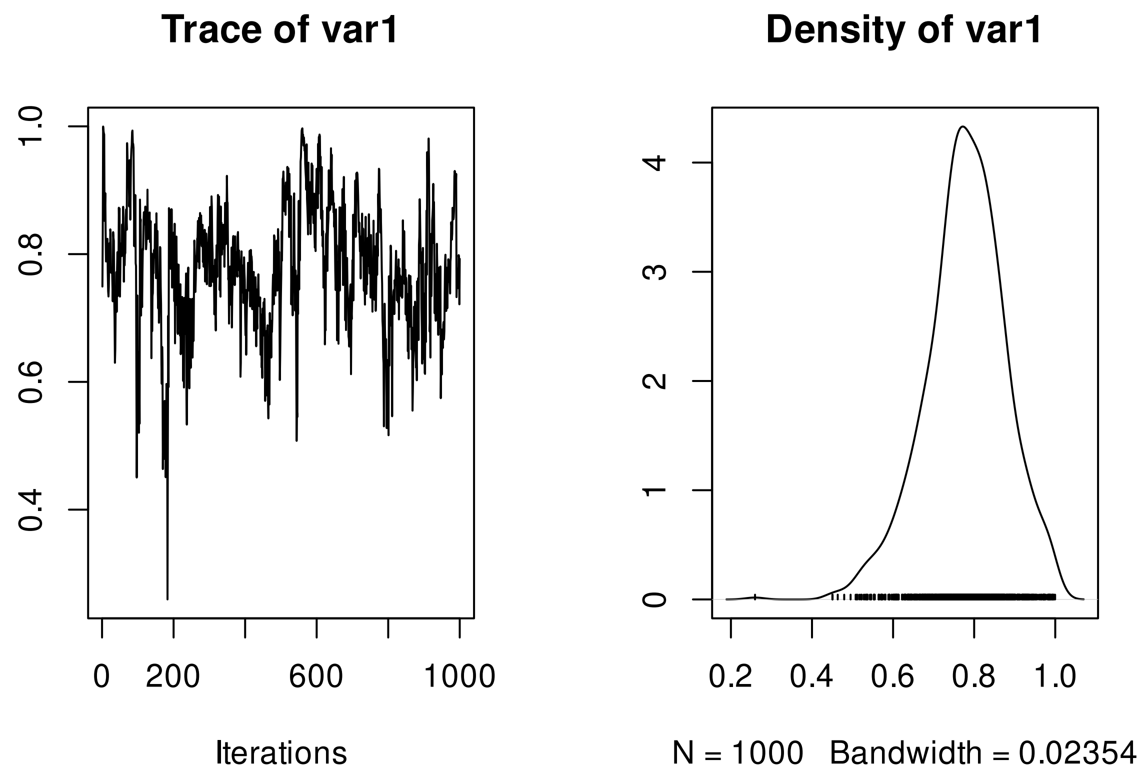
```
##
## Iterations = 1:1000
## Thinning interval = 1
## Number of chains = 1
## Sample size per chain = 1000
##
## 1. Empirical mean and standard deviation for each variable,
##    plus standard error of the mean:
##
##           Mean             SD       Naive SE Time-series SE
```

```
##        0.778166        0.098502        0.003115        0.013827
##
## 2. Quantiles for each variable:
##
##   2.5%    25%    50%    75%  97.5%
## 0.5640 0.7240 0.7805 0.8424 0.9700
```

```r
plot(cor_g_F)
```

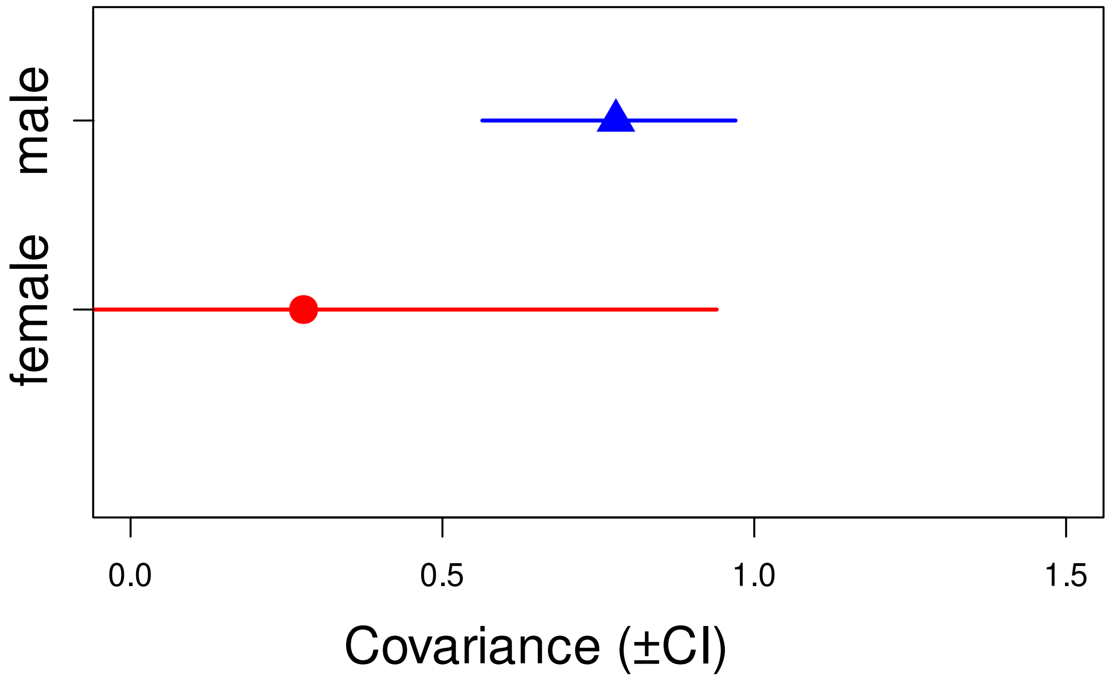



```r
plot(cor_g_M)
```



Here a plot to visualize the overlaps of covariances.

```
cor.est <- rbind(
  cbind(summary(cor_g_F)$statistics[1], summary(cor_g_F)$quantiles[1], summary(cor_g_F)$qu
  cbind(summary(cor_g_M)$statistics[1], summary(cor_g_M)$quantiles[1], summary(cor_g_M)$qu
)


plot(c(1, 2) ~ cor.est[, 1], xlim = c(0, 1.5), ylim = c(0, 2.5), xlab = "", ylab = "", col
segments(y0 = 1, x0 = cor.est[1, 2], y1 = 1, x1 = cor.est[1, 3], col = c("red"), lwd = 2)
segments(y0 = 2, x0 = cor.est[2, 2], y1 = 2, x1 = cor.est[2, 3], col = c("blue"), lwd = 2)
mtext("Covariance (±CI)", side = 1, las = 1, adj = 0.4, line = 3, cex = 1.6)
axis(2, at = 1, labels = c("female"), las = 3, cex.axis = 1.6)
axis(2, at = 2, labels = c("male"), las = 3, cex.axis = 1.6)
```

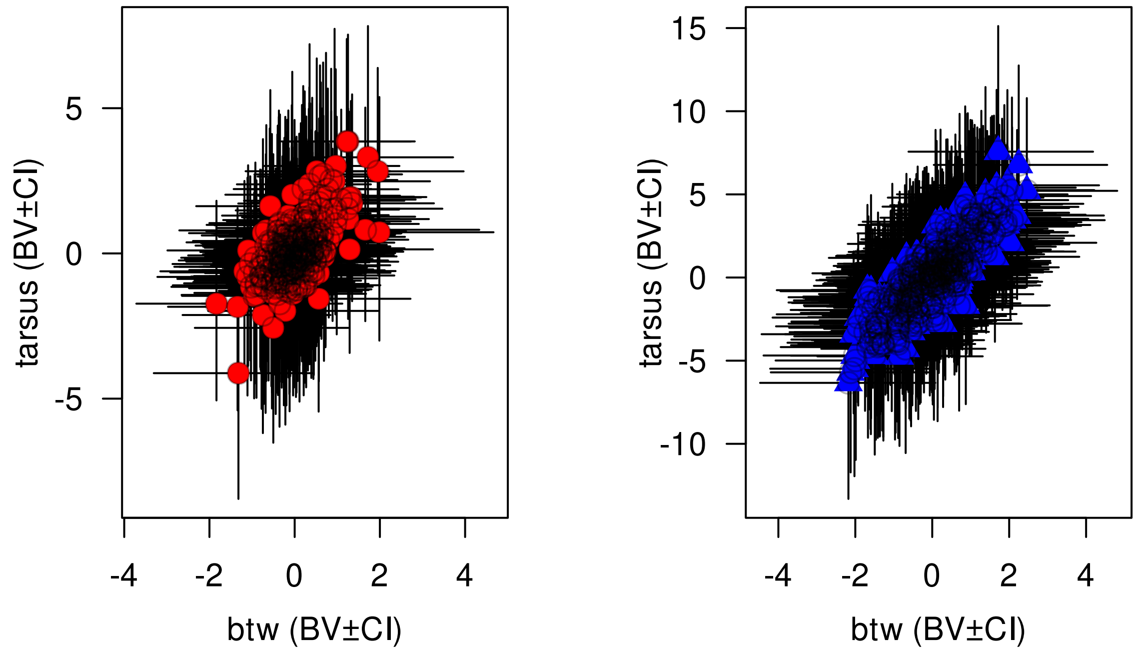


Here a simple plot of the sex-specific genetic correlation using the BLUPs

```
bls_m2.4 <- ranef(brms_m2.4)$animal
bl_m2.4 <- as.data.frame(abind::abind(lapply(1:dim(bls_m2.4)[3], function(x) bls_m2.4[, c(
colnames(bl_m2.4) <- paste0(rep(dimnames(bls_m2.4)[[3]], each = 3), c("", "_lo", "_up"))
bl_m2.4$id <- rownames(bl_m2.4)
bl_m2.4$sex <- attr(dimnames(bls_m2.4)[[1]], "by")
FEM <- subset(bl_m2.4, sex == "1")
MAL <- subset(bl_m2.4, sex == "2")
```

```
#
par(mfrow = c(1, 2))
plot(tarsus_Intercept ~ bwt_Intercept, FEM,
  xlab = "", ylab = "",
  xlim = c(min(FEM$bwt_Intercept_lo), max(FEM$bwt_Intercept_up)),
  ylim = c(min(FEM$tarsus_Intercept_lo), max(FEM$tarsus_Intercept_up)),
  las = 1.2, type = "n"
)
segments(
  x0 = FEM$bwt_Intercept, y0 = FEM$tarsus_Intercept_lo,
  x1 = FEM$bwt_Intercept, y1 = FEM$tarsus_Intercept_up,
  col = "black"
```

```
)
segments(
  x0 = FEM$bwt_Intercept_lo, y0 = FEM$tarsus_Intercept,
  x1 = FEM$bwt_Intercept_up, y1 = FEM$tarsus_Intercept,
  col = "black"
)
points(tarsus_Intercept ~ bwt_Intercept, FEM, pch = 16, col = "red", cex = 1.5)
points(tarsus_Intercept ~ bwt_Intercept, FEM, pch = 1, col = rgb(0, 0, 0, 0.3), cex = c(1.
mtext("btw (BV±CI)", side = 1, line = 2.4)
mtext("tarsus (BV±CI)", side = 2, line = 2, las = 3)
#
plot(tarsus_Intercept ~ bwt_Intercept, MAL,
  xlab = "", ylab = "",
  xlim = c(min(MAL$bwt_Intercept_lo), max(MAL$bwt_Intercept_up)),
  ylim = c(min(MAL$tarsus_Intercept_lo), max(MAL$tarsus_Intercept_up)),
  las = 1.2, type = "n"
)
segments(
  x0 = MAL$bwt_Intercept, y0 = MAL$tarsus_Intercept_lo,
  x1 = MAL$bwt_Intercept, y1 = MAL$tarsus_Intercept_up, col = "black"
)
segments(
  x0 = MAL$bwt_Intercept_lo, y0 = MAL$tarsus_Intercept,
  x1 = MAL$bwt_Intercept_up, y1 = MAL$tarsus_Intercept, col = "black"
)
points(tarsus_Intercept ~ bwt_Intercept, MAL, pch = 17, col = "blue", cex = 1.5)
points(tarsus_Intercept ~ bwt_Intercept, MAL, pch = 1, col = rgb(0, 0, 0, 0.3), cex = c(1.
mtext("btw (BV±CI)", side = 1, line = 2.4)
mtext("tarsus (BV±CI)", side = 2, line = 2, las = 3)
```



3.5.4 Between groups (co)variances and the B-matrix

Animal models are amazing model. With different group within a population, it is also possible to estimate how much the different groups shared the same genetic via the cross-group genetic covariance. This covariance is essential to understand ontogenic or sexual conflict, which can constraint or enhanced response to evolution. As an example, we estimate the cross-sex genetic correlation `r_{fm}`

It is important to keep in mind the covariance matrix at the residual level is zero and it is important to avoid estimating the cross-sex residual covariance because no individual switched sex during the experiment.

Note: the way of partitionning variance per sex is a bit different then the previous code ",by=sex". This code is faster and also easier to understand. Note, it is possible to play with the `|` or `||` to estimate or not covariance between sexes.

```
bf_bwt_5 <- bf(
  bwt ~ 1 + sex + (0 + sex | a | gr(animal, cov = Amat)) + (0 + sex | b | mother) + (0 + s
  sigma ~ sex - 1
)
bf_tarsus_5 <- bf(
  tarsus ~ 1 + sex + (0 + sex | a | gr(animal, cov = Amat)) + (0 + sex | b | mother) + (0
  sigma ~ sex - 1
```

```
)

brms_m2.5 <- brm(
  bf_bwt_5 + bf_tarsus_5 + set_rescor(TRUE),
  data = gryphon,
  data2 = list(Amat = Amat),
  chains = 2, cores = 2, iter = 1000
)
save(brms_m2.5, file = "data/brms_m2_5.rda")
```

Again we have provided the data from one such run. It can be accessed using the code:

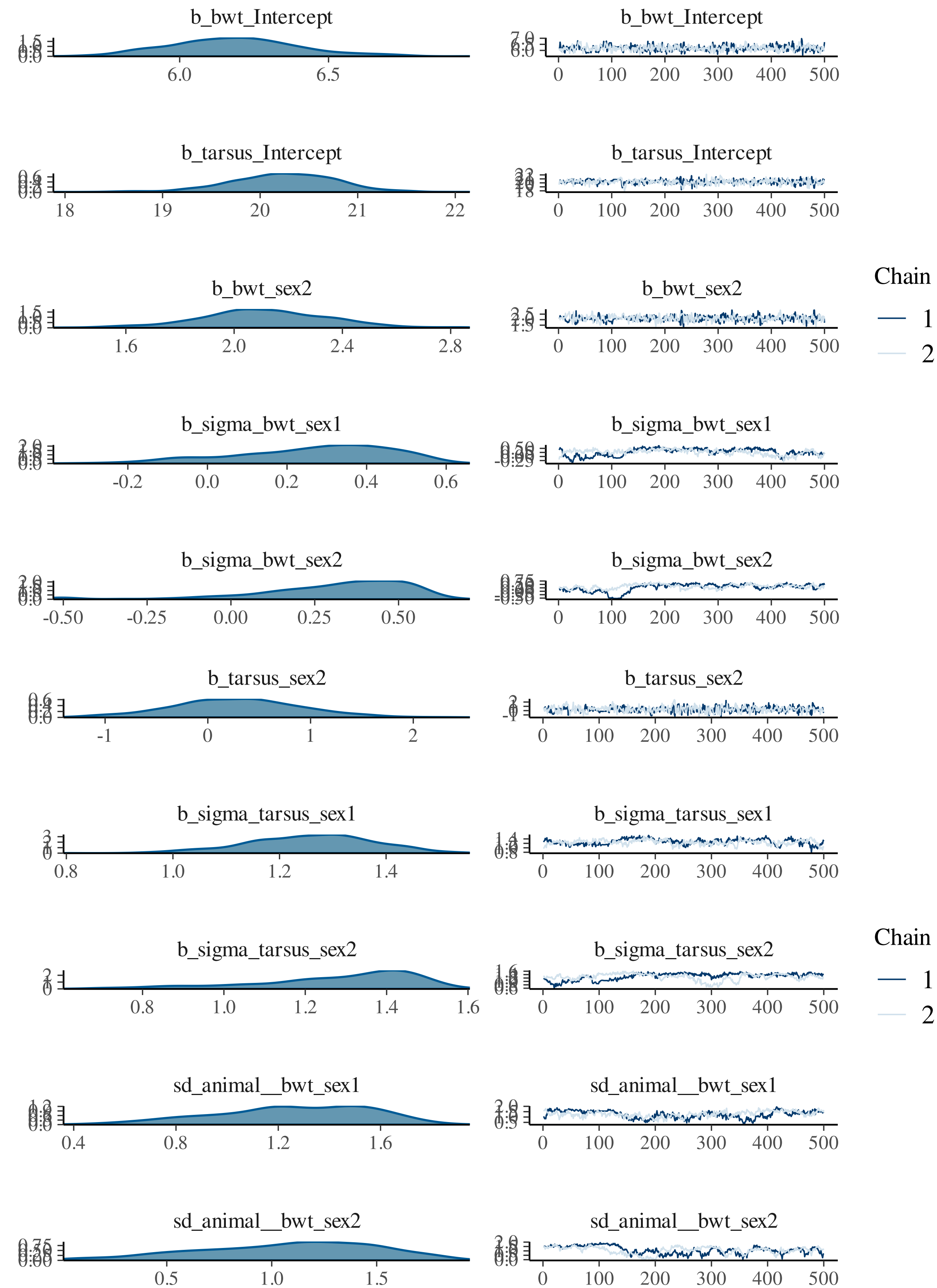
```
load("data/brms_m2_5.rda")
summary(brms_m2.5)
```

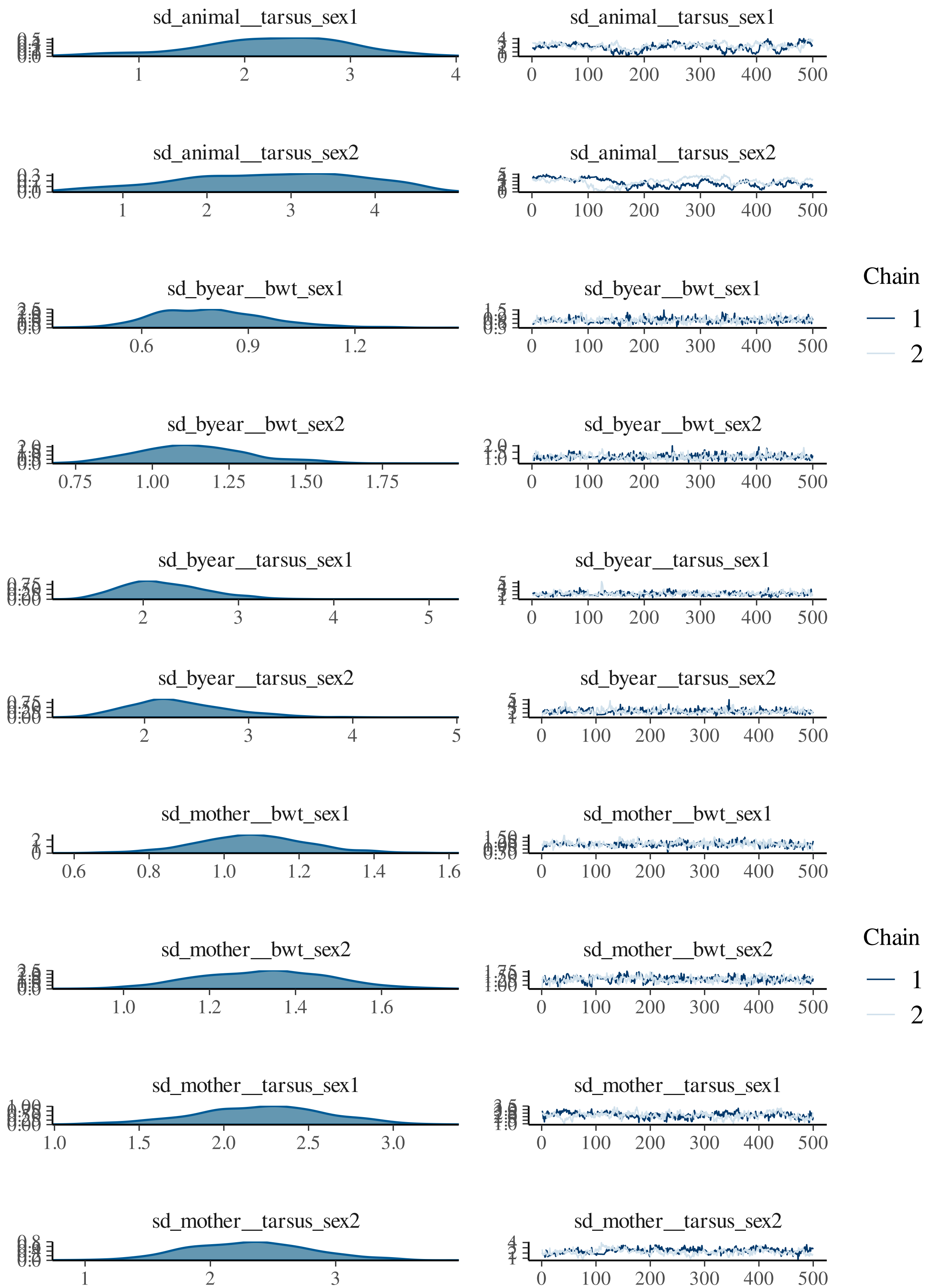
```
## Warning: Parts of the model have not converged (some Rhats are > 1.05). Be
## careful when analysing the results! We recommend running more iterations and/or
## setting stronger priors.

## Warning: There were 45 divergent transitions after warmup. Increasing
## adapt_delta above 0.8 may help. See http://mc-stan.org/misc/
## warnings.html#divergent-transitions-after-warmup

##  Family: MV(gaussian, gaussian)
##   Links: mu = identity; sigma = log
##          mu = identity; sigma = log
## Formula: bwt ~ 1 + sex + (0 + sex | a | gr(animal, cov = Amat)) + (0 + sex | b | mother
##          sigma ~ sex - 1
##          tarsus ~ 1 + sex + (0 + sex | a | gr(animal, cov = Amat)) + (0 + sex | b | mot
##          sigma ~ sex - 1
##    Data: gryphon (Number of observations: 683)
##   Draws: 2 chains, each with iter = 1000; warmup = 500; thin = 1;
##          total post-warmup draws = 1000
##
## Group-Level Effects:
## ~animal (Number of levels: 683)
##                               Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS
## sd(bwt_sex1)                      1.26      0.30     0.63     1.73 1.06       21
## sd(bwt_sex2)                      1.08      0.42     0.20     1.77 1.08       18
## sd(tarsus_sex1)                   2.26      0.72     0.61     3.57 1.04       40
## sd(tarsus_sex2)                   2.74      1.05     0.61     4.47 1.13       12
## cor(bwt_sex1,bwt_sex2)            0.48      0.29    -0.24     0.87 1.02       84
## cor(bwt_sex1,tarsus_sex1)         0.57      0.25    -0.07     0.89 1.14       10
## cor(bwt_sex2,tarsus_sex1)         0.38      0.38    -0.53     0.91 1.25        7
## cor(bwt_sex1,tarsus_sex2)         0.17      0.31    -0.49     0.75 1.04       60
## cor(bwt_sex2,tarsus_sex2)         0.52      0.33    -0.37     0.87 1.20        8
```

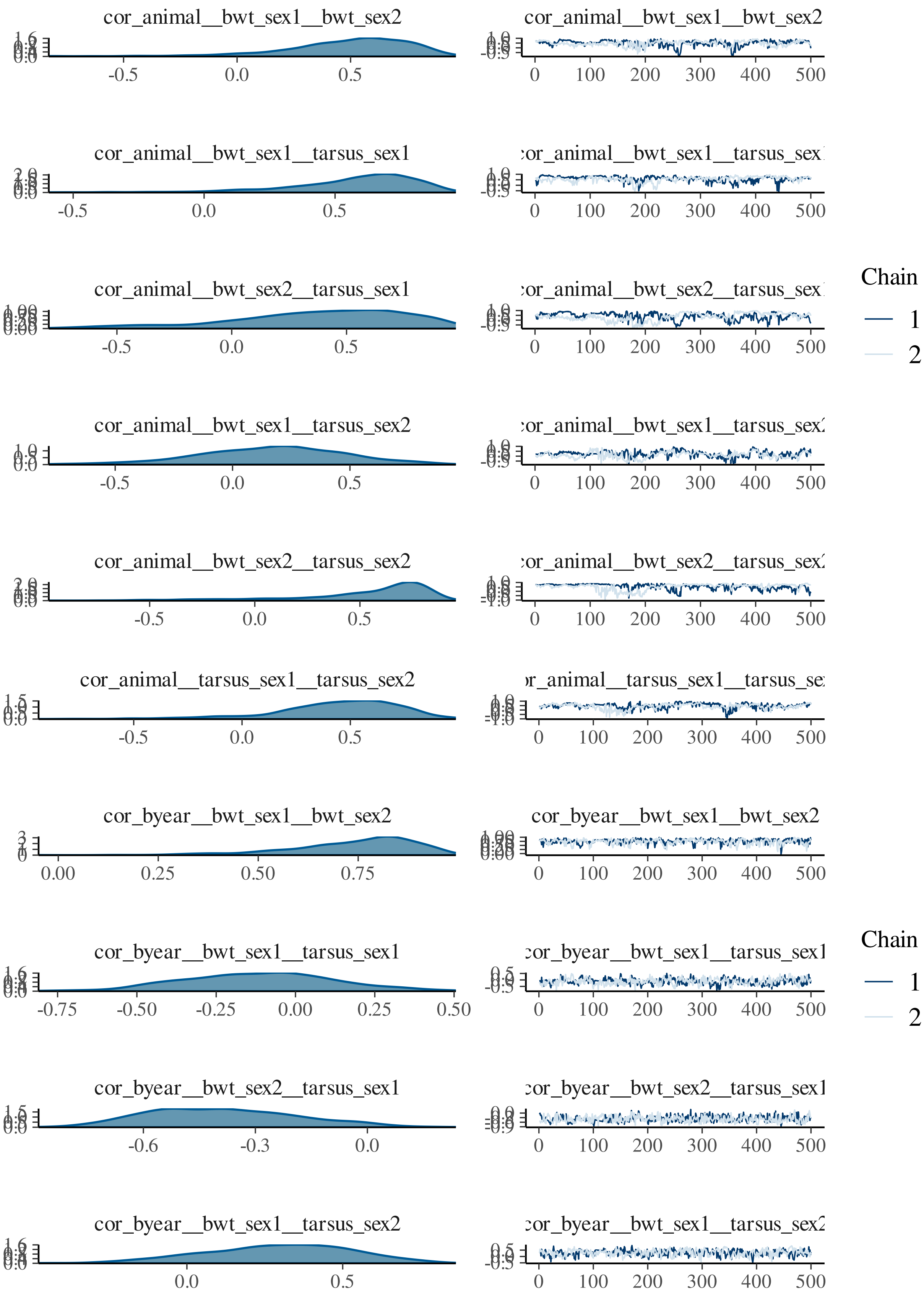
```
## cor(tarsus_sex1,tarsus_sex2)     0.44      0.29    -0.30     0.87 1.03       47
##                              Tail_ESS
## sd(bwt_sex1)                      104
## sd(bwt_sex2)                       25
## sd(tarsus_sex1)                    99
## sd(tarsus_sex2)                    42
## cor(bwt_sex1,bwt_sex2)            112
## cor(bwt_sex1,tarsus_sex1)         145
## cor(bwt_sex2,tarsus_sex1)          67
## cor(bwt_sex1,tarsus_sex2)          94
## cor(bwt_sex2,tarsus_sex2)          50
## cor(tarsus_sex1,tarsus_sex2)       44
##
## ~byear (Number of levels: 34)
##                              Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS
## sd(bwt_sex1)                     0.80      0.16     0.53     1.16 1.00      394
## sd(bwt_sex2)                     1.14      0.19     0.81     1.55 1.01      358
## sd(tarsus_sex1)                  2.23      0.46     1.50     3.18 1.01      297
## sd(tarsus_sex2)                  2.34      0.49     1.56     3.41 1.01      229
## cor(bwt_sex1,bwt_sex2)           0.74      0.15     0.35     0.96 1.01      266
## cor(bwt_sex1,tarsus_sex1)       -0.11      0.24    -0.55     0.35 1.01      190
## cor(bwt_sex2,tarsus_sex1)       -0.39      0.20    -0.73     0.00 1.01      410
## cor(bwt_sex1,tarsus_sex2)        0.29      0.23    -0.17     0.71 1.00      256
## cor(bwt_sex2,tarsus_sex2)        0.29      0.21    -0.16     0.66 1.01      327
## cor(tarsus_sex1,tarsus_sex2)     0.52      0.19     0.12     0.84 1.00      285
##                              Tail_ESS
## sd(bwt_sex1)                      619
## sd(bwt_sex2)                      653
## sd(tarsus_sex1)                   559
## sd(tarsus_sex2)                   239
## cor(bwt_sex1,bwt_sex2)            433
## cor(bwt_sex1,tarsus_sex1)         603
## cor(bwt_sex2,tarsus_sex1)         656
## cor(bwt_sex1,tarsus_sex2)         319
## cor(bwt_sex2,tarsus_sex2)         474
## cor(tarsus_sex1,tarsus_sex2)      600
##
## ~mother (Number of levels: 352)
##                              Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS
## sd(bwt_sex1)                     1.08      0.15     0.79     1.39 1.01      281
## sd(bwt_sex2)                     1.33      0.15     1.03     1.62 1.00      233
## sd(tarsus_sex1)                  2.21      0.40     1.36     2.95 1.01       72
## sd(tarsus_sex2)                  2.31      0.49     1.38     3.34 1.05       50
## cor(bwt_sex1,bwt_sex2)           0.83      0.11     0.57     0.98 1.01       68
## cor(bwt_sex1,tarsus_sex1)       -0.50      0.24    -0.91    -0.07 1.01       57
## cor(bwt_sex2,tarsus_sex1)       -0.64      0.17    -0.93    -0.28 1.06       50
## cor(bwt_sex1,tarsus_sex2)       -0.51      0.22    -0.88    -0.08 1.05       67
```

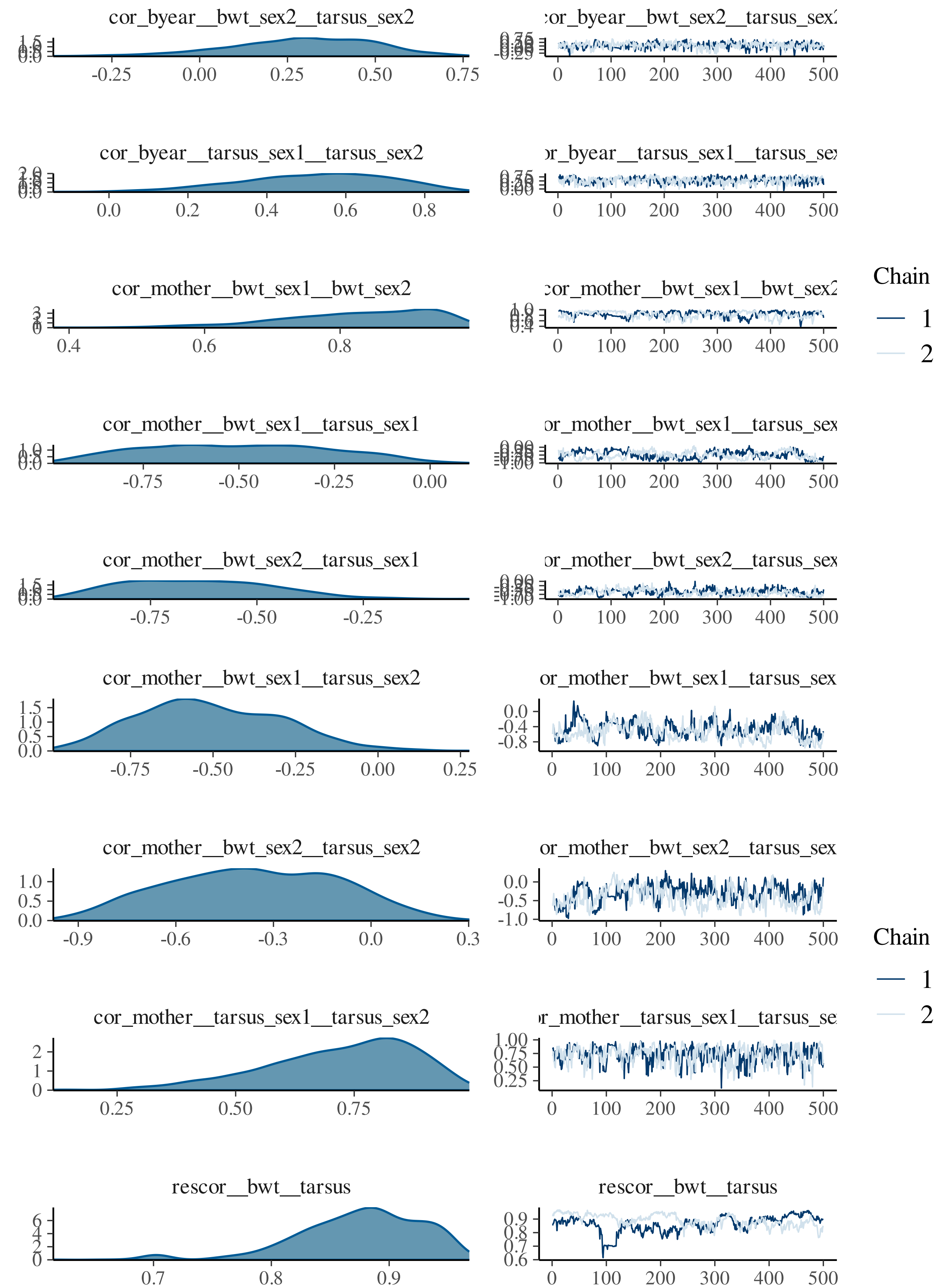
```
## cor(bwt_sex2,tarsus_sex2)       -0.36      0.26    -0.84      0.11 1.05       54
## cor(tarsus_sex1,tarsus_sex2)     0.72      0.16     0.37      0.95 1.01      249
##                              Tail_ESS
## sd(bwt_sex1)                      518
## sd(bwt_sex2)                      585
## sd(tarsus_sex1)                   224
## sd(tarsus_sex2)                   191
## cor(bwt_sex1,bwt_sex2)            296
## cor(bwt_sex1,tarsus_sex1)         156
## cor(bwt_sex2,tarsus_sex1)         268
## cor(bwt_sex1,tarsus_sex2)         124
## cor(bwt_sex2,tarsus_sex2)         297
## cor(tarsus_sex1,tarsus_sex2)      596
##
## Population-Level Effects:
##                  Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## bwt_Intercept        6.18      0.22     5.81     6.66 1.01      421      413
## tarsus_Intercept    20.24      0.55    19.12    21.25 1.01      497      527
## bwt_sex2             2.11      0.24     1.61     2.57 1.01      541      569
## sigma_bwt_sex1       0.27      0.20    -0.16     0.56 1.08       18       66
## sigma_bwt_sex2       0.31      0.23    -0.35     0.59 1.11       18       22
## tarsus_sex2          0.29      0.63    -0.96     1.56 1.00      490      535
## sigma_tarsus_sex1    1.26      0.12     1.01     1.47 1.02       50      109
## sigma_tarsus_sex2    1.28      0.20     0.80     1.53 1.13       12       42
##
## Residual Correlations:
##                   Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
## rescor(bwt,tarsus)     0.88      0.05     0.71     0.95 1.32        5       33
##
## Draws were sampled using sampling(NUTS). For each parameter, Bulk_ESS
## and Tail_ESS are effective sample size measures, and Rhat is the potential
## scale reduction factor on split chains (at convergence, Rhat = 1).
```

```
plot(brms_m2.5, ask = FALSE)
```


b_bwt_Intercept
6.0 6.5
b_bwt_Intercept
0 100 200 300 400 500
b_tarsus_Intercept
18 19 20 21 22
b_tarsus_Intercept
0 100 200 300 400 500
b_bwt_sex2
1.6 2.0 2.4 2.8
b_bwt_sex2
0 100 200 300 400 500
Chain
1
2
b_sigma_bwt_sex1
-0.2 0.0 0.2 0.4 0.6
b_sigma_bwt_sex1
0 100 200 300 400 500
b_sigma_bwt_sex2
-0.50 -0.25 0.00 0.25 0.50
b_sigma_bwt_sex2
0 100 200 300 400 500
b_tarsus_sex2
-1 0 1 2
b_tarsus_sex2
0 100 200 300 400 500
b_sigma_tarsus_sex1
0.8 1.0 1.2 1.4
b_sigma_tarsus_sex1
0 100 200 300 400 500
b_sigma_tarsus_sex2
0.8 1.0 1.2 1.4 1.6
b_sigma_tarsus_sex2
0 100 200 300 400 500
Chain
1
2
sd_animal__bwt_sex1
0.4 0.8 1.2 1.6
sd_animal__bwt_sex1
0 100 200 300 400 500
sd_animal__bwt_sex2
0.5 1.0 1.5
sd_animal__bwt_sex2
0 100 200 300 400 500


sd_animal__tarsus_sex1
sd_animal__tarsus_sex1
sd_animal__tarsus_sex2
sd_animal__tarsus_sex2
sd_byear__bwt_sex1
sd_byear__bwt_sex1
Chain
1
2
sd_byear__bwt_sex2
sd_byear__bwt_sex2
sd_byear__tarsus_sex1
sd_byear__tarsus_sex1
sd_byear__tarsus_sex2
sd_byear__tarsus_sex2
sd_mother__bwt_sex1
sd_mother__bwt_sex1
sd_mother__bwt_sex2
sd_mother__bwt_sex2
Chain
1
2
sd_mother__tarsus_sex1
sd_mother__tarsus_sex1
sd_mother__tarsus_sex2
sd_mother__tarsus_sex2


cor_animal__bwt_sex1__bwt_sex2
cor_animal__bwt_sex1__bwt_sex2
cor_animal__bwt_sex1__tarsus_sex1
cor_animal__bwt_sex1__tarsus_sex1
cor_animal__bwt_sex2__tarsus_sex1
cor_animal__bwt_sex2__tarsus_sex1
cor_animal__bwt_sex1__tarsus_sex2
cor_animal__bwt_sex1__tarsus_sex2
cor_animal__bwt_sex2__tarsus_sex2
cor_animal__bwt_sex2__tarsus_sex2
cor_animal__tarsus_sex1__tarsus_sex2
cor_animal__tarsus_sex1__tarsus_sex2
cor_byear__bwt_sex1__bwt_sex2
cor_byear__bwt_sex1__bwt_sex2
cor_byear__bwt_sex1__tarsus_sex1
cor_byear__bwt_sex1__tarsus_sex1
cor_byear__bwt_sex2__tarsus_sex1
cor_byear__bwt_sex2__tarsus_sex1
cor_byear__bwt_sex1__tarsus_sex2
cor_byear__bwt_sex1__tarsus_sex2
Chain
1
2
Chain
1
2


cor_byear__bwt_sex2__tarsus_sex2
-0.25 0.00 0.25 0.50 0.75
0 100 200 300 400 500
cor_byear__tarsus_sex1__tarsus_sex2
0.0 0.2 0.4 0.6 0.8
0 100 200 300 400 500
cor_mother__bwt_sex1__bwt_sex2
0.4 0.6 0.8
0 100 200 300 400 500
Chain
1
2
cor_mother__bwt_sex1__tarsus_sex1
-0.75 -0.50 -0.25 0.00
0 100 200 300 400 500
cor_mother__bwt_sex2__tarsus_sex1
-0.75 -0.50 -0.25
0 100 200 300 400 500
cor_mother__bwt_sex1__tarsus_sex2
1.5 1.0 0.5 0.0
-0.75 -0.50 -0.25 0.00 0.25
0.0 -0.4 -0.8
0 100 200 300 400 500
cor_mother__bwt_sex2__tarsus_sex2
1.0 0.5 0.0
-0.9 -0.6 -0.3 0.0 0.3
0.0 -0.5 -1.0
0 100 200 300 400 500
Chain
1
2
cor_mother__tarsus_sex1__tarsus_sex2
2 1 0
0.25 0.50 0.75
1.00 0.75 0.50 0.25
0 100 200 300 400 500
rescor__bwt__tarsus
6 4 2 0
0.7 0.8 0.9
rescor__bwt__tarsus
0.9 0.8 0.7 0.6
0 100 200 300 400 500

```r
VarCorr(brms_m2.5)
```

```
## $animal
## $animal$sd
##              Estimate Est.Error      Q2.5    Q97.5
## bwt_sex1     1.256797 0.3027123 0.6293789 1.733715
## bwt_sex2     1.077842 0.4168427 0.1958640 1.767136
## tarsus_sex1 2.259727 0.7239967 0.6135135 3.567762
## tarsus_sex2 2.744785 1.0537686 0.6051135 4.468542
##
## $animal$cor
## , , bwt_sex1
##
##               Estimate Est.Error        Q2.5     Q97.5
## bwt_sex1     1.0000000 0.0000000  1.00000000 1.0000000
## bwt_sex2     0.4823461 0.2872049 -0.23539931 0.8699222
## tarsus_sex1 0.5711397 0.2473353 -0.06616842 0.8936581
## tarsus_sex2 0.1685774 0.3102320 -0.48914110 0.7539686
##
## , , bwt_sex2
##
##               Estimate Est.Error       Q2.5     Q97.5
## bwt_sex1     0.4823461 0.2872049 -0.2353993 0.8699222
## bwt_sex2     1.0000000 0.0000000  1.0000000 1.0000000
## tarsus_sex1 0.3772862 0.3765302 -0.5312556 0.9085651
## tarsus_sex2 0.5246223 0.3336679 -0.3678213 0.8692250
##
## , , tarsus_sex1
##
##               Estimate Est.Error        Q2.5     Q97.5
## bwt_sex1     0.5711397 0.2473353 -0.06616842 0.8936581
## bwt_sex2     0.3772862 0.3765302 -0.53125561 0.9085651
## tarsus_sex1 1.0000000 0.0000000  1.00000000 1.0000000
## tarsus_sex2 0.4401433 0.2929178 -0.29616405 0.8720453
##
## , , tarsus_sex2
##
##               Estimate Est.Error       Q2.5     Q97.5
## bwt_sex1     0.1685774 0.3102320 -0.4891411 0.7539686
## bwt_sex2     0.5246223 0.3336679 -0.3678213 0.8692250
## tarsus_sex1 0.4401433 0.2929178 -0.2961641 0.8720453
## tarsus_sex2 1.0000000 0.0000000  1.0000000 1.0000000
##
##
## $animal$cov
```

```
## , , bwt_sex1
##
##               Estimate Est.Error        Q2.5    Q97.5
## bwt_sex1    1.6710810 0.7317405  0.39611874 3.005768
## bwt_sex2    0.7428820 0.5579922 -0.10600955 2.049110
## tarsus_sex1 1.8733421 1.2159805 -0.05815667 4.340959
## tarsus_sex2 0.6471034 1.0646022 -1.25297349 2.930019
##
## , , bwt_sex2
##
##             Estimate Est.Error        Q2.5    Q97.5
## bwt_sex1    0.742882 0.5579922 -0.10600955 2.049110
## bwt_sex2    1.335327 0.8557561  0.03836336 3.122771
## tarsus_sex1 1.105102 1.0991534 -0.68104784 3.388813
## tarsus_sex2 2.171388 1.8198507 -0.18718074 5.946047
##
## , , tarsus_sex1
##
##             Estimate Est.Error        Q2.5     Q97.5
## bwt_sex1    1.873342  1.215980 -0.05815667  4.340959
## bwt_sex2    1.105102  1.099153 -0.68104784  3.388813
## tarsus_sex1 5.630014  3.143741  0.37639882 12.728924
## tarsus_sex2 3.150235  2.476892 -0.67170548  8.755673
##
## , , tarsus_sex2
##
##               Estimate Est.Error       Q2.5     Q97.5
## bwt_sex1    0.6471034  1.064602 -1.2529735  2.930019
## bwt_sex2    2.1713876  1.819851 -0.1871807  5.946047
## tarsus_sex1 3.1502347  2.476892 -0.6717055  8.755673
## tarsus_sex2 8.6431609  5.649764  0.3661935 19.967865
##
##
##
## $byear
## $byear$sd
##               Estimate Est.Error      Q2.5    Q97.5
## bwt_sex1    0.7989572 0.1620838 0.5318383 1.156162
## bwt_sex2    1.1420876 0.1912205 0.8090083 1.549360
## tarsus_sex1 2.2286834 0.4609182 1.4995560 3.183107
## tarsus_sex2 2.3428101 0.4941316 1.5596304 3.405106
##
## $byear$cor
## , , bwt_sex1
##
##                Estimate Est.Error       Q2.5     Q97.5
## bwt_sex1     1.0000000 0.0000000  1.0000000 1.0000000
```

```
## bwt_sex2     0.7404024 0.1542690  0.3534945 0.9558481
## tarsus_sex1 -0.1137836 0.2357386 -0.5534464 0.3543949
## tarsus_sex2  0.2922708 0.2345550 -0.1749420 0.7113421
##
## , , bwt_sex2
##
##               Estimate Est.Error       Q2.5       Q97.5
## bwt_sex1     0.7404024 0.1542690  0.3534945 0.955848060
## bwt_sex2     1.0000000 0.0000000  1.0000000 1.000000000
## tarsus_sex1 -0.3874250 0.1987378 -0.7323699 0.004258363
## tarsus_sex2  0.2937354 0.2059346 -0.1577533 0.659531338
##
## , , tarsus_sex1
##
##               Estimate Est.Error       Q2.5       Q97.5
## bwt_sex1    -0.1137836 0.2357386 -0.5534464 0.354394929
## bwt_sex2    -0.3874250 0.1987378 -0.7323699 0.004258363
## tarsus_sex1  1.0000000 0.0000000  1.0000000 1.000000000
## tarsus_sex2  0.5226217 0.1897518  0.1183176 0.839911077
##
## , , tarsus_sex2
##
##              Estimate Est.Error       Q2.5     Q97.5
## bwt_sex1    0.2922708 0.2345550 -0.1749420 0.7113421
## bwt_sex2    0.2937354 0.2059346 -0.1577533 0.6595313
## tarsus_sex1 0.5226217 0.1897518  0.1183176 0.8399111
## tarsus_sex2 1.0000000 0.0000000  1.0000000 1.0000000
##
##
## $byear$cov
## , , bwt_sex1
##
##               Estimate Est.Error       Q2.5     Q97.5
## bwt_sex1     0.6645776 0.2761781  0.2828520 1.3367115
## bwt_sex2     0.6843681 0.2597687  0.2749460 1.2955568
## tarsus_sex1 -0.1581409 0.4589758 -1.0281983 0.8339776
## tarsus_sex2  0.5456796 0.5013040 -0.3608892 1.5951028
##
## , , bwt_sex2
##
##               Estimate Est.Error       Q2.5       Q97.5
## bwt_sex1     0.6843681 0.2597687  0.2749460 1.295556807
## bwt_sex2     1.3408929 0.4593417  0.6544951 2.400516888
## tarsus_sex1 -1.0167438 0.6693667 -2.4775184 0.009371017
## tarsus_sex2  0.8646682 0.7242669 -0.3384814 2.623722863
##
## , , tarsus_sex1
```

```
##
##              Estimate Est.Error      Q2.5       Q97.5
## bwt_sex1    -0.1581409 0.4589758 -1.0281983  0.833977585
## bwt_sex2    -1.0167438 0.6693667 -2.4775184  0.009371017
## tarsus_sex1  5.1792626 2.3047474  2.2486683 10.132170288
## tarsus_sex2  2.7818157 1.5318128  0.5297591  5.970346660
##
## , , tarsus_sex2
##
##             Estimate Est.Error      Q2.5     Q97.5
## bwt_sex1    0.5456796 0.5013040 -0.3608892  1.595103
## bwt_sex2    0.8646682 0.7242669 -0.3384814  2.623723
## tarsus_sex1 2.7818157 1.5318128  0.5297591  5.970347
## tarsus_sex2 5.7326811 2.5639312  2.4324504 11.594758
##
##
##
## $mother
## $mother$sd
##             Estimate Est.Error      Q2.5    Q97.5
## bwt_sex1    1.076447 0.1526711 0.7866154 1.390273
## bwt_sex2    1.325206 0.1540539 1.0256350 1.621175
## tarsus_sex1 2.214033 0.3976449 1.3647309 2.946910
## tarsus_sex2 2.310902 0.4940802 1.3795156 3.339175
##
## $mother$cor
## , , bwt_sex1
##
##              Estimate Est.Error      Q2.5       Q97.5
## bwt_sex1     1.0000000 0.0000000  1.0000000  1.00000000
## bwt_sex2     0.8260360 0.1110784  0.5676601  0.97826511
## tarsus_sex1 -0.5024557 0.2385053 -0.9137423 -0.06798800
## tarsus_sex2 -0.5073494 0.2162931 -0.8806394 -0.07677131
##
## , , bwt_sex2
##
##              Estimate Est.Error      Q2.5      Q97.5
## bwt_sex1     0.8260360 0.1110784  0.5676601  0.9782651
## bwt_sex2     1.0000000 0.0000000  1.0000000  1.0000000
## tarsus_sex1 -0.6373889 0.1744852 -0.9272366 -0.2775698
## tarsus_sex2 -0.3593672 0.2577845 -0.8364419  0.1135921
##
## , , tarsus_sex1
##
##              Estimate Est.Error      Q2.5      Q97.5
## bwt_sex1    -0.5024557 0.2385053 -0.9137423 -0.0679880
## bwt_sex2    -0.6373889 0.1744852 -0.9272366 -0.2775698
```

```
## tarsus_sex1  1.0000000 0.0000000  1.0000000  1.0000000
## tarsus_sex2  0.7206209 0.1561300  0.3688228  0.9518425
##
## , , tarsus_sex2
##
##                Estimate Est.Error       Q2.5       Q97.5
## bwt_sex1    -0.5073494 0.2162931 -0.8806394 -0.07677131
## bwt_sex2    -0.3593672 0.2577845 -0.8364419  0.11359208
## tarsus_sex1  0.7206209 0.1561300  0.3688228  0.95184250
## tarsus_sex2  1.0000000 0.0000000  1.0000000  1.00000000
##
##
## $mother$cov
## , , bwt_sex1
##
##               Estimate Est.Error       Q2.5      Q97.5
## bwt_sex1     1.182023 0.3330334  0.6187659  1.9328578
## bwt_sex2     1.179468 0.2744898  0.6821359  1.7479435
## tarsus_sex1 -1.110068 0.4557029 -1.9379754 -0.2103052
## tarsus_sex2 -1.223308 0.5582766 -2.3558658 -0.1900476
##
## , , bwt_sex2
##
##                Estimate Est.Error       Q2.5      Q97.5
## bwt_sex1     1.1794683 0.2744898  0.6821359  1.7479435
## bwt_sex2     1.7798788 0.4088241  1.0519272  2.6282093
## tarsus_sex1 -1.8437371 0.5678929 -2.9129058 -0.7723013
## tarsus_sex2 -0.9438083 0.6393327 -2.0044262  0.4581811
##
## , , tarsus_sex1
##
##               Estimate Est.Error      Q2.5      Q97.5
## bwt_sex1    -1.110068 0.4557029 -1.937975 -0.2103052
## bwt_sex2    -1.843737 0.5678929 -2.912906 -0.7723013
## tarsus_sex1  5.059904 1.7495725  1.862491  8.6842757
## tarsus_sex2  3.692391 1.3309441  1.432767  6.5202798
##
## , , tarsus_sex2
##
##                Estimate Est.Error      Q2.5      Q97.5
## bwt_sex1    -1.2233079 0.5582766 -2.355866 -0.1900476
## bwt_sex2    -0.9438083 0.6393327 -2.004426  0.4581811
## tarsus_sex1  3.6923914 1.3309441  1.432767  6.5202798
## tarsus_sex2  5.5841373 2.3245515  1.903063 11.1500916
```

The cross-sex genetic correlation can estimate form the output of the model. For tarsus length at fledging, sexes shared a lot of genetic variance which is commun for a trait with low sexual dimorphism. If the selection is antagonistic between males and females, sexes can not evolve freely from the other sexes and a intralocus sexual conflict can appeared.

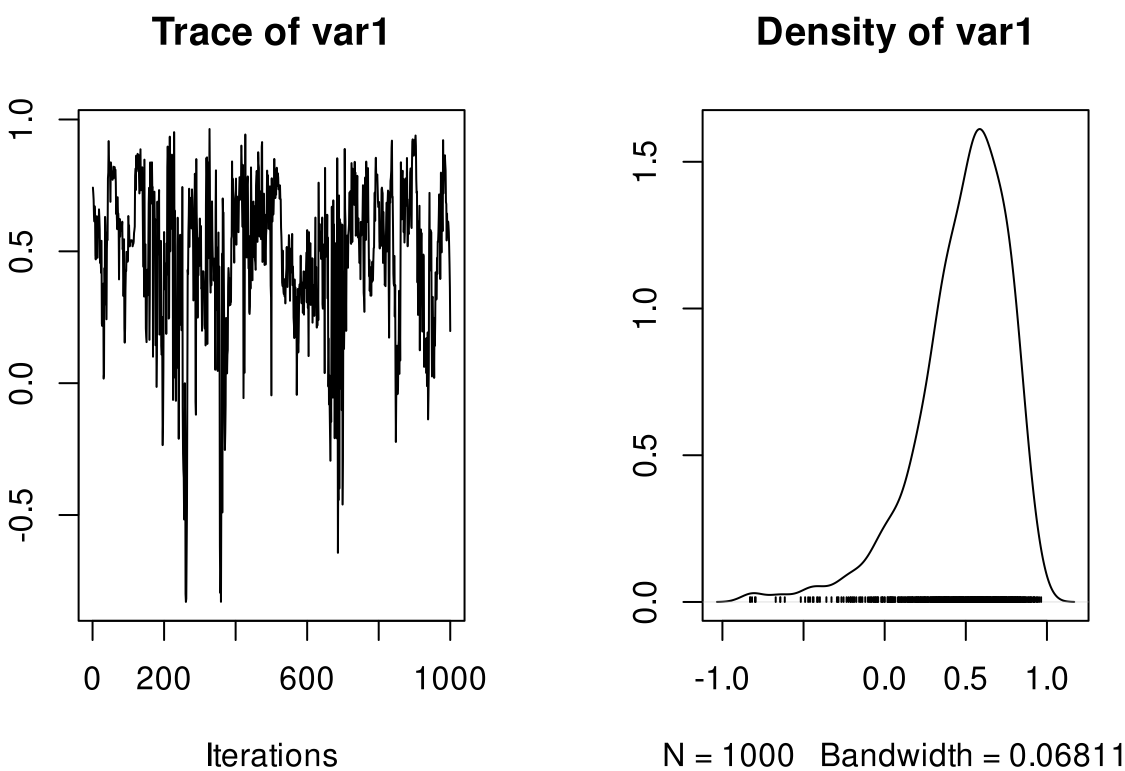
```
cross_sex.cor.btw <- as.mcmc((VarCorr(brms_m2.5, summary = FALSE)$animal$cor[, 1, 2]))
cross_sex.cor.tarsus <- as.mcmc((VarCorr(brms_m2.5, summary = FALSE)$animal$cor[, 3, 4]))

summary(cross_sex.cor.btw)
```

```
##
## Iterations = 1:1000
## Thinning interval = 1
## Number of chains = 1
## Sample size per chain = 1000
##
## 1. Empirical mean and standard deviation for each variable,
##    plus standard error of the mean:
##
##           Mean             SD       Naive SE Time-series SE
##       0.482346       0.287205       0.009082       0.032430
##
## 2. Quantiles for each variable:
##
##    2.5%     25%     50%     75%   97.5%
## -0.2354  0.3433  0.5365  0.6861  0.8699
```

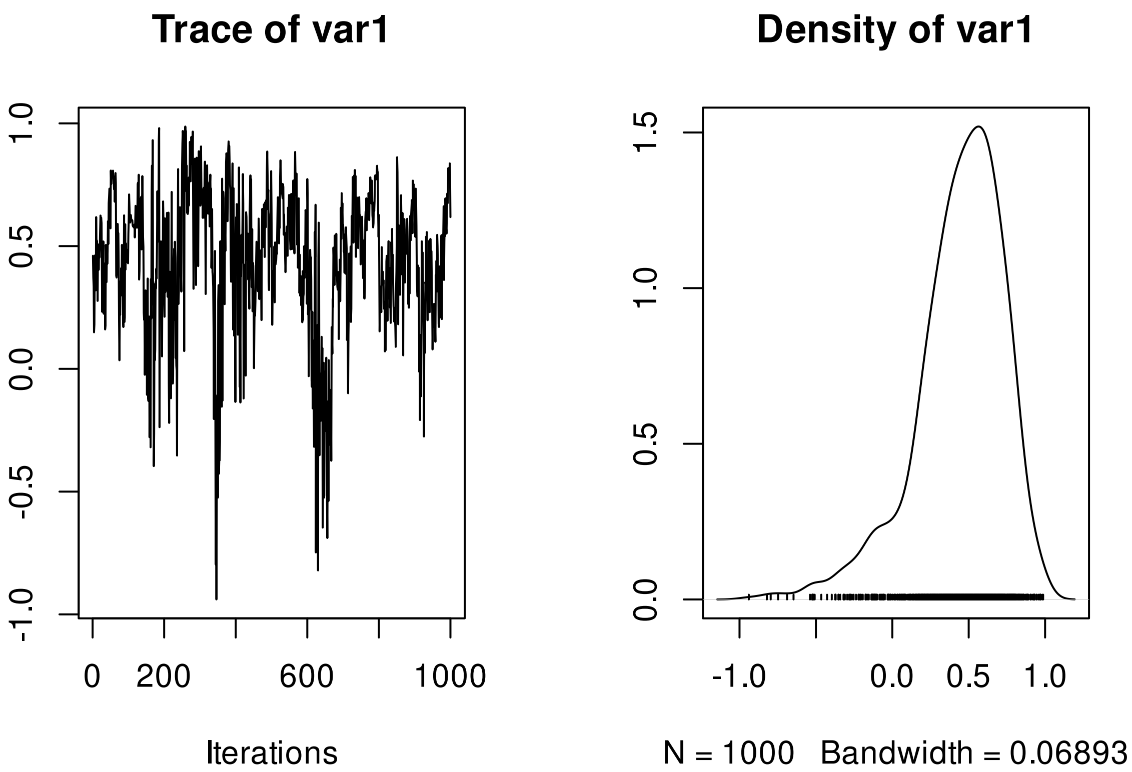
```
summary(cross_sex.cor.tarsus)
```

```
##
## Iterations = 1:1000
## Thinning interval = 1
## Number of chains = 1
## Sample size per chain = 1000
##
## 1. Empirical mean and standard deviation for each variable,
##    plus standard error of the mean:
##
##           Mean             SD       Naive SE Time-series SE
##       0.440143       0.292918       0.009263       0.048863
##
## 2. Quantiles for each variable:
##
##    2.5%     25%     50%     75%   97.5%
## -0.2962  0.2950  0.4846  0.6419  0.8720
```

```r
plot(cross_sex.cor.btw)
```




```r
plot(cross_sex.cor.tarsus)
```



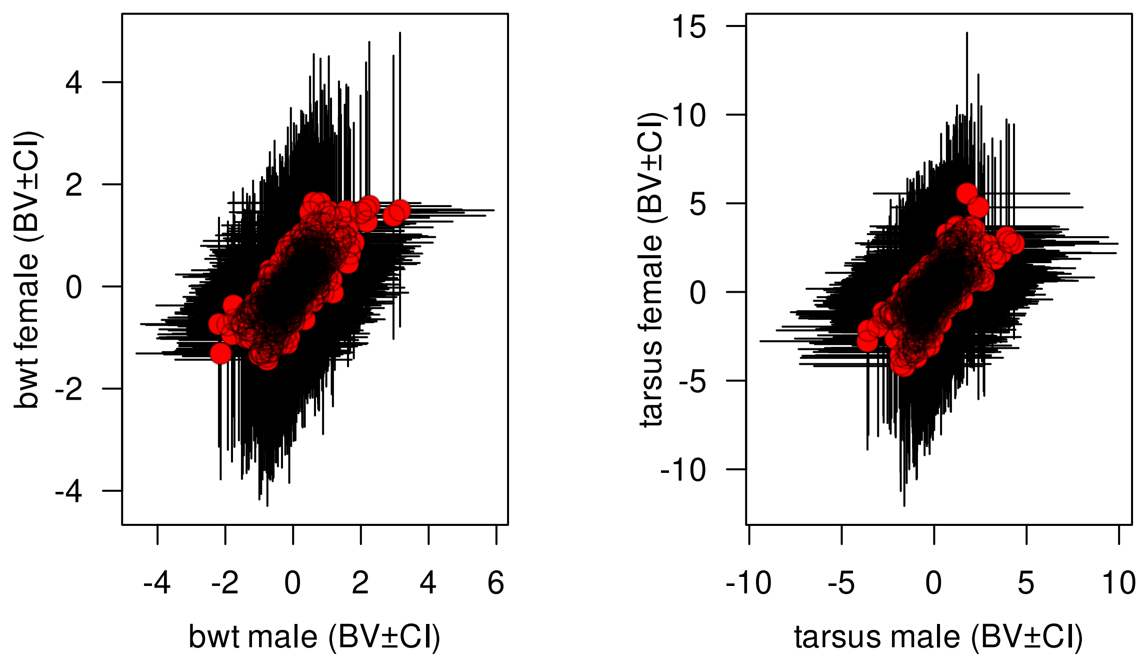
Here, some simple code to extract the BLUP.

```
bls_m2.5 <- ranef(brms_m2.5)$animal
bl_m2.5 <- as.data.frame(abind::abind(lapply(1:4, function(x) bls_m2.5[, c(1, 3, 4), x])))
colnames(bl_m2.5) <- paste0(rep(dimnames(bls_m2.5)[[3]], each = 3), c("", "_lo", "_up"))
bl_m2.5$id <- rownames(bl_m2.5)
```

Here, some simple code to plot the cross-sex genetic correlation.

```
par(mfrow = c(1, 2))
plot(bwt_sex2 ~ bwt_sex1, bl_m2.5,
  xlab = "", ylab = "", las = 1.2, type = "n",
  xlim = c(min(bl_m2.5$bwt_sex1_lo), max(bl_m2.5$bwt_sex1_up)),
  ylim = c(min(bl_m2.5$bwt_sex2_lo), max(bl_m2.5$bwt_sex2_up))
)
with(bl_m2.5, segments(x0 = bwt_sex1, y0 = bwt_sex2_lo, x1 = bwt_sex1, y1 = bwt_sex2_up, c
with(bl_m2.5, segments(x0 = bwt_sex1_lo, y0 = bwt_sex2, x1 = bwt_sex1_up, y1 = bwt_sex2, c
points(bwt_sex2 ~ bwt_sex1, bl_m2.5, pch = 16, col = "red", cex = 1.5)
points(bwt_sex2 ~ bwt_sex1, bl_m2.5, pch = 1, col = rgb(0, 0, 0, 0.3), cex = c(1.5))
mtext("bwt male (BV±CI)", side = 1, line = 2.4)
mtext("bwt female (BV±CI)", side = 2, line = 2, las = 3)
```

```
plot(tarsus_sex2 ~ tarsus_sex1, bl_m2.5,
  xlab = "", ylab = "", las = 1.2, type = "n",
  xlim = c(min(bl_m2.5$tarsus_sex1_lo), max(bl_m2.5$tarsus_sex1_up)),
  ylim = c(min(bl_m2.5$tarsus_sex2_lo), max(bl_m2.5$tarsus_sex2_up))
)
with(bl_m2.5, segments(x0 = tarsus_sex1, y0 = tarsus_sex2_lo, x1 = tarsus_sex1, y1 = tarsu
with(bl_m2.5, segments(x0 = tarsus_sex1_lo, y0 = tarsus_sex2, x1 = tarsus_sex1_up, y1 = ta
points(tarsus_sex2 ~ tarsus_sex1, bl_m2.5, pch = 16, col = "red", cex = 1.5)
points(tarsus_sex2 ~ tarsus_sex1, bl_m2.5, pch = 1, col = rgb(0, 0, 0, 0.3), cex = c(1.5))
mtext("tarsus male (BV±CI)", side = 1, line = 2.4)
mtext("tarsus female (BV±CI)", side = 2, line = 2, las = 3)
```



Within this model, we also have acces to the rest of the B-matrix. Note, the cross-sex genetic correlation is just the diagonal of the B matrix. For now on, you can explore this matrix and estimate the cross-sex-cross-trait genetic correlation.

3.6 stan

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Chapitre 4

A repeated measures animal model

This tutorial will demonstrate how to run a univariate animal model for a trait with repeated observations using different R packages with an example data files provided.

4.1 Scenario and data

4.1.1 scenario

Since gryphons are iteroparous, multiple observations of reproductive traits are available for some individuals. Here we have repeated measures of lay date (measured in days after January 1) for individual females varying in age from 2 (age of sexual maturation) up until age 6. Not all females lay every year so the number of observations per female is variable (between 1 to 5). We want to know how repeatable the trait is, and (assuming it is repeatable) how heritable it is.

4.1.2 Data files

The pedigree file `gryphonped.csv` is that used in the preceding tutorials but we now use a new data file `gryphonRM.csv`. Columns correspond to individual identity (`animal`), birth year (`byear`), age in years (`age`), year of measurement (`year`) and lay date (`laydate`). Each row of the data file corresponds to a single phenotypic observation. Here the data is sorted by identity and then age so that the repeated observations on individuals are apparent. However this is not a requirement for analysis - data could equally be sorted by some other variable (*e.g.*, measurement year) or be in a random order.

```
str(gryphonRM)
```

```
## 'data.frame':    1607 obs. of  5 variables:
##  $ animal : Factor w/ 469 levels "1","2","3","8",..: 1 1 1 1 1 2 2 2 3 3 ...
##  $ byear  : Factor w/ 34 levels "968","970","971",..: 22 22 22 22 22 22 22 22 22 22 ...
##  $ age    : Factor w/ 5 levels "2","3","4","5",..: 1 2 3 4 5 1 2 3 1 2 ...
##  $ year   : Factor w/ 39 levels "970","971","972",..: 23 24 25 26 27 23 24 25 23 24 ...
##  $ laydate: num  19 23 24 23 29 21 17 21 20 20 ...
```

```r
summary(gryphonRM)
```

```
##       animal          byear        age          year          laydate     
##  1       :   5   1000   : 109   2:308   1004   :  79   Min.   : 0.00  
##  3       :   5   1001   :  98   3:322   1005   :  78   1st Qu.:20.00  
##  9       :   5   999    :  86   4:339   1003   :  69   Median :24.00  
##  17      :   5   1002   :  85   5:315   1006   :  64   Mean   :23.54  
##  42      :   5   987    :  70   6:323   1002   :  60   3rd Qu.:27.00  
##  50      :   5   989    :  66           988    :  54   Max.   :41.00  
##  (Other):1577   (Other):1093           (Other):1203
```

```r
head(gryphonRM)
```

```
##   animal byear age year laydate
## 1      1   990   2  992      19
## 2      1   990   3  993      23
## 3      1   990   4  994      24
## 4      1   990   5  995      23
## 5      1   990   6  996      29
## 6      2   990   2  992      21
```

4.2 Asreml-R

First we need to load the `asreml` library:

```r
library(asreml)
```

4.2.1 Estimating repeatability

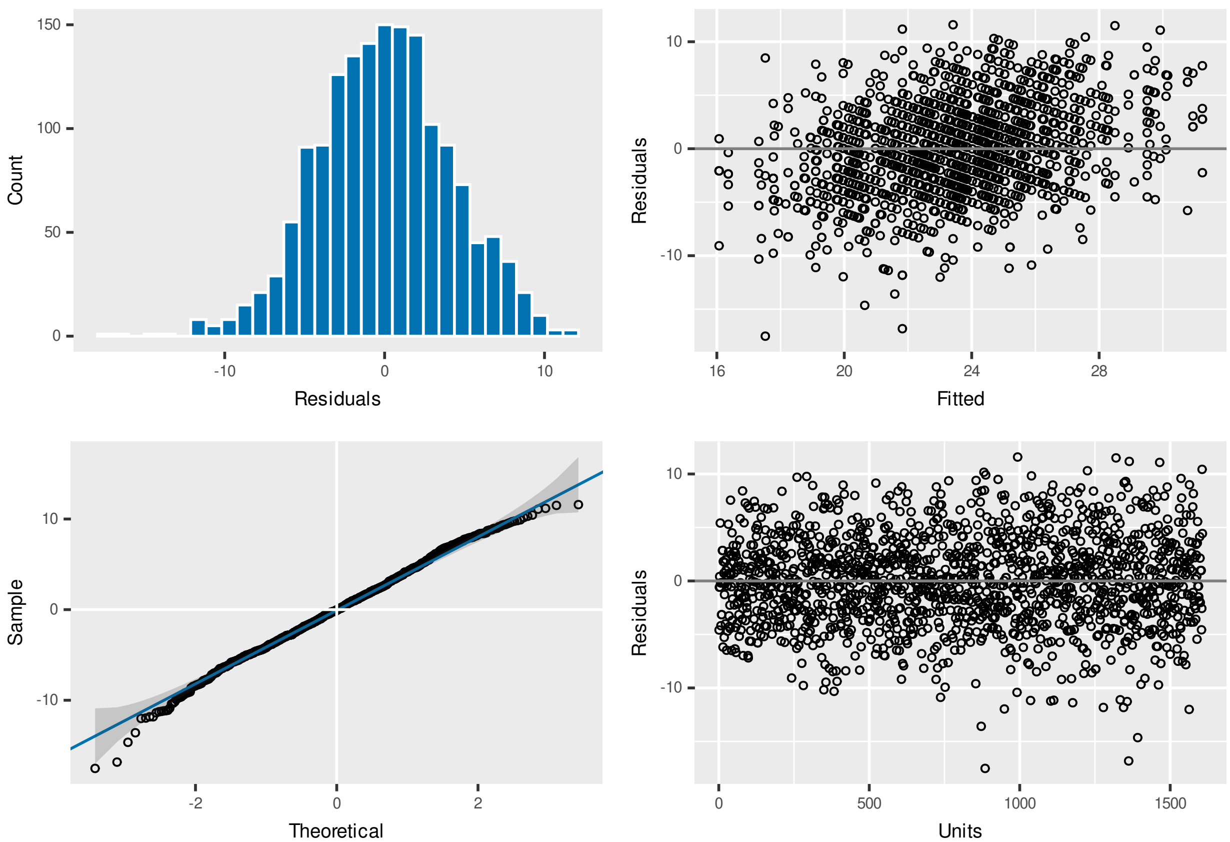
With repeated measures on individuals it is often of interest to see how repeatable a trait is. We can estimate the repeatability of a trait as the proportion of phenotypic variance V_P explained by individual variance V_{ind}; $R = V_{ind}/V_P = V_{ind}/(V_{ind} + V_R)$.

```r
modelv <- asreml(
  fixed = laydate ~ 1,
  random = ~animal,
  residual = ~ idv(units),
  data = gryphonRM,
  na.action = na.method(x = "omit", y = "omit")
)
```

```
## Model fitted using the sigma parameterization.
## ASReml 4.1.0 Tue Nov 29 16:56:53 2022
```

```
##          LogLik        Sigma2     DF      wall     cpu
## 1      -10182.83         1.0   1606 16:56:53     0.0
## 2       -8266.10         1.0   1606 16:56:53     0.0
## 3       -6145.01         1.0   1606 16:56:53     0.0
## 4       -4651.57         1.0   1606 16:56:53     0.0
## 5       -3819.31         1.0   1606 16:56:53     0.0
## 6       -3554.22         1.0   1606 16:56:53     0.0
## 7       -3501.56         1.0   1606 16:56:53     0.0
## 8       -3497.58         1.0   1606 16:56:53     0.0
## 9       -3497.54         1.0   1606 16:56:53     0.0
## 10      -3497.54         1.0   1606 16:56:53     0.0
```

```
plot(modelv)
```



The model assumption seems correct, so we can look at the different estimates. Note that since we want to estimate the amount of variance explained by individual identity (rather than by additive genetic effects), we fit `animal` as a normal random effect and we don't associate it with the pedigree. Here, we also ask the model to remove any `NA` in `laydate`.

This model partitions the phenotypic variance in `laydate` as follows:

```
summary(modelv)$varcomp
```

```
##                component std.error   z.ratio bound %ch
```

```
## animal       11.08634 1.1794319  9.399728     P   0
## units!units  21.29643 0.8896196 23.938798     P   0
## units!R       1.00000        NA        NA     F   0
```

Between-individual (or among-individual) variance is given by the `animal` component, while the residual component (`units!units`) represents within-individual variance. Here then the repeatability of the trait can be determined by hand as 0.34 (*i.e.*, as 11.086/(11.086 + 21.296)).

Mean lay date might change with age, so we could ask what the repeatability of lay date is after conditioning on age. This would be done by adding `age` into the model as a fixed effect.

```
modelw <- asreml(
  fixed = laydate ~ age,
  random = ~animal,
  residual = ~ idv(units),
  data = gryphonRM,
  na.action = na.method(x = "omit", y = "omit")
)
```

```
## Model fitted using the sigma parameterization.
## ASReml 4.1.0 Tue Nov 29 16:56:54 2022
##          LogLik        Sigma2     DF     wall    cpu
##  1     -8402.968           1.0   1602 16:56:54    0.0
##  2     -6912.361           1.0   1602 16:56:54    0.0
##  3     -5274.379           1.0   1602 16:56:54    0.0
##  4     -4143.634           1.0   1602 16:56:54    0.0
##  5     -3541.895           1.0   1602 16:56:54    0.0
##  6     -3372.909           1.0   1602 16:56:54    0.0
##  7     -3347.670           1.0   1602 16:56:54    0.0
##  8     -3346.655           1.0   1602 16:56:54    0.0
##  9     -3346.652           1.0   1602 16:56:54    0.0
```

```
summary(modelw)$varcomp
```

```
##             component std.error  z.ratio bound %ch
## animal       12.28982  1.156115 10.63027     P   0
## units!units  16.37989  0.686619 23.85586     P   0
## units!R       1.00000        NA       NA     F   0
```

The repeatability of lay date, after accounting for age effects, is now estimated as 0.43 (*i.e.*, as 12.29/(12.29 + 16.38)). So, just as we saw when estimating h^2 in Tutorial 1, the inclusion of fixed effects will alter the estimated effect size if we determine total phenotypic variance as the sum of the variance components. Thus, proper interpretation is vital.

```
summary(modelw, coef = TRUE)$coef.fixed
wald.asreml(modelw, ssType = "conditional", denDF = "numeric")
```

```
##             solution std error   z.ratio
## age_2       0.000000        NA        NA
## age_3       2.577777 0.3355253  7.682811
## age_4       4.247276 0.3309028 12.835418
## age_5       6.094490 0.3375537 18.054872
## age_6       3.132675 0.3371074  9.292811
## (Intercept) 20.305073 0.2899515 70.029214
```

```
## Model fitted using the sigma parameterization.
## ASReml 4.1.0 Tue Nov 29 16:56:54 2022
##          LogLik        Sigma2     DF     wall    cpu
##  1     -3346.652          1.0   1602 16:56:54    0.0
##  2     -3346.652          1.0   1602 16:56:54    0.0
##  3     -3346.652          1.0   1602 16:56:54    0.0
```

```
##
##             Df  denDF   F.inc   F.con Margin          Pr
## (Intercept)  1  460.2 14880.0 14880.0        0.00000e+00
## age          4 1225.3    88.7    88.7      A 2.89474e-66
```

Here age is modeled as a 5-level factor (specified using the function `as.factor()` at the beginning of the analysis). We could equally have fitted it as a continuous variable, in which case, given potential for a late life decline, we would probably also include a quadratic term. In addition, using `age` as continuous variable can help in saving some degree of freedom in the analysis.

4.2.2 Partitioning additive and permanent environment effects

Generally we expect that the repeatability will set the upper limit for heritability since among individual variation can be decomposed in the additive genetic variation and non additive genetic variation. In other word, the additive genetic variation is a subcomponent of the difference between individuals. Non-additive contributions to fixed among-individual differences are normally referred to as *permanent environment effects*. If a trait has repeated measures then it is necessary to model permanent environment effects in an animal model to prevent upward bias in V_A.

To illustrate it, we first fit the animal model:

```
gryphonped <- read.csv("data/gryphonped.csv")
gryphonped$id <- as.factor(gryphonped$id)
gryphonped$father <- as.factor(gryphonped$father)
gryphonped$mother <- as.factor(gryphonped$mother)

ainv <- ainverse(gryphonped)

modelx <- asreml(
  fixed = laydate ~ age,
  random = ~ vm(animal, ainv),
  residual = ~ idv(units),
  data = gryphonRM,
```

```
  na.action = na.method(x = "omit", y = "omit")
)
```

```
## Model fitted using the sigma parameterization.
## ASReml 4.1.0 Tue Nov 29 16:56:54 2022
##          LogLik        Sigma2     DF     wall    cpu
##  1     -8751.390          1.0   1602 16:56:54    0.0
##  2     -7169.205          1.0   1602 16:56:54    0.0
##  3     -5427.604          1.0   1602 16:56:54    0.0
##  4     -4219.598          1.0   1602 16:56:54    0.0
##  5     -3569.815          1.0   1602 16:56:54    0.0
##  6     -3382.341          1.0   1602 16:56:54    0.0
##  7     -3352.867          1.0   1602 16:56:54    0.0
##  8     -3351.565          1.0   1602 16:56:54    0.0
##  9     -3351.560          1.0   1602 16:56:54    0.0
```

Variance components are almost unchanged if we compare the previous model:

```
summary(modelx)$varcomp
```

```
##                    component std.error   z.ratio bound %ch
## vm(animal, ainv)  13.91784  1.443968  9.638607     P   0
## units!units       16.84008  0.707365 23.806768     P   0
## units!R            1.00000        NA        NA     F   0
```

```
summary(modelw)$varcomp
```

```
##               component std.error  z.ratio bound %ch
## animal         12.28982  1.156115 10.63027     P   0
## units!units    16.37989  0.686619 23.85586     P   0
## units!R         1.00000        NA       NA     F   0
```

This suggests that most of the among-individual variance is – rightly or wrongly – being partitioned as V_A here. To instead to obtain an unbiased estimate of V_A, we need to partition for both additive genetic *and* non-genetic sources of individual variation. We do it by fitting `animal` twice, once with a pedigree, and once without a pedigree (using `ide()`). Here, the command `ide` allow to create a second effect using a similar variable.

```
modely <- asreml(
  fixed = laydate ~ age,
  random = ~ vm(animal, ainv) + ide(animal),
  residual = ~ idv(units),
  data = gryphonRM,
  na.action = na.method(x = "omit", y = "omit")
)
```

```
## Model fitted using the sigma parameterization.
## ASReml 4.1.0 Tue Nov 29 16:56:54 2022
##          LogLik        Sigma2     DF     wall    cpu
##  1     -7731.394          1.0   1602 16:56:54    0.0
##  2     -6426.548          1.0   1602 16:56:54    0.0
##  3     -4997.252          1.0   1602 16:56:54    0.0
##  4     -4018.486          1.0   1602 16:56:54    0.0
##  5     -3504.988          1.0   1602 16:56:54    0.0
##  6     -3363.160          1.0   1602 16:56:54    0.0
##  7     -3341.611          1.0   1602 16:56:54    0.0
##  8     -3340.682          1.0   1602 16:56:54    0.0
##  9     -3340.679          1.0   1602 16:56:54    0.0
```

```r
summary(modely)$varcomp
```

```
##                    component std.error   z.ratio bound %ch
## vm(animal, ainv)  4.876101 1.8087709  2.695809     P   0
## ide(animal)       7.400983 1.7280113  4.282948     P   0
## units!units      16.380188 0.6866189 23.856300     P   0
## units!R           1.000000        NA        NA     F   0
```

The estimate of V_A is now much lower since the additive and permanent environment effects are being properly separated. We can estimate h^2 and the repeatability from this model:

```r
vpredict(modely, h2 ~ V1 / (V1 + V2 + V3))
```

```
##     Estimate         SE
## h2 0.1701523 0.06073974
```

```r
vpredict(modely, repeatability ~ (V1 + V2) / (V1 + V2 + V3))
```

```
##                Estimate         SE
## repeatability 0.4284108 0.02741602
```

4.2.3 Adding additional effects and testing significance

Models of repeated measures can be extended to include other fixed or random effects. For example try including year of measurement (`year`) and birth year (`byear`) as random effects.

```r
modelz <- asreml(
  fixed = laydate ~ age,
  random = ~ vm(animal, ainv) + ide(animal) +
    year + byear,
  residual = ~ idv(units),
  data = gryphonRM,
```

```r
  na.action = na.method(x = "omit", y = "omit")
)
```

```
## Model fitted using the sigma parameterization.
## ASReml 4.1.0 Tue Nov 29 16:56:54 2022
##           LogLik        Sigma2     DF     wall    cpu
##  1     -4650.748           1.0   1602 16:56:54    0.0
##  2     -4088.264           1.0   1602 16:56:54    0.0
##  3     -3494.147           1.0   1602 16:56:54    0.0
##  4     -3127.161           1.0   1602 16:56:54    0.0 (1 restrained)
##  5     -2976.449           1.0   1602 16:56:54    0.0 (1 restrained)
##  6     -2955.785           1.0   1602 16:56:54    0.0 (1 restrained)
##  7     -2955.097           1.0   1602 16:56:54    0.0 (1 restrained)
##  8     -2955.095           1.0   1602 16:56:54    0.0 (1 restrained)
##  9     -2955.095           1.0   1602 16:56:54    0.0
```

```r
summary(modelz)$varcomp
```

```
##                       component std.error   z.ratio bound %ch
## byear              1.650876e-07        NA        NA     B   0
## year               7.938576e+00 1.9344619  4.103765     P   0
## vm(animal, ainv)   4.815136e+00 1.6682351  2.886365     P   0
## ide(animal)        8.433325e+00 1.5495778  5.442337     P   0
## units!units        7.795560e+00 0.3324411 23.449443     P   0
## units!R            1.000000e+00        NA        NA     F   0
```

This model will return additional variance components corresponding to variation in lay dates between years of measurement and between birth cohorts of females. V_{byear} is very low and `B` appeared which tell us that the model had fixed the variance as a boundary. If you compare this model to a reduced model with byear excluded the log-likelihood remains unchanged.

```r
modelz_2 <- asreml(
  fixed = laydate ~ age,
  random = ~ vm(animal, ainv) + ide(animal) +
    year,
  residual = ~ idv(units),
  data = gryphonRM,
  na.action = na.method(x = "omit", y = "omit")
)
```

```
## Model fitted using the sigma parameterization.
## ASReml 4.1.0 Tue Nov 29 16:56:54 2022
##           LogLik        Sigma2     DF     wall    cpu
##  1     -4665.606           1.0   1602 16:56:54    0.0
##  2     -4097.928           1.0   1602 16:56:54    0.0
```

```
## 3     -3498.611           1.0   1602 16:56:54    0.0
## 4     -3128.789           1.0   1602 16:56:54    0.0
## 5     -2976.883           1.0   1602 16:56:54    0.0
## 6     -2955.806           1.0   1602 16:56:54    0.0
## 7     -2955.096           1.0   1602 16:56:54    0.0
## 8     -2955.095           1.0   1602 16:56:54    0.0
```

```
summary(modelz_2)$varcomp
```

```
##                    component std.error   z.ratio bound %ch
## year                7.938576 1.9344829  4.103720     P   0
## vm(animal, ainv)    4.815137 1.6682366  2.886364     P   0
## ide(animal)         8.433324 1.5495828  5.442319     P   0
## units!units         7.795560 0.3324384 23.449637     P   0
## units!R             1.000000        NA        NA     F   0
```

```
modelz$loglik
```

```
## [1] -2955.095
```

```
modelz_2$loglik
```

```
## [1] -2955.095
```

```
1 - pchisq(2 * (modelz_2$loglik - modelz$loglik), 1)
```

```
## [1] 0.9990425
```

year effects could alternatively be included as fixed effects (try it!). This will reduce V_R and increase the estimates of heritability and repeatability, which must now be interpreted as proportions of phenotypic variance after conditioning on both age and year of measurement effects.

```
modelz_3 <- asreml(
  fixed = laydate ~ age + byear,
  random = ~ vm(animal, ainv) + ide(animal) +
    year,
  residual = ~ idv(units),
  data = gryphonRM,
  na.action = na.method(x = "omit", y = "omit")
)
```

```
## Model fitted using the sigma parameterization.
## ASReml 4.1.0 Tue Nov 29 16:56:55 2022
##          LogLik        Sigma2     DF     wall    cpu
## 1     -4623.985           1.0   1569 16:56:55    0.0
```

```
## 2      -4063.535           1.0   1569 16:56:55    0.0
## 3      -3471.618           1.0   1569 16:56:55    0.0
## 4      -3105.972           1.0   1569 16:56:55    0.0
## 5      -2955.436           1.0   1569 16:56:55    0.0
## 6      -2934.435           1.0   1569 16:56:55    0.0
## 7      -2933.721           1.0   1569 16:56:55    0.0
## 8      -2933.720           1.0   1569 16:56:55    0.0
```

```
summary(modelz_3)$varcomp
```

```
##                    component std.error   z.ratio bound %ch
## year                8.029139 1.9920127  4.030666     P   0
## vm(animal, ainv)    5.060775 1.7855255  2.834334     P   0
## ide(animal)         8.412539 1.6494894  5.100087     P   0
## units!units         7.805139 0.3331474 23.428484     P   0
## units!R             1.000000        NA        NA     F   0
```

```
summary(modelw, coef = TRUE)$coef.fixed
wald.asreml(modelz_3, ssType = "conditional", denDF = "numeric")
```

```
##              solution std error   z.ratio
## age_2        0.000000        NA        NA
## age_3        2.577777 0.3355253  7.682811
## age_4        4.247276 0.3309028 12.835418
## age_5        6.094490 0.3375537 18.054872
## age_6        3.132675 0.3371074  9.292811
## (Intercept) 20.305073 0.2899515 70.029214

## Model fitted using the sigma parameterization.

## Warning in asreml(fixed = laydate ~ age + byear, random = ~vm(animal, ainv) + :
## Algebraic derivatives for denominator df not available.

## ASReml 4.1.0 Tue Nov 29 16:56:55 2022
##           LogLik        Sigma2     DF     wall    cpu
## 1      -2933.720           1.0   1569 16:56:55    0.0
## 2      -2933.720           1.0   1569 16:56:55    0.0
## Calculating denominator DF

##
##              Df denDF   F.inc   F.con Margin      Pr
## (Intercept)  1   55.3 1894.00 1894.00        0.00000
## age          4  845.2  152.70  132.90      A 0.00000
## byear       33  466.5    0.77    0.77      A 0.81646
```

4.3 gremlin

TODO (maybe just bother Matthew to do it)

Meanwhile

Figure 4.1: Keep it dry and do no feed after midnight.

4.4 MCMCglmm

4.4.1 Estimating repeatability

With repeated measures on individuals it is often of interest to see how repeatable a trait is. We can estimate the repeatability of a trait as the proportion of phenotypic variance V_P explained by individual variance V_{ind}; $R = V_{ind}/V_P = V_{ind}/(V_{ind} + V_R)$. As you already know, bayesian modelisation requires prior. Here, we create a unformative prior with one estimate for the G matrix and one estimate for the Residual matrix, in addition

```
# p.var <- var(gryphonRM$laydate, na.rm = TRUE)
prior3.1 <- list(G = list(G1 = list(V = 1, nu = 0.002)), R = list(
  V = 1,
  nu = 0.002
))
model3.1 <- MCMCglmm(laydate ~ 1,
  random = ~animal, data = gryphonRM,
```

```
  prior = prior3.1, verbose = FALSE
)
posterior.mode(model3.1$VCV)
```

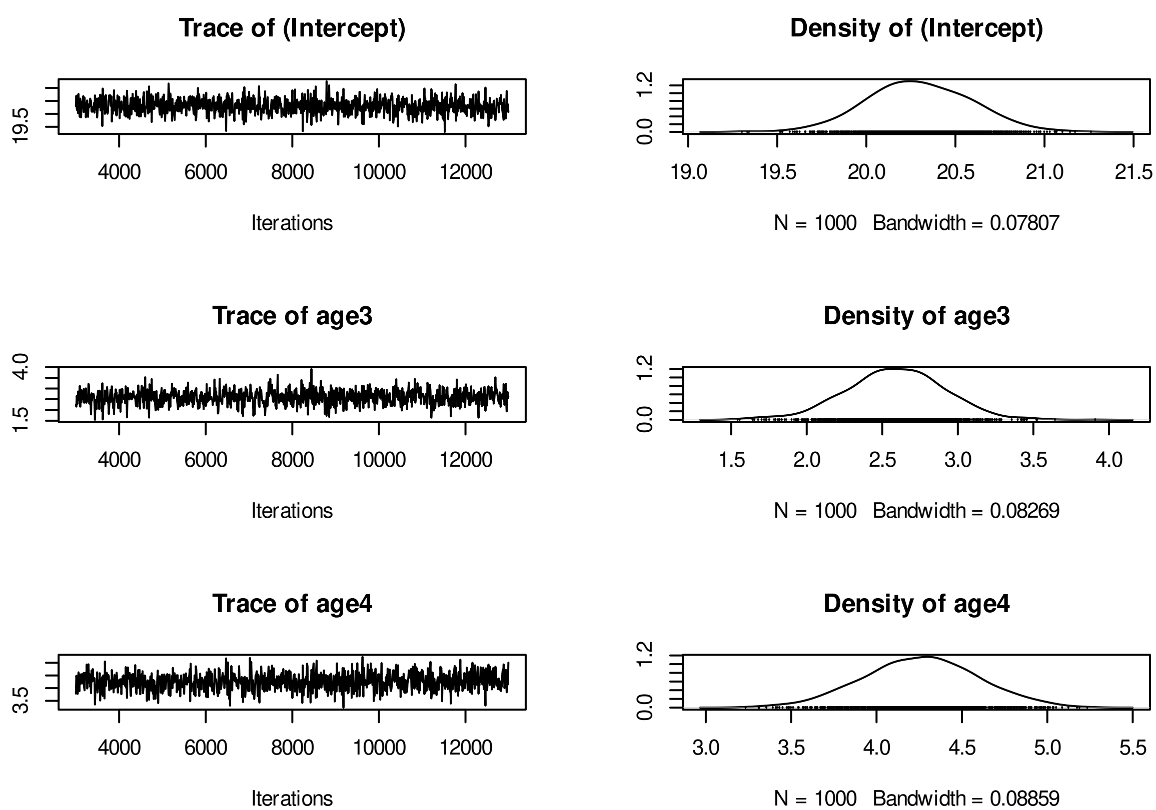
```
##   animal    units
## 11.14136 21.22028
```

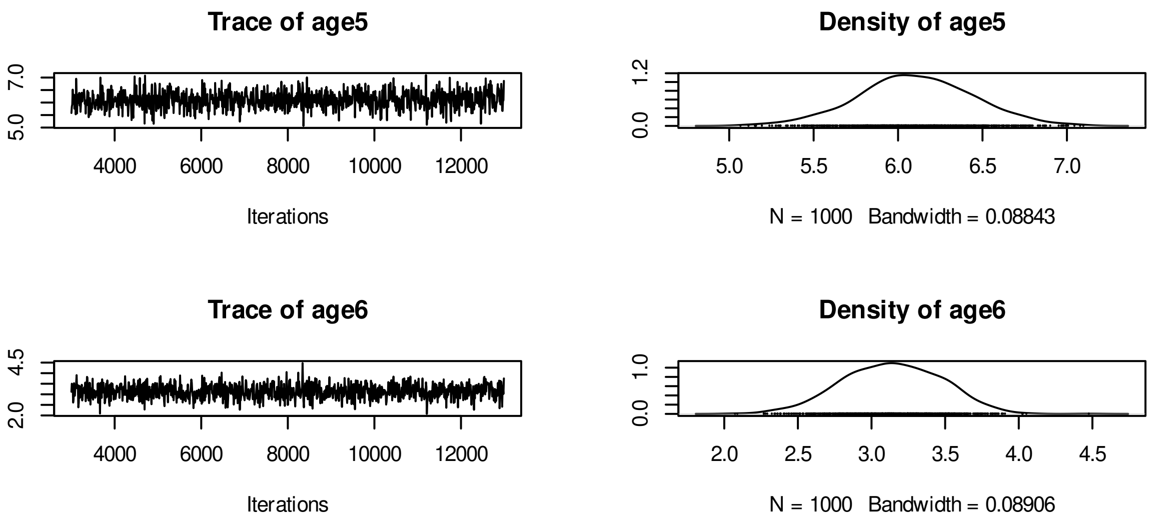
Note the use of the term `animal` as random allowed to partition the phenotypic variance V_P into among individual variance V_{ind} associated with `animal` and residual variance V_R associated with `units`.

Here then the repeatability of the `laydate` can be determined as: 22.22 (*i.e.*, as 11.141/(11.141 + 21.22)). Just a friendly remember, we work with Monte Carlo chain with model iteration, so the point estimate can be different (but very similar) each time you run the model.

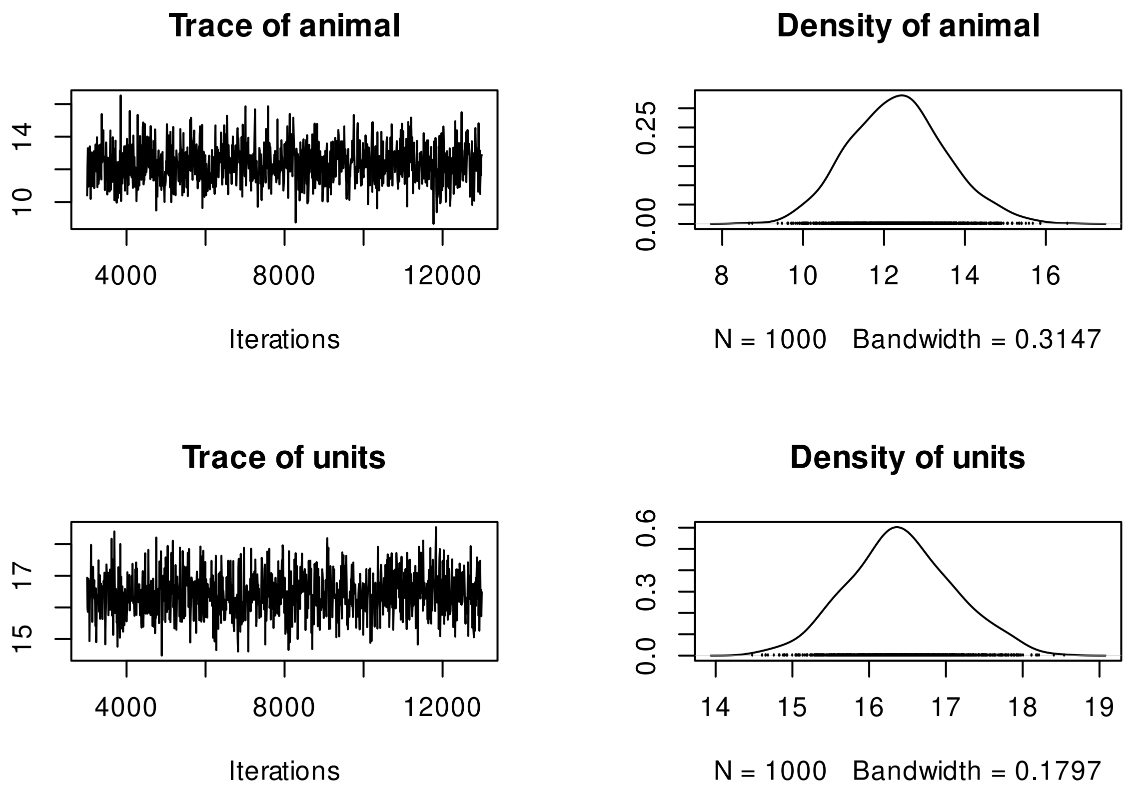
Mean lay date might change with age, so we could ask what the repeatability of lay date is after conditioning on age. This would be done by adding `age` into the model as a fixed effect.

```
model3.2 <- MCMCglmm(laydate ~ age,
  random = ~animal, data = gryphonRM,
  prior = prior3.1, verbose = FALSE
)
plot(model3.2$Sol)
```






```
plot(model3.2$VCV)
```

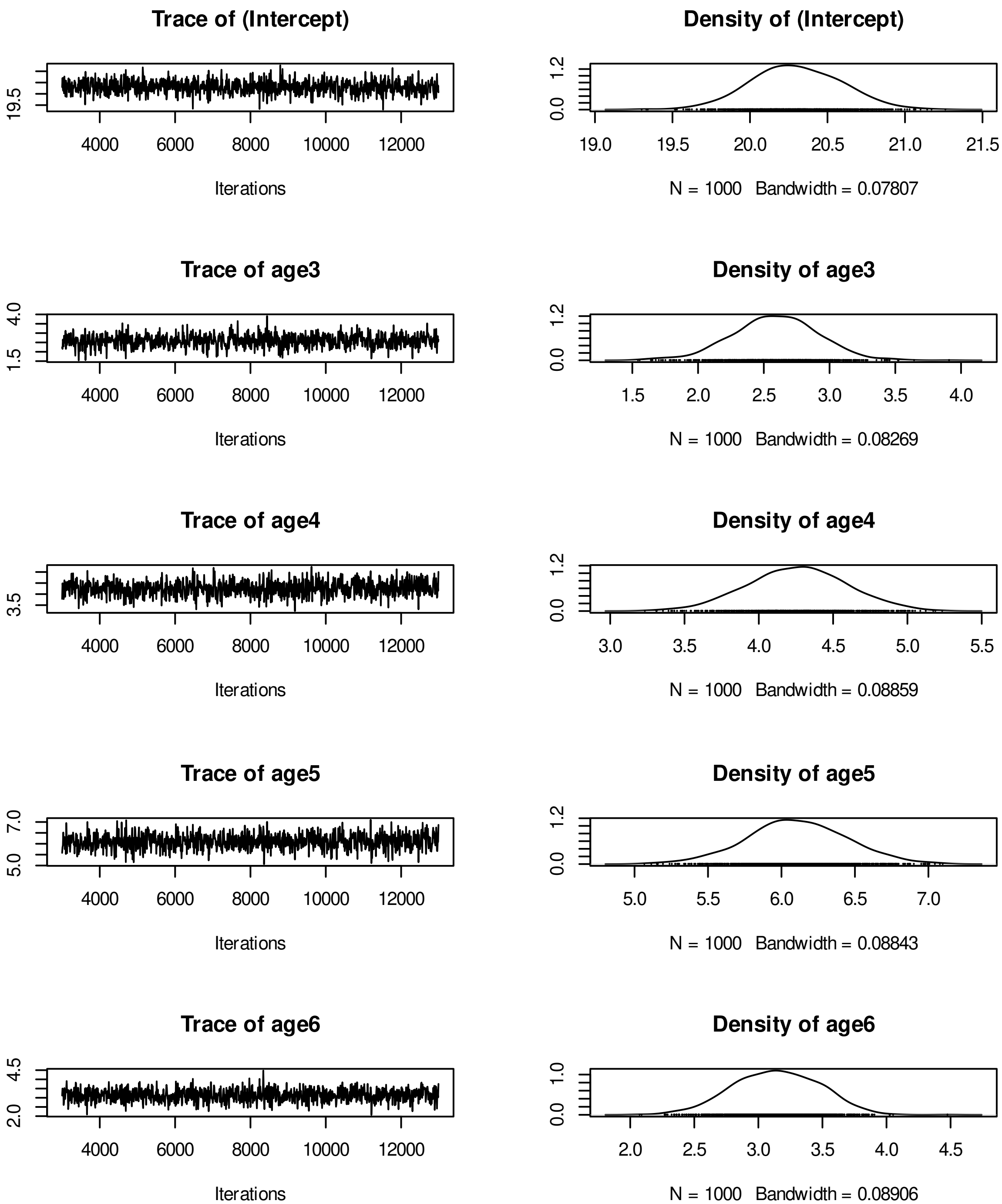



```
posterior.mode(model3.2$VCV)
```

```
##   animal    units
## 12.74460 16.27617
```

The model assumption seems correct, so we can look at the different estimates. Note that the random effect structure has remained unchanged because we did not modified the prior `prior3.1`. The repeatability of `laydate`, after accounting for age effects, is now estimated as 22.22 (*i.e.*, as 11.141/(11.141 + 21.22)). Just as we saw when estimating h_2 in tutorial 1, the inclusion of fixed effects will alter the estimated effect size if we determine total phenotypic variance as the sum of the variance components. Thus, proper interpretation is vital.

```
plot(model3.2$Sol)
```


Trace of (Intercept)
19.5
4000 6000 8000 10000 12000
Iterations
Density of (Intercept)
0.0 1.2
19.0 19.5 20.0 20.5 21.0 21.5
N = 1000 Bandwidth = 0.07807
Trace of age3
1.5 4.0
4000 6000 8000 10000 12000
Iterations
Density of age3
0.0 1.2
1.5 2.0 2.5 3.0 3.5 4.0
N = 1000 Bandwidth = 0.08269
Trace of age4
3.5
4000 6000 8000 10000 12000
Iterations
Density of age4
0.0 1.2
3.0 3.5 4.0 4.5 5.0 5.5
N = 1000 Bandwidth = 0.08859
Trace of age5
5.0 7.0
4000 6000 8000 10000 12000
Iterations
Density of age5
0.0 1.2
5.0 5.5 6.0 6.5 7.0
N = 1000 Bandwidth = 0.08843
Trace of age6
2.0 4.5
4000 6000 8000 10000 12000
Iterations
Density of age6
0.0 1.0
2.0 2.5 3.0 3.5 4.0 4.5
N = 1000 Bandwidth = 0.08906

```r
posterior.mode(model3.2$Sol)
```

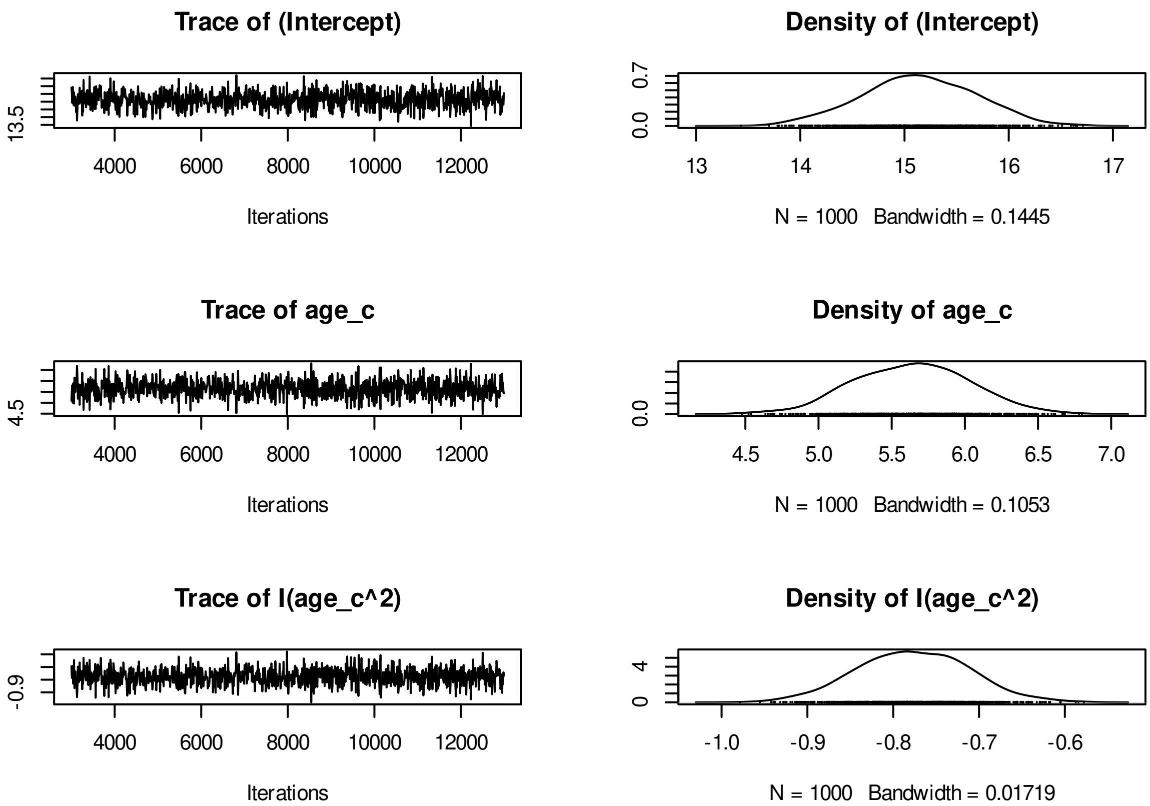
```
## (Intercept)       age3       age4       age5       age6
##   20.169385   2.492732   4.327622   5.998775   3.123463
```

```r
HPDinterval(model3.2$Sol, 0.95)
```

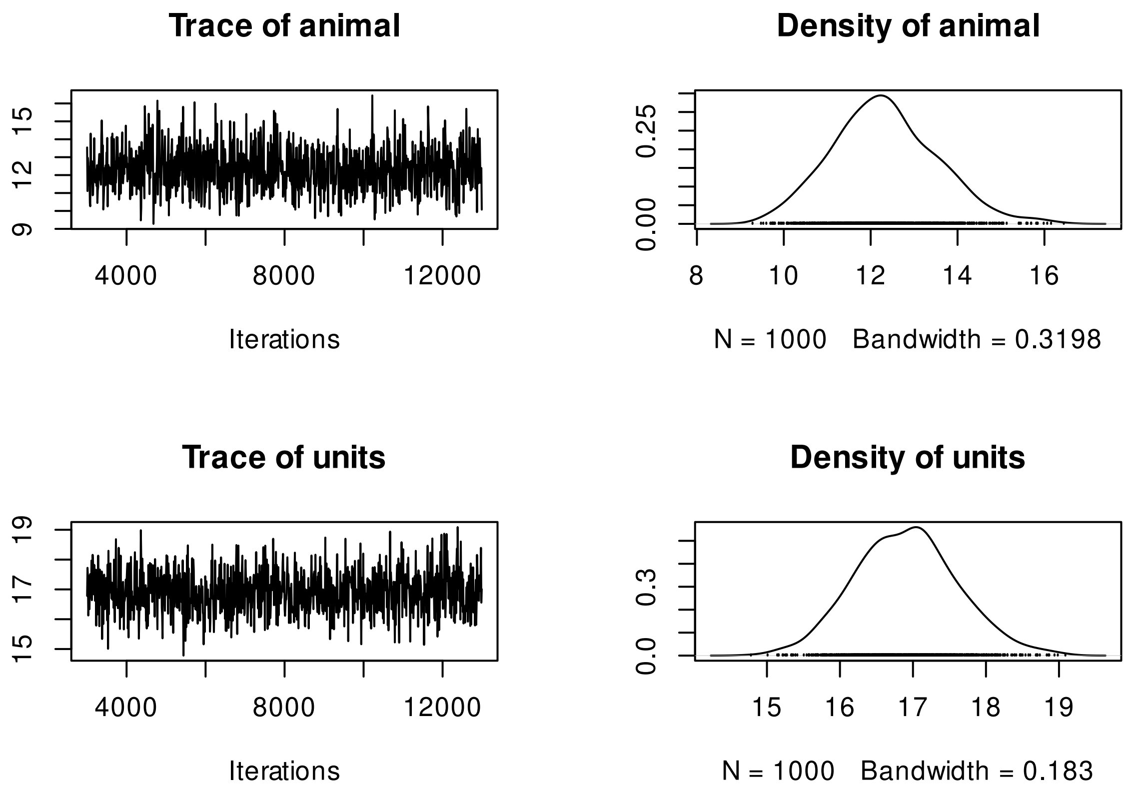
```
##                 lower     upper
## (Intercept) 19.728159 20.862694
## age3         1.928464  3.201445
## age4         3.640339  4.940057
## age5         5.444036  6.778223
## age6         2.554508  3.825944
## attr(,"Probability")
## [1] 0.95
```

Here age is modeled as a 5-level factor (specified using the function `as.factor()` at the beginning of the analysis). We could equally have fitted it as a continuous variable, in which case, given potential for a late life decline, we would probably also include a quadratic term. In addition, using `age` as continuous variable can help in saving some degree of freedom in the analysis.

```r
gryphonRM$age_c <- as.numeric(gryphonRM$age)

model3.2_2 <- MCMCglmm(laydate ~ age_c + I(age_c^2),
  random = ~animal, data = gryphonRM,
  prior = prior3.1, verbose = FALSE
)
plot(model3.2_2$Sol)
```




```
plot(model3.2_2$VCV)
```




```r
posterior.mode(model3.2_2$VCV)
```

```
##   animal    units
## 11.47883 17.00732
```

```r
posterior.mode(model3.2_2$Sol)
```

```
## (Intercept)       age_c  I(age_c^2)
##   15.126910    5.696353   -0.783416
```

```r
HPDinterval(model3.2_2$Sol, 0.95)
```

```
##                 lower      upper
## (Intercept) 13.986362 16.0715658
## age_c        4.976011  6.5004344
## I(age_c^2)  -0.907706 -0.6549909
## attr(,"Probability")
## [1] 0.95
```

4.4.2 Partitioning additive and permanent environment effects

Generally we expect that the repeatability will set the upper limit for heritability since among individual variation can be decomposed in the additive genetic variation and non additive genetic variation. In other word, the additive genetic variation is a subcomponent of the difference between individuals. Non-additive contributions to fixed among-individual differences are normally referred to as *permanent environment effects*. If a trait has repeated measures then it is necessary to model permanent environment effects in an animal model to prevent upward bias in V_A.

To illustrate it, we first fit the animal model:

```
Ainv <- inverseA(gryphonped)$Ainv
model3.3 <- MCMCglmm(laydate ~ 1 + age,
  random = ~animal, ginv = list(animal = Ainv),
  data = gryphonRM, prior = prior3.1, verbose = FALSE
)
```

Variance components are almost unchanged if we compare the previous model:

```
posterior.mode(model3.3$VCV)
```

```
##   animal    units
## 13.36499 16.93964
```

```
posterior.mode(model3.2$VCV)
```

```
##   animal    units
## 12.74460 16.27617
```

This suggests that most of the among-individual variance is – rightly or wrongly – being partitioned as V_A here. In fact here the partition is wrong since the simulation included both additive genetic effects and additional fixed heterogeneity that was not associated with the pedigree structure (i.e. permanent environment effects). In order to o obtain an unbiased estimate of V_A, we need to fit the individual identity twice in the model: once linked to the pedigree (genetic effect) and once not linked to the pedigree (permanent environment effect).To do so, we need to duplicate the variable containing the individual identity `animal` and give it a new name. In addition, the prior need to be modified to integrate a seconf random effect.An more appropriate estimate of V_A is given by the model:

```
gryphonRM$animal_pe <- gryphonRM$animal
# p.var <- var(gryphonRM$laydate, na.rm = TRUE)
prior3.4 <- list(G = list(G1 = list(V = 1, nu = 0.002), G2 = list(
  V = 1,
  nu = 0.002
)), R = list(V = 1, nu = 0.002))
model3.4 <- MCMCglmm(laydate ~ 1 + age,
```

```
  random = ~ animal + animal_pe,
  ginv = list(animal = Ainv), data = gryphonRM, prior = prior3.4, verbose = FALSE
)
posterior.mode(model3.4$VCV)
```

```
##    animal animal_pe     units
##  4.159477  7.576943 16.219255
```

The estimate ofV_A is now much lower (reduced from 13.6735 to 5.1238) due to a proper separation in the additive and permanent environment effects. We can estimate h^2 and the repeatability from this model:

```
model3.4.VP <- model3.4$VCV[, "animal"] + model3.4$VCV[, "animal_pe"] + model3.4$VCV[, "un
model3.4.PE_VA <- model3.4$VCV[, "animal"] + model3.4$VCV[, "animal_pe"]
posterior.mode(model3.4.PE_VA / model3.4.VP)
```

```
##      var1
## 0.4135483
```

```
posterior.mode(model3.4$VCV[, "animal"] / model3.4.VP)
```

```
##     var1
## 0.169229
```

4.4.3 Adding additional effects and testing significance

Models of repeated measures can be extended to include other fixed or random effects. For example we can try including year of measurement (`year`) and birth year (`byear`) as other random effects.

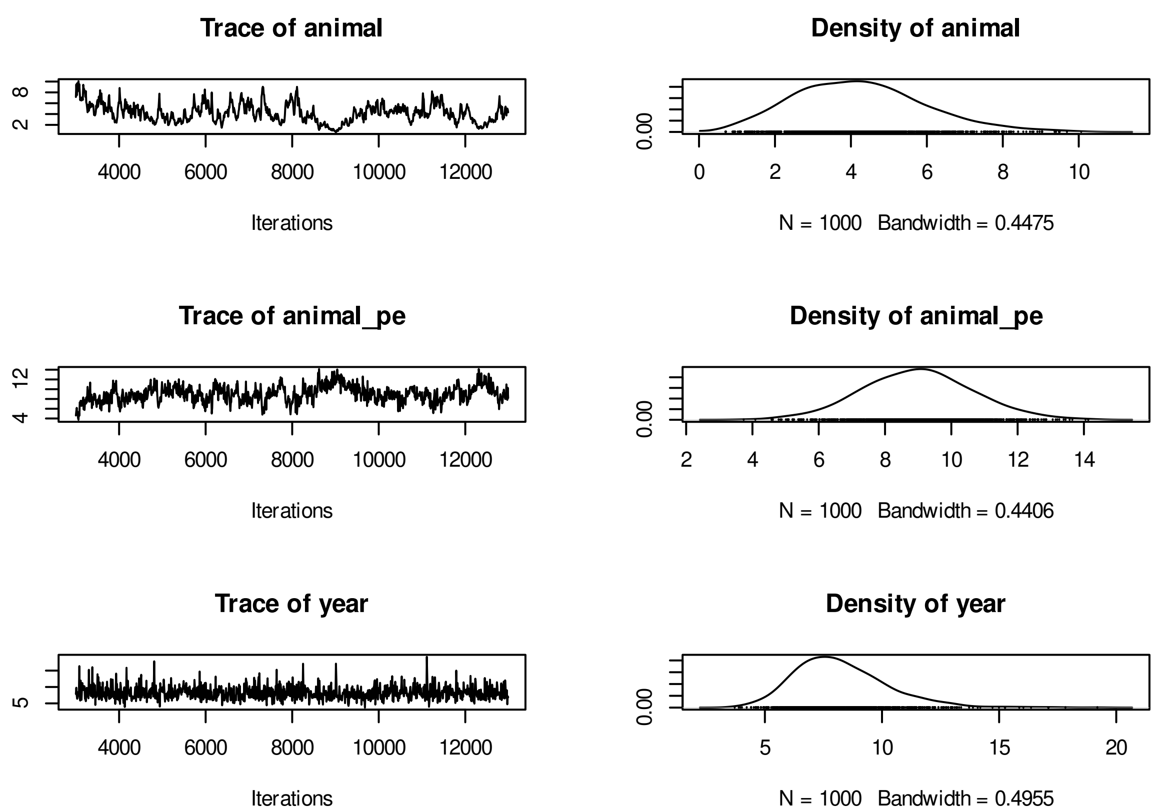
```
# p.var <- var(gryphonRM$laydate, na.rm = TRUE)
prior3.5 <- list(G = list(G1 = list(V = 1, nu = 0.002), G2 = list(
  V = 1,
  nu = 0.002
), G3 = list(V = 1, nu = 0.002), G4 = list(
  V = 1,
  nu = 0.002
)), R = list(V = 1, nu = 0.002))

model3.5 <- MCMCglmm(laydate ~ 1 + age,
  random = ~ animal + animal_pe +
    year + byear, ginv = list(animal = Ainv), data = gryphonRM, prior = prior3.5,
  verbose = FALSE
)
posterior.mode(model3.5$VCV)
```

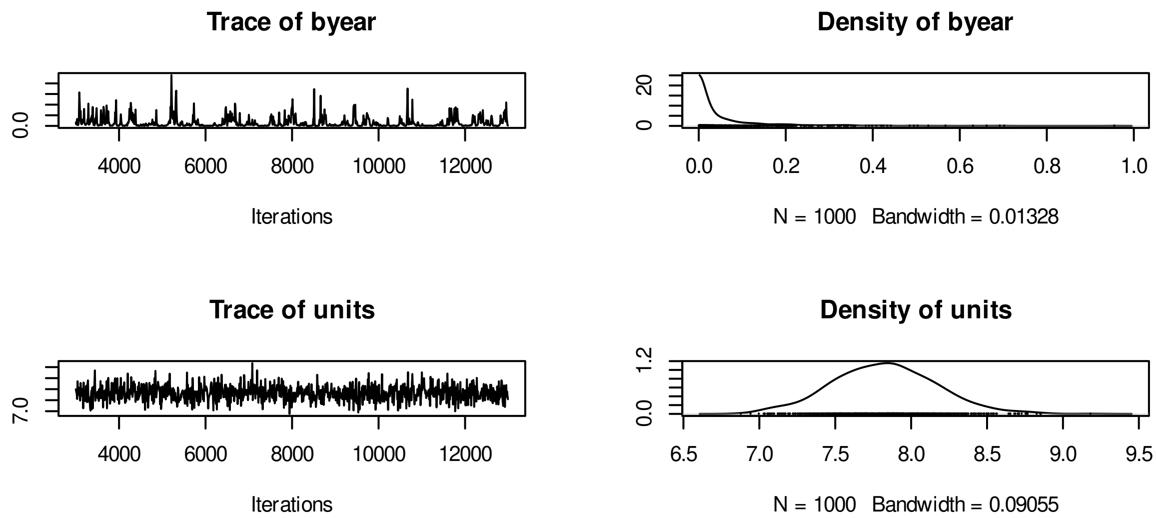
```
##      animal   animal_pe        year       byear       units
## 3.265010495 8.924558498 7.557087451 0.002605666 7.884707995
```

```r
HPDinterval(model3.5$VCV, 0.95)
```

```
##                  lower      upper
## animal    0.8798128012  7.3118109
## animal_pe 5.7782140304 12.3829408
## year      4.5928409666 12.1586746
## byear     0.0003427203  0.2808403
## units     7.1211681107  8.4819224
## attr(,"Probability")
## [1] 0.95
```

```r
plot(model3.5$VCV)
```





This model will return additional variance components corresponding to year of measurement effects and birth year of the female effects.

V_{byear} is very low and its posterior distribution (via the function `HPDinterval` or `plot`) is very close to zero indicating its not significance. You have to remember bayesian model never estimate variable to 0 or passing zero, so you will never see a credible interval `CI` crossing zero for a variance. If you compared the DIC of model3.5 to a reduced model without `byear`, it should be very similar.

```
prior3.5_2 <- list(
  G = list(G1 = list(V = 1, nu = 0.002), G2 = list(
    V = 1,
    nu = 0.002
  ), G3 = list(V = 1, nu = 0.002)),
  R = list(V = 1, nu = 0.002)
)

model3.5_2 <- MCMCglmm(laydate ~ 1 + age,
  random = ~ animal + animal_pe +
    year, ginv = list(animal = Ainv), data = gryphonRM, prior = prior3.5_2,
  verbose = FALSE
)
posterior.mode(model3.5_2$VCV)
```

```
##     animal animal_pe      year     units
```

```
## 3.774539 8.762062 7.215465 7.813281
```

```
model3.5$DIC
```

```
## [1] 8291.123
```

```
model3.5_2$DIC
```

```
## [1] 8290.812
```

`year` effects could alternatively be included as fixed effects (try it!, you should be able to handle the new prior specification at this point). This will reduce V_R and increase the estimates of heritability and repeatability, which must now be interpreted as proportions of phenotypic variance after conditioning on both age and year of measurement effects.

4.5 brms

```
library(brms)

Amat <- as.matrix(nadiv::makeA(gryphonped))
gryphonRM$animal_pe <- gryphonRM$animal



model_simple1.1 <- brm(
  laydate ~ 1 + (1 | gr(animal, cov = Amat)) + (1 | animal_pe),
  data = gryphonRM,
  family = gaussian(),
  data2 = list(Amat = Amat),
  chains = 2, cores = 2, iter = 1000
)

summary(model_simple1.1)
plot(model_simple1.1)
```

4.6 stan

to do

Chapitre 5

Quick comparison of codes

5.1 Univariate model with repeated measures

5.1.1 Asreml-R

5.1.2 gremlin

5.1.3 MCMCglmm

5.1.4 brms

5.2 bivariate model

5.2.1 Asreml-R

5.2.2 gremlin

5.2.3 MCMCglmm

5.2.4 brms