

How to fit an animal model

An ecologist guide

Julien Martin & Mathieu Videlier



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Preface

This book is a collection of tutorial from the excellent paper by (Wilson et al. 2010). The tutorials have been updated to work with the latest version of the softwares, extended with extra information and other softwares have been added. Eric Postma kindly provided an updated version of the original asreml-r tutorial from asreml-r v3 to asreml-r v4.

This is a living document and information is updated/added regularly

Citing the book

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Image credit

The cover image was generated by Julien Martin using the Nightcafe AI image generator using the call “Family tree of legendary beast”.

Who are we ?



Julien Martin is a Professor at the University of Ottawa working on Evolutionary Ecology and has discovered R with version 1.8.1 and teaches R since v2.4.0. He developed the first version of the book in February 2021 and now continues to develop the book and maintains the site for all languages (currently only english but french and spanish comin soon).

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Mathieu Videlier is currently a postdoctoral fellow collaborating with [Pr. Jacqueline Sztepanacz](#) at University of Toronto. In joined the project in May 2021 . He added and continues to add more details in the document. He is also spearheading the translation fo French and Spanish.

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- : [BioBipbip](#)
- : [MathieuVID](#)

Hex Sticker



Chapter 1

Introduction

The book 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](#) We 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/~bkingham/pedigree.htm>. pedtricks an R package deveopped by ([pedtricks?](#)) and distributed through [CRAN](#) 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 pedtricks.

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](#)

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 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 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: (Hadfield 2010).

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 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://devillemerueil.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**.

Part I.

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.

Scenario and data

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.

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 751 987 490 906 591 ...
 $ mother: Factor w/ 429 levels "1","2","3","8",...: 362 268 216 375 396 289 328 255 347 240 ...
 $ 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 ...
 $ mother: int 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 1283 1282 ...
 $ father: Factor w/ 158 levels "4","13","18",...: NA ...
 $ mother: Factor w/ 429 levels "1","2","3","8",...: NA ...
```

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

Chapter 2

Asreml-R

2.0.1. Running the model

First we need to load the `asreml` library:

```
library(asreml)
```

```
Loading required package: Matrix
```

```
Online License checked out Tue Oct  8 11:02:02 2024
```

```
Loading ASReml-R version 4.2
```

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")  
)
```

ASReml Version 4.2 08/10/2024 11:02:03

	LogLik	Sigma2	DF	wall
1	-4128.454	1.0	853	11:02:03
2	-3284.272	1.0	853	11:02:03
3	-2354.992	1.0	853	11:02:03
4	-1710.357	1.0	853	11:02:03
5	-1363.555	1.0	853	11:02:03
6	-1263.516	1.0	853	11:02:03
7	-1247.854	1.0	853	11:02:03
8	-1247.185	1.0	853	11:02:03
9	-1247.183	1.0	853	11:02:03

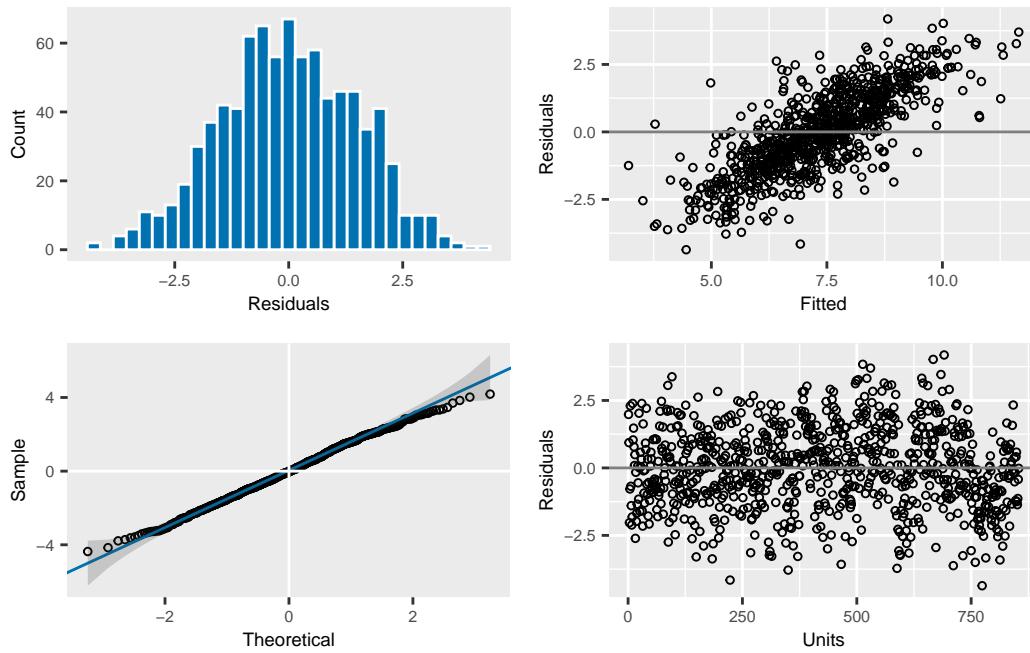
In this model, `bwt` is the response variable and the only fixed effect is the intercept, denoted as 1. The only random effect we have fitted is `animal`, which will provide an estimate of V_A . Our random `animal` effect is connected to the inverse related matrix `ainv` which integrate the relatedness or pedigree information.

`data=` specifies the name of the dataframe that contains our variables. Finally, we inform `asreml()` what to do when it encounters NAs 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 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 plotted which help visualizing the distribution of the model residual and check the different assumptions.

```
plot(model1)
```



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

```
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

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.

2.0.2. 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	0.0765088

2.0.3. 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")  
)
```

ASReml Version 4.2 08/10/2024 11:02:04

	LogLik	Sigma2	DF	wall
1	-3364.126	1.0	852	11:02:04
2	-2702.117	1.0	852	11:02:04
3	-1978.916	1.0	852	11:02:04
4	-1487.834	1.0	852	11:02:04
5	-1236.350	1.0	852	11:02:04
6	-1172.771	1.0	852	11:02:04
7	-1165.270	1.0	852	11:02:04
8	-1165.093	1.0	852	11:02:04
9	-1165.093	1.0	852	11:02:04

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

```
      solution std.error z.ratio
(Intercept) 6.058669 0.1718244 35.26082
sex_1        0.000000       NA       NA
sex_2        2.206996 0.1619974 13.62365
```

ASReml Version 4.2 08/10/2024 11:02:05

	LogLik	Sigma2	DF	wall
1	-1165.093	1.0	852	11:02:05
2	-1165.093	1.0	852	11:02:05

\$Wald

	Df	denDF	F.inc	F.con	Margin	Pr
(Intercept)	1	251	3491.0	3491.0		0
sex	1	831	185.6	185.6	A	0

\$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 (± 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

component	std.error	z.ratio	bound	%ch

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	0.0765088

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

	Estimate	SE
h2.bwt	0.510171	0.0743239

Here h^2 has increased slightly from || Estimate| :——|——:| |h2.bwt | 0.47| to || Estimate| :——|——:| |h2.bwt | 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).

2.0.4. Adding random effects

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

```

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

```

ASReml Version 4.2 08/10/2024 11:02:05

	LogLik	Sigma2	DF	wall
1	-2742.658	1.0	852	11:02:05
2	-2237.268	1.0	852	11:02:05
3	-1690.453	1.0	852	11:02:05
4	-1328.910	1.0	852	11:02:05
5	-1154.597	1.0	852	11:02:05
6	-1116.992	1.0	852	11:02:05
7	-1113.809	1.0	852	11:02:05
8	-1113.772	1.0	852	11:02:05
9	-1113.772	1.0	852	11:02:05

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

	component	std.error	z.ratio	bound	%ch
byear	0.8862604	0.2695918	3.287415	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

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

	Estimate	SE
h2.bwt	0.4586068	0.0674036

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:

```
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")
)
```

ASReml Version 4.2 08/10/2024 11:02:05

	LogLik	Sigma2	DF	wall
1	-2033.178	1.0	852	11:02:05
2	-1723.734	1.0	852	11:02:05
3	-1396.354	1.0	852	11:02:05
4	-1193.012	1.0	852	11:02:05
5	-1107.946	1.0	852	11:02:05
6	-1095.327	1.0	852	11:02:05
7	-1094.816	1.0	852	11:02:05
8	-1094.815	1.0	852	11:02:05

```
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

	component	std.error	z.ratio	bound	%ch
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	0.0386155

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).

2.0.5. 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.

2.0.6. 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")
)

```

ASReml Version 4.2 08/10/2024 11:02:05

	LogLik	Sigma2	DF	wall
1	-1142.164	1.0	852	11:02:05
2	-1126.308	1.0	852	11:02:06
3	-1111.536	1.0	852	11:02:06
4	-1105.383	1.0	852	11:02:06
5	-1104.375	1.0	852	11:02:06
6	-1104.364	1.0	852	11:02:06

```
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 ($|h2.bwt| = 0.25$ and $|h2.bwt| = 0.33$), 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 = "", c
arrows(y0 = 0.95, x0 = h2.sex[1, 1] - h2.sex[1, 2], y1 = 0.95, x1 = h2.sex[1, 1] + h2.sex[1, 2],
arrows(y0 = 1.05, x0 = h2.sex[2, 1] - h2.sex[2, 2], y1 = 1.05, x1 = h2.sex[2, 1] + h2.sex[2, 2],
mtext("Narrow-sense heritability ( $\pm$ 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)

```

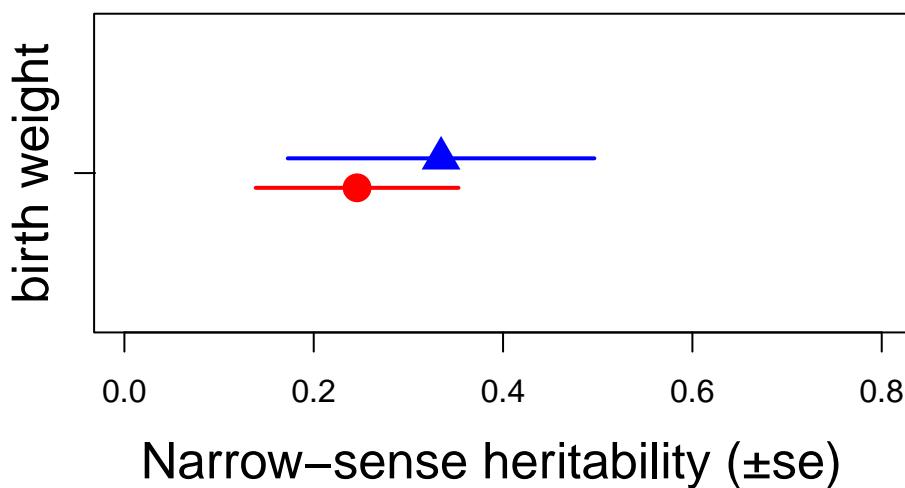


Figure 2.1.: Female and male heritability of birth weight

2.0.7. 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
)
```

ASReml Version 4.2 08/10/2024 11:02:06

	LogLik	Sigma2	DF	wall
1	-2033.178	1.0	852	11:02:06
2	-1723.734	1.0	852	11:02:06
3	-1396.354	1.0	852	11:02:06
4	-1193.012	1.0	852	11:02:06
5	-1107.946	1.0	852	11:02:06
6	-1095.327	1.0	852	11:02:06

```

7      -1094.816      1.0     852  11:02:06
8      -1094.815      1.0     852  11:02:06

```

```
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.

2.0.8. 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

```

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.

Chapter 3

MCMCglmm

3.0.1. Running the model

First load MCMCglmm:

```
library(MCMCglmm)
```

Loading required package: Matrix

Loading required package: coda

Loading required package: ape

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 $\text{nu}>0$ 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)
```

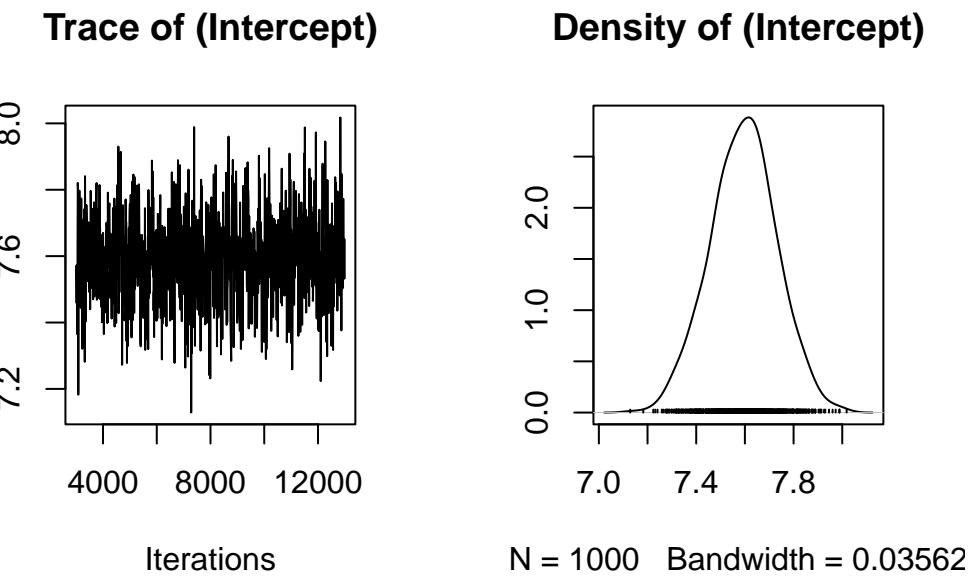


Figure 3.1.: The posterior distribution of the fixed effect (the intercept, or mean) in model 1.1

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)
```

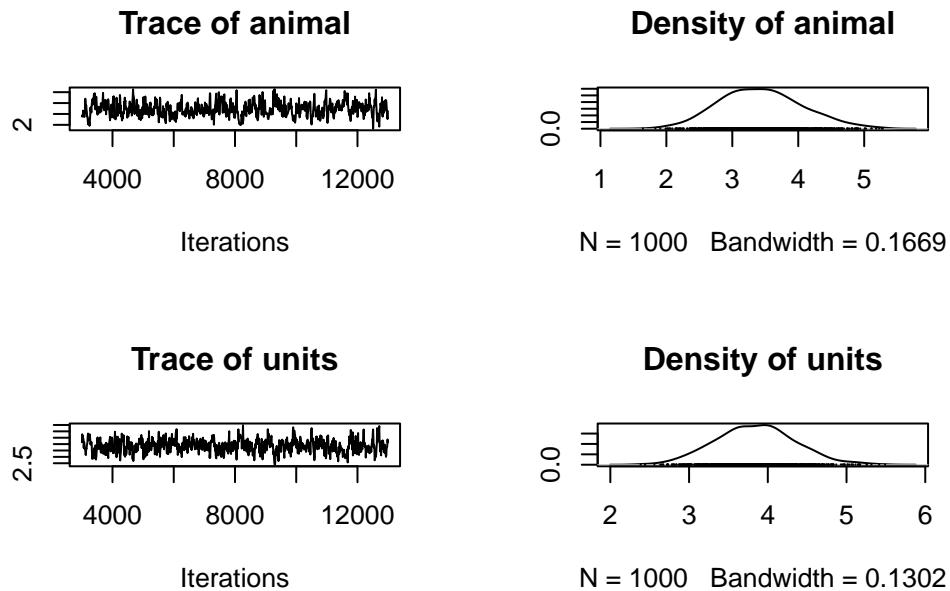


Figure 3.2.: The posterior distributions of the variance components of model 1.1, based on an analysis with the default values for nitt, burnin, and thin in MCMCglmm

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.

3.0.2. 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	1.00000000	1.00000000
Lag 50	0.19000363	0.19720861
Lag 250	0.03080980	0.01546578
Lag 500	-0.01505963	-0.05286184
Lag 2500	-0.01755035	-0.02538836

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
	3.324804	3.789779

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 2.249203 4.764617
units  2.929122 4.923796
attr(,"Probability")
[1] 0.95
```

3.0.3. 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
3.324804 3.789779
```

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

```
animal      units  
3.769996 3.812074
```

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.

3.0.4. 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.herditability1.1 <- model1.1$VCV[, "animal"] /  
(model1.1$VCV[, "animal"] + model1.1$VCV[, "units"])  
  
posterior.mode(posterior.herditability1.1)
```

```
var1  
0.4674414
```

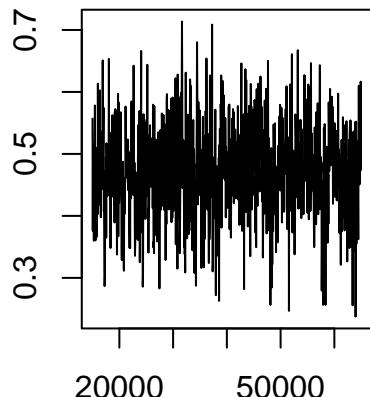
```
HPDinterval(posterior.herditability1.1, 0.95)
```

```
lower      upper  
var1 0.3287511 0.6268801  
attr(,"Probability")  
[1] 0.95
```

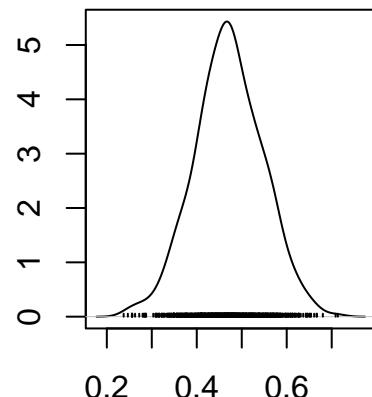
Generate a plot of the posterior distribution of this heritability estimate:

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

Trace of var1



Density of var1



Iterations

N = 1000 Bandwidth = 0.02011

Figure 3.3.: The posterior distributions the heritability from model 1.1

3.0.5. 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: 3717.393

G-structure: ~animal

```
post.mean l-95% CI u-95% CI eff.samp
animal      3.083     2.05    4.016    755.1
```

R-structure: ~units

```
post.mean l-95% CI u-95% CI eff.samp
units      2.944     2.189    3.779    805.6
```

Location effects: bwt ~ sex

```
post.mean l-95% CI u-95% CI eff.samp pMCMC
(Intercept)   6.065    5.760    6.394    1000 <0.001 ***
sex2          2.207    1.849    2.492    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
2.22336
```

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

```
lower      upper
var1 1.849157 2.491577
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  
3.356471  2.875270
```

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  
0.5494853
```

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

```
lower      upper  
var1 0.3719122 0.6471908  
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).

3.0.6. 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
2.7101798	0.8393404	2.3517527

Here the variance in birth weight explained by birth year is 0.84. 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
2.2100541  0.8649762  1.0710032  1.5762728

```

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"] + model1.4$VCV[, "units"])
posterior.mode(posterior.heritability1.2)

```

```

var1
0.5494853

posterior.mode(posterior.heritability1.3)

```

```

var1
0.4500106

```

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

```
var1  
0.3812813
```

3.0.7. 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] 3547.575
```

```
model1.4$DIC
```

```
[1] 3297.787
```

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.

3.0.8. 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 = 1, nu = 0.002)),
  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
0.6470916	2.5074849	0.8829385	1.4621951	2.3933947	1.6630896

```

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
0.1742903

```

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

	lower	upper
var1	0.04975175	0.4445928
attr(,"Probability")		
[1]	0.95	

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

var1
0.2857213

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

	lower	upper
var1	0.08249098	0.6198509
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.heritability1.4.FEM),
  cbind(posterior.mode(posterior.heritability1.4.MAL), HPDinterval(posterior.heritability1.4.MAL,
))

plot(c(0.95, 1.05) ~ h2.sex[, 1], xlim = c(0, 0.8), ylim = c(0.5, 1.5), , xlab = "", ylab = "", c
arrows(y0 = 0.95, x0 = h2.sex[1, 2], y1 = 0.95, x1 = h2.sex[1, 3], code = 3, angle = 90, length =
arrows(y0 = 1.05, x0 = h2.sex[2, 2], y1 = 1.05, x1 = h2.sex[2, 3], code = 3, angle = 90, length =
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)
```

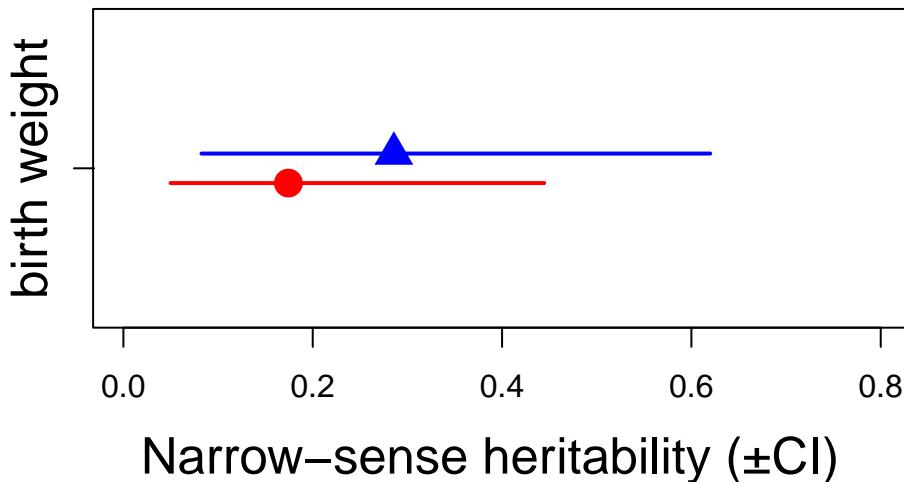


Figure 3.4.: Female and male heritability of birth weight

3.0.9. Modification of model parameter

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

3.0.10. 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

```
prior1.5 <- list(
  G = list(G1 = list(V = diag(2), nu = 0.002)),
  R = list(V = 1, nu = 0.002)
)

model1.5 <- MCMCglmm(bwt ~ sex,
  random = ~ str(animal + mother), ginv = list(animal = Ainv),
  rcov = ~ idh(1):units,
```

```
data = gryphon, nitt = 65000, thin = 50, burnin = 15000,  
prior = prior1.5, verbose = FALSE  
)  
  
posterior.mode(model1.5$VCV)
```

Chapter 4

brms

4.0.1. Running the model

First we need to load the `brms` library:

```
library(brms)
```

Loading required package: Rcpp

Loading 'brms' package (version 2.21.0). Useful instructions
can be found by typing `help('brms')`. A more detailed introduction
to the package is available through `vignette('brms_overview')`.

Attaching package: 'brms'

The following object is masked from 'package:stats':

ar

To be able to fit an animal model, `brms` needs the relativity (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 relativity. 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), `cores` 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>)

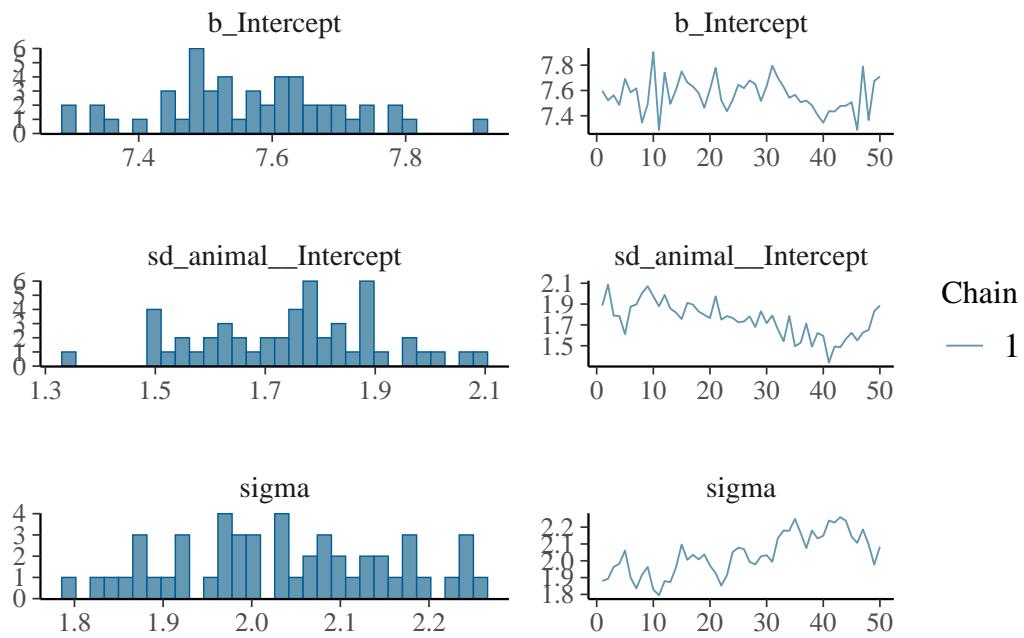
`bmrs` is a Bayesian Multilevel Models using Stan, doing so we can apply a prior to the model to better shape the distribution of the different variances estimated by the model. Given that `bmrs` fit the model using a Bayesian approach via the software `stan`, we need to specify priors for the model. 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")
```

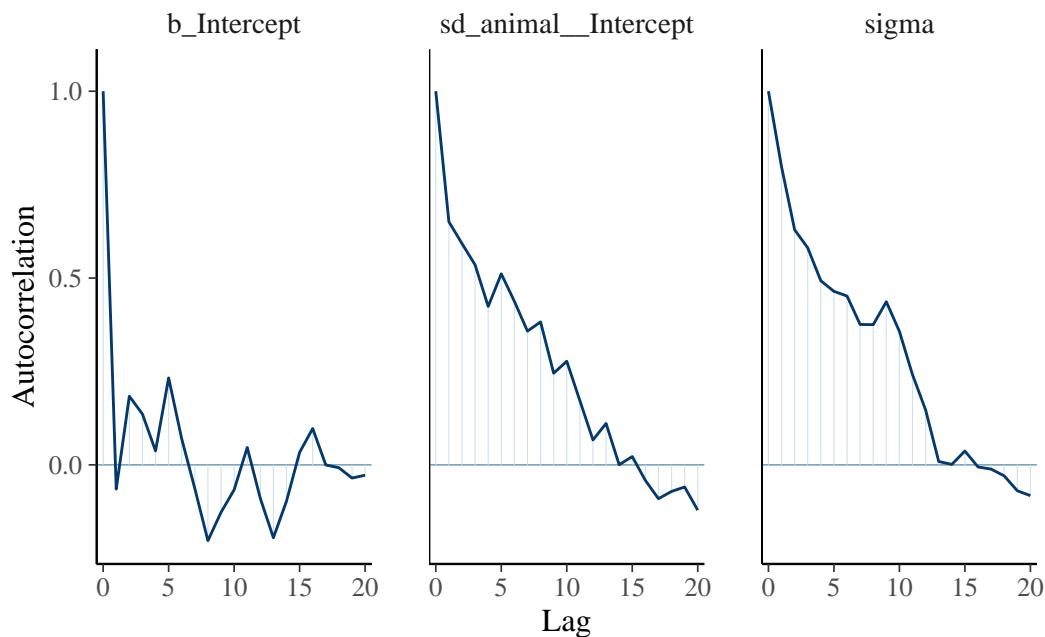
The result of the long model calculation is save in a spare file `brms_m1_1.rda`. To help readers, we can directly reloading it. Two distinct plot can be produce to produce some diagnostics graphs `mcmc_plot`. Note, that `sigma` represents the residual standard deviation.

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")
```



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

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: gaussian

```
Links: mu = identity; sigma = identity
Formula: bwt ~ 1 + (1 | gr(animal, cov = Amat))
Data: gryphon (Number of observations: 854)
Draws: 1 chains, each with iter = 100; warmup = 50; thin = 1;
      total post-warmup draws = 50
```

Multilevel Hyperparameters:

~animal (Number of levels: 1084)

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(Intercept)	1.75	0.17	1.49	2.06	1.55	2	20

Regression Coefficients:

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
Intercept	7.57	0.13	7.30	7.79	1.00	27	63

Further Distributional Parameters:

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sigma	2.04	0.12	1.83	2.25	1.68	2	20

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’

```

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 = 1:50
 Thinning interval = 1
 Number of chains = 1
 Sample size per chain = 50

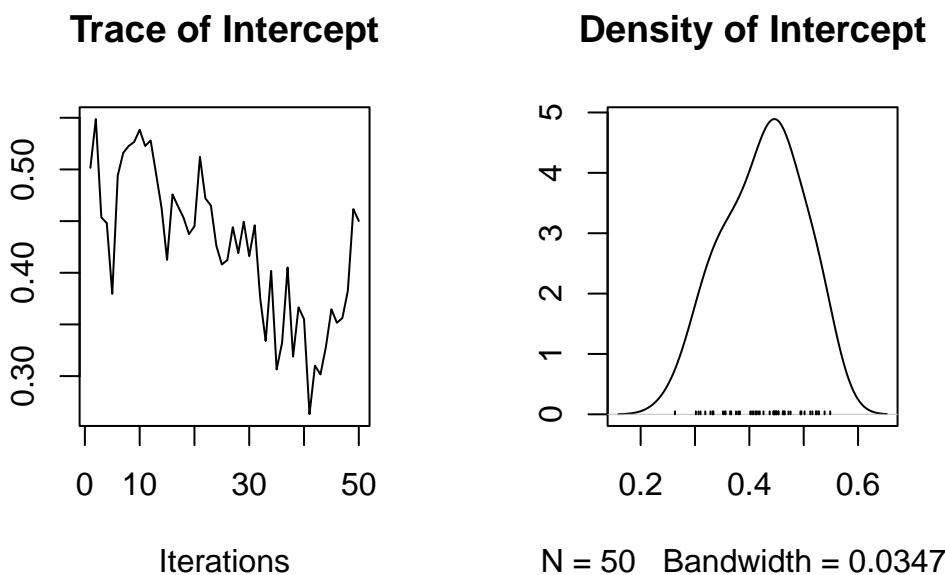
1. Empirical mean and standard deviation for each variable,
plus standard error of the mean:

Mean	SD	Naive SE	Time-series SE
0.42526	0.07162	0.01013	0.02854

2. Quantiles for each variable:

2.5% 25% 50% 75% 97.5%
 0.3027 0.3687 0.4408 0.4702 0.5361

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



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_Intercept)^2 + Var.table\$sd_error)^2)

Iterations = 1:50

Thinning interval = 1

Number of chains = 1

Sample size per chain = 50

1. Empirical mean and standard deviation for each variable,

plus standard error of the mean:

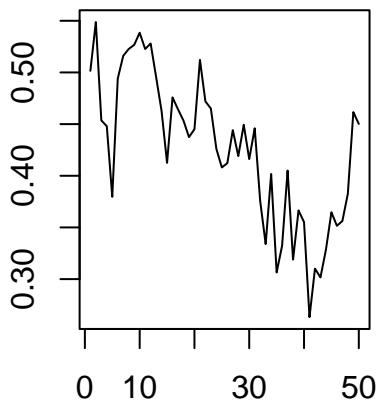
Mean	SD	Naive SE	Time-series SE
0.42526	0.07162	0.01013	0.02854

2. Quantiles for each variable:

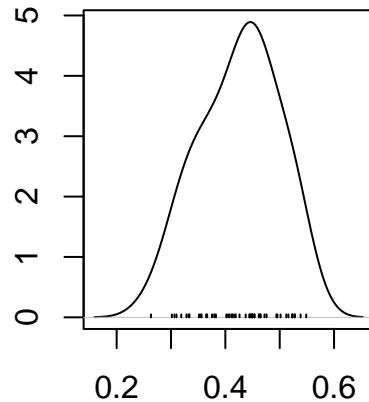
2.5% 25% 50% 75% 97.5%

0.3027 0.3687 0.4408 0.4702 0.5361

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

Trace of var1

Iterations

Density of var1

N = 50 Bandwidth = 0.03472

4.0.2. 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)
```

```
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
```

Multilevel Hyperparameters:

```
~animal (Number of levels: 1084)  
Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS  
sd(Intercept)     1.67      0.14     1.39     1.97 1.02      93     120
```

Regression Coefficients:

```
Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
```

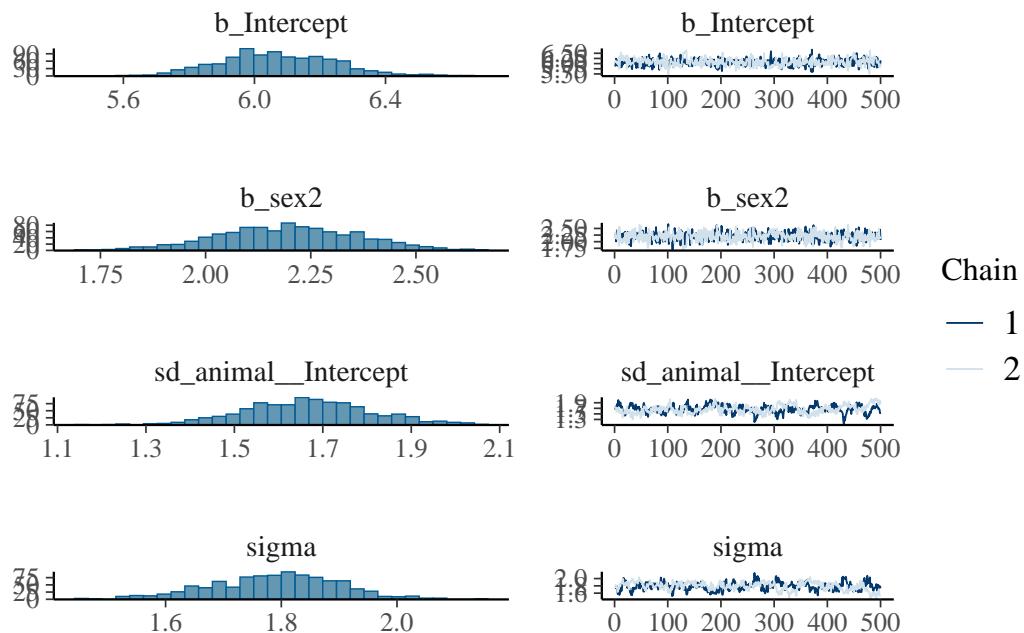
Intercept	6.07	0.18	5.75	6.43	1.00	616	451
sex2	2.20	0.17	1.87	2.52	1.00	749	502

Further Distributional Parameters:

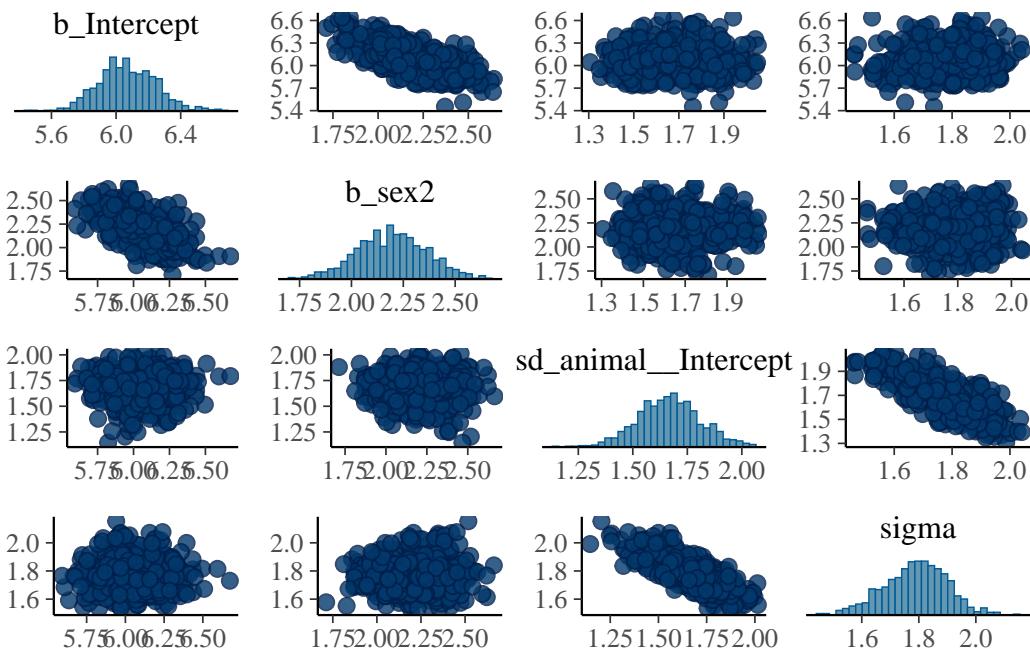
	Estimate	Est.Error	l-95%	CI	u-95%	CI	Rhat	Bulk_ESS	Tail_ESS
sigma	1.79	0.11	1.56		1.99	1.03	1.00	96	119

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)
```



```
mcmc_trace(brms_m1.2, type = "pairs")
```



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

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
Intercept	6.071245	0.1774787	5.748606	6.428933	1.001657	615.7726	451.3620
sex2	2.195386	0.1667400	1.872125	2.518738	1.002985	749.4558	502.4438

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

\$animal

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(Intercept)	1.667668	0.1442392	1.393627	1.967308	1.023006	93.37621	119.8231

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:

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

\$animal

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(Intercept)	1.667668	0.1442392	1.393627	1.967308	1.023006	93.37621	119.8231

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.

```
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
0.464637	0.068645	0.002171	0.007561

2. Quantiles for each variable:

2.5%	25%	50%	75%	97.5%
0.3375	0.4183	0.4620	0.5089	0.6030

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

```
Iterations = 1:50  
Thinning interval = 1
```

```
Number of chains = 1
Sample size per chain = 50
```

1. Empirical mean and standard deviation for each variable,
plus standard error of the mean:

Mean	SD	Naive SE	Time-series SE
0.42526	0.07162	0.01013	0.02854

2. Quantiles for each variable:

```
2.5%    25%    50%    75%   97.5%
0.3027  0.3687  0.4408  0.4702  0.5361
```

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).

4.0.3. 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:

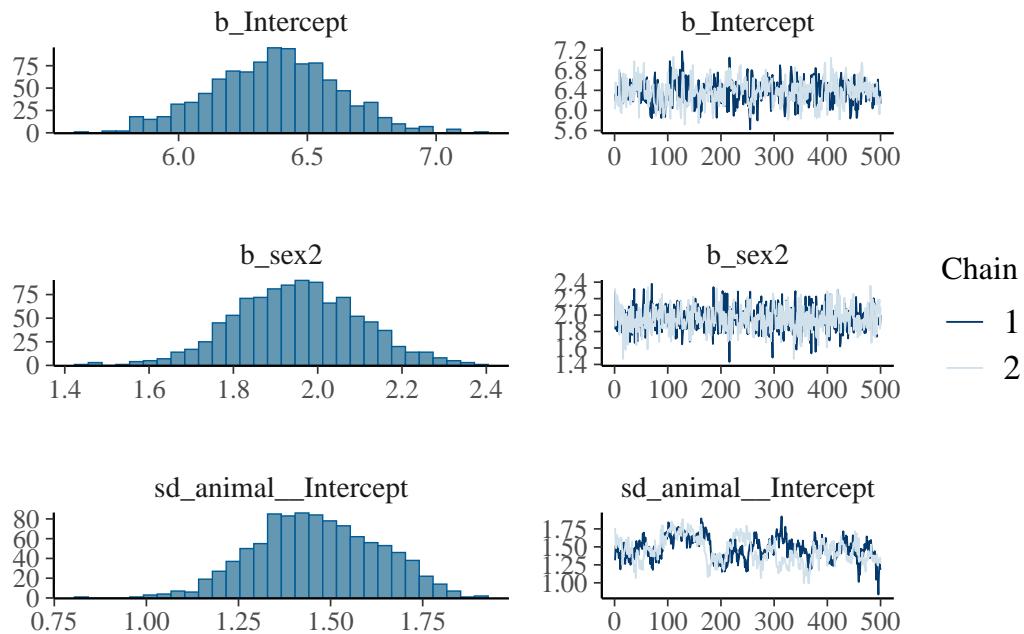
```
brms_m1.3 <- brm(
  bwt ~ 1 + sex + (1 | gr(animal, cov = Amat)) + (1 | byear) + (1 | mother),
  data = gryphon,
  data2 = list(Amat = Amat),
  family = gaussian(),
  chains = 2, cores = 2, iter = 1000
)
```

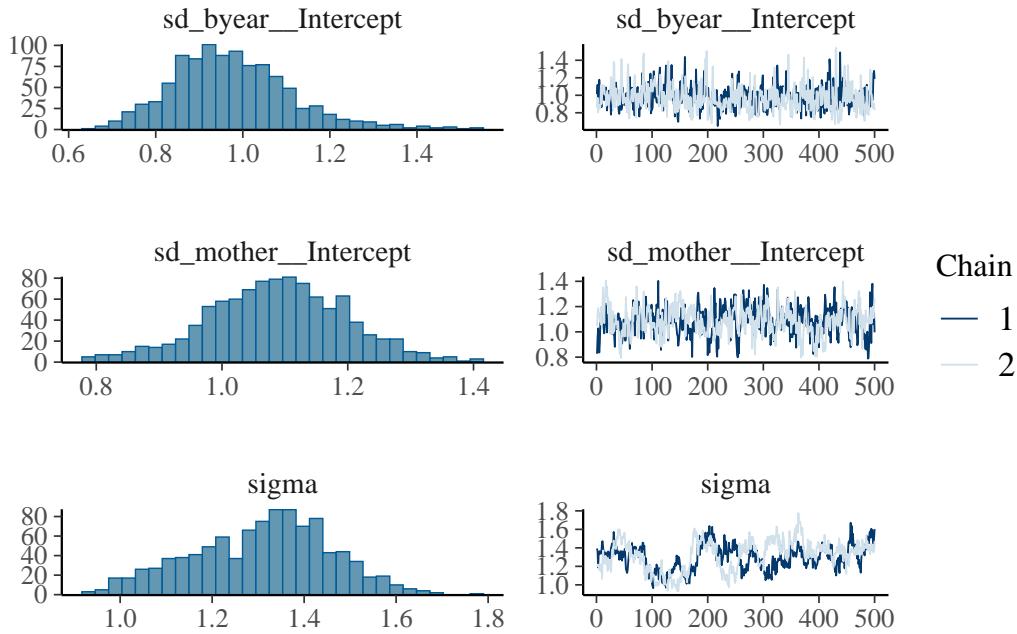
```
save(brms_m1.3, file = "data/brms_m1_3.rda")
```

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)
```

Warning: Argument 'N' is deprecated. Please use argument 'nvariables' instead.





```
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	1-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(Intercept)	1.462757	0.1673822	1.153225	1.768881	1.079817	32.11486	156.8095

\$byear

	Estimate	Est.Error	1-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(Intercept)	0.9767418	0.140156	0.7415211	1.306467	1.007016	469.316	407.5334

\$mother

	Estimate	Est.Error	1-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(Intercept)	1.086973	0.1107873	0.8507715	1.296683	1.001921	228.2474	380.5216

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
0.356562	0.073890	0.002337	0.010196

2. Quantiles for each variable:

```
2.5%    25%    50%    75%  97.5%  
0.2208 0.3042 0.3517 0.4111 0.5045
```

```
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
0.464637	0.068645	0.002171	0.007561

2. Quantiles for each variable:

```
2.5%    25%    50%    75%  97.5%
0.3375 0.4183 0.4620 0.5089 0.6030
```

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

```
Iterations = 1:50
```

```
Thinning interval = 1
```

```
Number of chains = 1
```

```
Sample size per chain = 50
```

1. Empirical mean and standard deviation for each variable,
plus standard error of the mean:

Mean	SD	Naive SE	Time-series SE
0.42526	0.07162	0.01013	0.02854

2. Quantiles for each variable:

```
2.5%    25%    50%    75%  97.5%
0.3027 0.3687 0.4408 0.4702 0.5361
```

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_Intercept)^2 + Var.table\$sd_error)^2)

Iterations = 1:1000
 Thinning interval = 1
 Number of chains = 1
 Sample size per chain = 1000

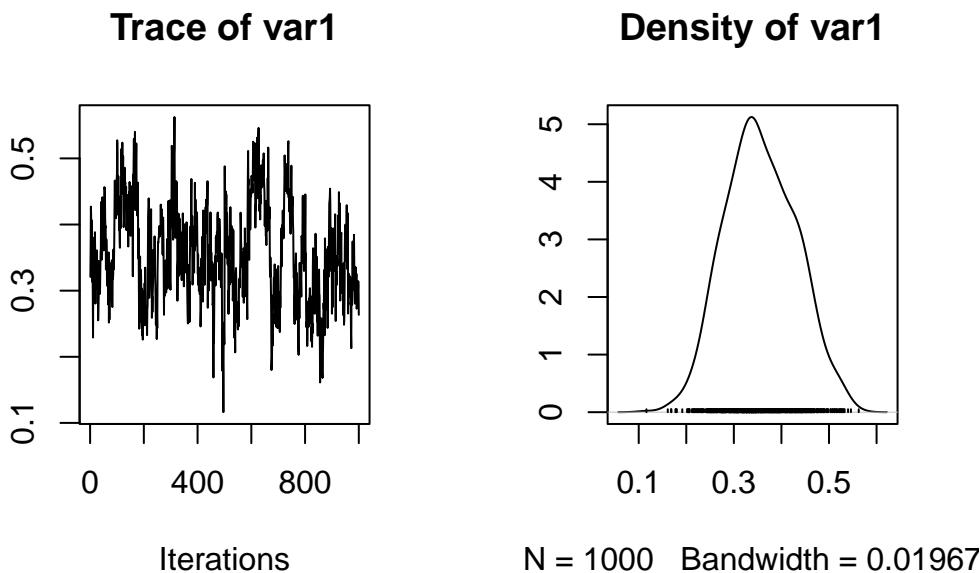
- Empirical mean and standard deviation for each variable,
 plus standard error of the mean:

Mean	SD	Naive SE	Time-series SE
0.356562	0.073890	0.002337	0.010196

- Quantiles for each variable:

2.5%	25%	50%	75%	97.5%
0.2208	0.3042	0.3517	0.4111	0.5045

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



4.0.4. 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, "loo")
```

```
Warning: Found 364 observations with a pareto_k > 0.67 in model 'brms_m1.3'. We
recommend to run more iterations to get at least about 2200 posterior draws to
improve LOO-CV approximation accuracy.
```

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

```
Warning: Found 476 observations with a pareto_k > 0.41 in model 'brms_m1.1'. We
recommend to run more iterations to get at least about 2200 posterior draws to
improve LOO-CV approximation accuracy.
```

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

	elpd_diff	se_diff
brms_m1.3	0.0	0.0
brms_m1.1	-208.3	15.7

4.0.5. 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 approach 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
  bwt ~ 1 + sex + (0 + sex || gr(animal, cov = Amat)) + (0 + sex || byear) + (0 + sex || mother),
  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 + sex || m
Data: gryphon (Number of observations: 854)
Draws: 2 chains, each with iter = 1000; warmup = 500; thin = 1;
      total post-warmup draws = 1000

```

Multilevel Hyperparameters:

`~animal` (Number of levels: 1084)

	Estimate	Est.Error	1-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
<code>sd(sex1)</code>	1.32	0.24	0.81	1.75	1.02	40	124
<code>sd(sex2)</code>	0.91	0.38	0.12	1.53	1.07	22	70

`~byear` (Number of levels: 34)

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(sex1)	0.91	0.17	0.62	1.26	1.00	632	604
sd(sex2)	1.08	0.20	0.76	1.50	1.00	429	614

~mother (Number of levels: 429)

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(sex1)	0.91	0.24	0.33	1.33	1.03	93	93
sd(sex2)	1.39	0.16	1.09	1.69	1.02	210	262

Regression Coefficients:

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
Intercept	6.28	0.23	5.85	6.74	1.00	635	490
sex2	2.05	0.34	1.39	2.67	1.00	636	698

Further Distributional Parameters:

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sigma	1.49	0.17	1.15	1.76	1.05	22	53

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 || byear),
  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 + sex ||  
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
```

Multilevel Hyperparameters:

`~animal` (Number of levels: 854)

	Estimate	Est.Error	1-95% 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	1-95% 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

Regression Coefficients:

	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$sd_animal__sex1)^2 + (Var.table$sd_animal__sex2)^2))
Var.table$h.bwt.m <- as.mcmc((Var.table$sd_animal__sex2)^2 / ((Var.table$sd_animal__sex1)^2 + (Var.table$sd_animal__sex2)^2))
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
```

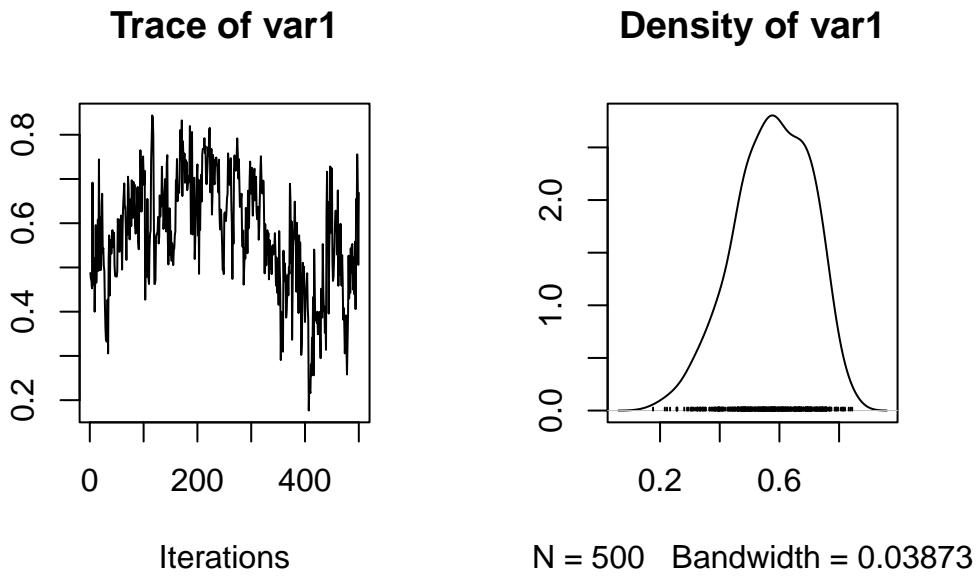
1. Empirical mean and standard deviation for each variable,
plus standard error of the mean:

Mean	SD	Naive SE	Time-series SE
0.463879	0.155395	0.006949	0.078323

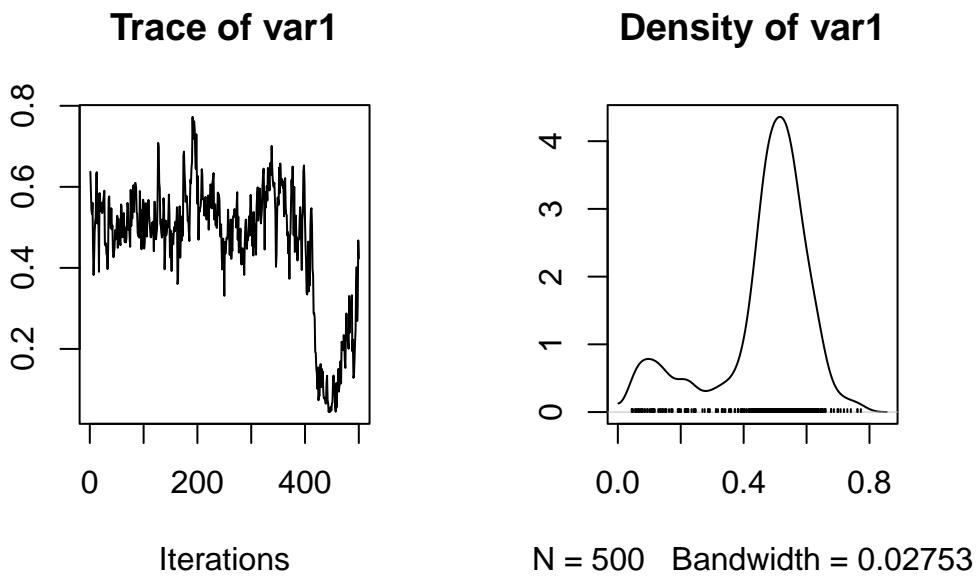
2. Quantiles for each variable:

```
2.5%     25%     50%     75%   97.5%
0.06693  0.43668  0.50150  0.55729  0.66016
```

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



```
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], 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 = "", c)
arrows(y0 = 0.95, x0 = h2.sex[1, 2], y1 = 0.95, x1 = h2.sex[1, 3], code = 3, angle = 90, length =
arrows(y0 = 1.05, x0 = h2.sex[2, 2], y1 = 1.05, x1 = h2.sex[2, 3], code = 3, angle = 90, length =
```

```
mtext("Narrow-sense heritability (\u00b1CI)", 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)
```

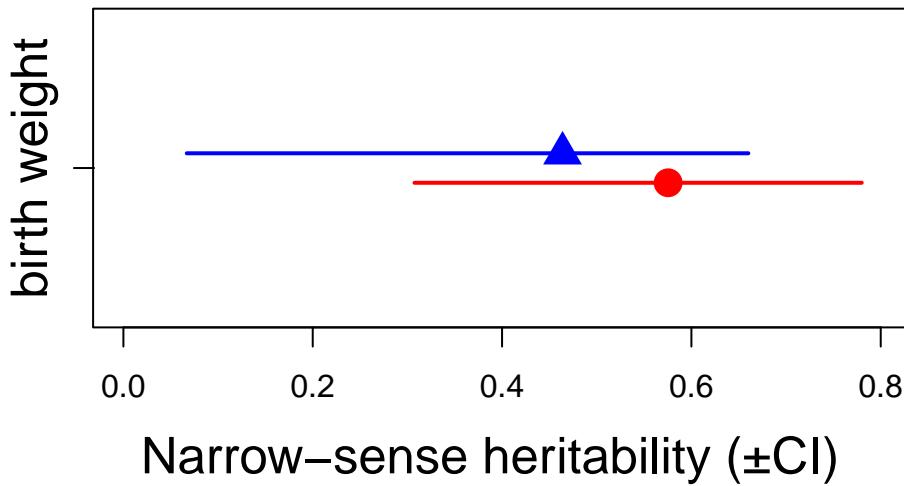


Figure 4.1.: Female and male heritability of birth weight

4.0.6. Modification of model parameter

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

4.0.7. 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.

Part II.

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.

Scenario and data

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.

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)
```

Chapter 5

Asreml-R

5.0.1. Running the model

First we need to load the `asreml` library:

```
library(asreml)
```

Loading required package: Matrix

Attaching package: 'Matrix'

The following objects are masked from 'package:tidyverse':

expand, pack, unpack

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Loading ASReml-R version 4.2

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 respectively. We can also specify some starting values for the variance matrices. These can be

very approximate *guesimates* 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
)
```

ASReml Version 4.2 08/10/2024 11:28:59

	LogLik	Sigma2	DF	wall
1	-7108.741	1.0	1535	11:28:59
2	-5837.803	1.0	1535	11:28:59
3	-4437.495	1.0	1535	11:28:59
4	-3459.378	1.0	1535	11:28:59
5	-2914.034	1.0	1535	11:28:59
6	-2729.131	1.0	1535	11:28:59
7	-2684.659	1.0	1535	11:28:59
8	-2679.838	1.0	1535	11:28:59
9	-2679.742	1.0	1535	11:28:59
10	-2679.741	1.0	1535	11:28:59

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

ASReml Version 4.2 08/10/2024 11:28:59

LogLik	Sigma2	DF	wall

```
1 -2679.741      1.0   1535  11:28:59
2 -2679.741      1.0   1535  11:28:59
```

`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	%ch
trait:vm(animal, ainv)!trait_bwt:bwt	3.368397	0.6348307	5.305977	P	0
trait:vm(animal, ainv)!trait_tarsus:bwt	2.459809	1.0732644	2.291895	P	0
trait:vm(animal, ainv)!trait_tarsus:tarsus	12.345792	3.0744285	4.015638	P	0
units:trait!R	1.000000	NA	NA	F	0
units:trait!trait_bwt:bwt	3.849916	0.5200101	7.403542	P	0
units:trait!trait_tarsus:bwt	3.313282	0.9129234	3.629310	P	0
units:trait!trait_tarsus:tarsus	17.646432	2.6670380	6.616491	P	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:trait!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 disequilibrium, 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:

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

	Estimate	SE
r_A	0.3814436	0.1299759

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

	Estimate	SE
r_res	0.4019799	0.086071

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

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

	Estimate	SE
h2.bwt	0.466646	0.0767153

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

	Estimate	SE
h2.tarsus	0.4116331	0.0930586

5.0.2. 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
)
```

ASReml Version 4.2 08/10/2024 11:28:59

	LogLik	Sigma2	DF	wall
1	-4672.301	1.0	1533	11:28:59
2	-4005.616	1.0	1533	11:28:59
3	-3271.484	1.0	1533	11:28:59 (1 restrained)
4	-2761.414	1.0	1533	11:29:00 (1 restrained)
5	-2481.355	1.0	1533	11:29:00
6	-2395.858	1.0	1533	11:29:00
7	-2381.050	1.0	1533	11:29:00
8	-2380.251	1.0	1533	11:29:00
9	-2380.246	1.0	1533	11:29:00

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

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	LogLik	Sigma2	DF	wall
1	-2380.246	1.0	1533	11:29:00
2	-2380.246	1.0	1533	11:29:00

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	bound	%ch
trait:byear!trait_bwt:bwt	0.9746385	0.2825727	3.4491602	P	0
trait:byear!trait_tarsus:bwt	0.1624076	0.4185079	0.3880635	P	0
trait:byear!trait_tarsus:tarsus	3.7383721	1.2065992	3.0982716	P	0
trait:mother!trait_bwt:bwt	1.1445184	0.2302182	4.9714512	P	0
trait:mother!trait_tarsus:bwt	-1.5567306	0.4051848	-3.8420260	P	0
trait:mother!trait_tarsus:tarsus	4.8206132	1.3201300	3.6516202	P	0
trait:vm(animal, ainv)!trait_bwt:bwt	1.9893546	0.4410246	4.5107569	P	0
trait:vm(animal, ainv)!trait_tarsus:bwt	3.3170404	0.9032323	3.6724110	P	0
trait:vm(animal, ainv)!trait_tarsus:tarsus	10.2294887	2.8077066	3.6433610	P	0
units:trait!R	1.0000000	NA	NA	F	0
units:trait!trait_bwt:bwt	1.8443110	0.3443178	5.3564203	P	0
units:trait!trait_tarsus:bwt	4.0142841	0.7412540	5.4155308	P	0
units:trait!trait_tarsus:tarsus	12.4845955	2.2893363	5.4533690	P	0

we can estimate the different correlations using vpredict:

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

	Estimate	SE
r_byear	0.0850831	0.2134209

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

	Estimate	SE
r_M	-0.6627518	0.2487963

```
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	0.0736676

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

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

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	LogLik	Sigma2	DF	wall
1	-2380.246	1.0	1533	11:29:01
2	-2380.246	1.0	1533	11:29:01

	Df	denDF	F.inc	F.con	Margin	Pr
trait	2	52.6	1.396e+03	1.396e+03		0.000000
at(trait, 'bwt'):sex	1	812.8	2.984e+02	1.735e+02	B	0.000000

	Df	denDF	F.inc	F.con	Margin	Pr
at(trait, 'tarsus'):sex	1	747.9	3.204e-02	3.204e-02	B	0.857984

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
)
```

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	LogLik	Sigma2	DF	wall
1	-4810.563	1.0	1534	11:29:01
2	-4129.799	1.0	1534	11:29:01
3	-3382.529	1.0	1534	11:29:01 (1 restrained)
4	-2864.076	1.0	1534	11:29:01
5	-2574.891	1.0	1534	11:29:01
6	-2478.879	1.0	1534	11:29:01
7	-2458.305	1.0	1534	11:29:01
8	-2456.425	1.0	1534	11:29:01
9	-2456.377	1.0	1534	11:29:01
10	-2456.376	1.0	1534	11:29:01
	solution	std error	z.ratio	
trait_bwt	7.636226	0.2389515	31.95722	
trait_tarsus	22.703658	0.4827348	47.03133	

```
at(trait, 'tarsus'):sex_1  0.000000      NA      NA
at(trait, 'tarsus'):sex_2 -3.267042  0.2953279 -11.06242
```

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	LogLik	Sigma2	DF	wall
1	-2456.376	1.0	1534	11:29:02
2	-2456.376	1.0	1534	11:29:02

	Df	denDF	F.inc	F.con	Margin	Pr
trait	2	50.7	1233.0	1233.0		0
at(trait, 'tarsus'):sex	1	522.9	122.4	122.4	B	0

5.0.3. 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
)

```

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	LogLik	Sigma2	DF	wall
1	-4677.820	1.0	1533	11:29:02
2	-4010.442	1.0	1533	11:29:02
3	-3275.409	1.0	1533	11:29:02
4	-2763.519	1.0	1533	11:29:02
5	-2483.732	1.0	1533	11:29:02
6	-2400.242	1.0	1533	11:29:02
7	-2386.663	1.0	1533	11:29:02
8	-2386.049	1.0	1533	11:29:02
9	-2386.045	1.0	1533	11:29:02

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 $\chi^2_1 = 11.6$. 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
)
```

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	LogLik	Sigma2	DF	wall
1	-4672.708	1.0	1533	11:29:03
2	-4005.954	1.0	1533	11:29:03
3	-3271.738	1.0	1533	11:29:03 (1 restrained)
4	-2761.626	1.0	1533	11:29:03 (1 restrained)
5	-2481.647	1.0	1533	11:29:03
6	-2395.992	1.0	1533	11:29:04
7	-2381.136	1.0	1533	11:29:04
8	-2380.331	1.0	1533	11:29:04
9	-2380.326	1.0	1533	11:29:04

```

2 * (modelb$loglik - modeld$loglik)

[1] 0.1600641

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

[1] 0.6890975

```

5.0.4. 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
)

```

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	LogLik	Sigma2	DF	wall
1	-4672.301	1.0	1533	11:29:04
2	-4003.183	1.0	1533	11:29:05
3	-3266.521	1.0	1533	11:29:05 (1 restrained)
4	-2757.188	1.0	1533	11:29:05 (1 restrained)
5	-2479.291	1.0	1533	11:29:05

```

6      -2395.476      1.0    1533  11:29:05
7      -2381.026      1.0    1533  11:29:05
8      -2380.251      1.0    1533  11:29:05
9      -2380.246      1.0    1533  11:29:05

```

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

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	LogLik	Sigma2	DF	wall
1	-2380.246	1.0	1533	11:29:06
2	-2380.246	1.0	1533	11:29:06

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

	component	std.error	z.ratio	bound	%ch
trait:byear!trait_bwt:bwt	0.9746386	0.2825728	3.449159	P	0
trait:byear!trait_tarsus:bwt	0.1624071	0.4185082	0.388062	P	0
trait:byear!trait_tarsus:tarsus	3.7383734	1.2066018	3.098266	P	0
trait:mother!trait_bwt:bwt	1.1445186	0.2302183	4.971450	P	0
trait:mother!trait_tarsus:bwt	-1.5567316	0.4051850	-3.842027	P	0
trait:mother!trait_tarsus:tarsus	4.8206154	1.3201324	3.651615	P	0
trait:vm(animal, ainv)!trait!tarsus:!trait!bwt.cor	0.7353061	0.1094807	6.716310	U	0
trait:vm(animal, ainv)!trait_bwt	1.9893543	0.4410243	4.510758	P	0
trait:vm(animal, ainv)!trait_tarsus	10.2294850	2.8077055	3.643361	P	0
units:trait!R	1.0000000	NA	NA	F	0
units:trait!trait_bwt:bwt	1.8443112	0.3443178	5.356422	P	0
units:trait!trait_tarsus:bwt	4.0142825	0.7412540	5.415529	P	0
units:trait!trait_tarsus:tarsus	12.4845977	2.2893355	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.

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

```
[1] -2380.246
```

```
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.

```
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
)
```

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	LogLik	Sigma2	DF	wall
1	-2545.233	1.0	1533	11:29:06
2	-2483.883	1.0	1533	11:29:06

```
3      -2423.504          1.0   1533  11:29:06
4      -2392.509          1.0   1533  11:29:07
5      -2383.661          1.0   1533  11:29:07
6      -2383.084          1.0   1533  11:29:07
7      -2383.033          1.0   1533  11:29:07
8      -2383.022          1.0   1533  11:29:07
9      -2383.019          1.0   1533  11:29:07
10     -2383.019          1.0   1533  11:29:07
```

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

```
[1] 5.544679
```

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

```
[1] 0.006598676
```

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

5.0.5. 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 normally 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
)

```

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	LogLik	Sigma2	DF	wall
1	-4672.301	1.0	1533	11:29:07
2	-4003.183	1.0	1533	11:29:07
3	-3266.521	1.0	1533	11:29:07 (1 restrained)
4	-2757.188	1.0	1533	11:29:07 (1 restrained)
5	-2479.291	1.0	1533	11:29:07
6	-2395.476	1.0	1533	11:29:07
7	-2381.026	1.0	1533	11:29:07
8	-2380.251	1.0	1533	11:29:07
9	-2380.246	1.0	1533	11:29:08

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

ASReml Version 4.2 08/10/2024 11:29:08

	LogLik	Sigma2	DF	wall
1	-2380.246	1.0	1533	11:29:08
2	-2380.246	1.0	1533	11:29:08

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

	component	std.error	z.ratio	bound	%ch
trait:byear!trait_T1:T1	0.9746386	0.2825728	3.449159	P	0
trait:byear!trait_T2:T1	0.1624071	0.4185082	0.388062	P	0
trait:byear!trait_T2:T2	3.7383734	1.2066018	3.098266	P	0
trait:mother!trait_T1:T1	1.1445186	0.2302183	4.971450	P	0

	component	std.error	z.ratio	bound	%ch
trait:mother!trait_T2:T1	-1.5567316	0.4051850	-3.842027	P	0
trait:mother!trait_T2:T2	4.8206154	1.3201324	3.651615	P	0
trait:vm(animal, ainv)!trait!T2:!trait!T1.cor	0.7353061	0.1094807	6.716310	U	0
trait:vm(animal, ainv)!trait_T1	1.9893543	0.4410243	4.510758	P	0
trait:vm(animal, ainv)!trait_T2	10.2294850	2.8077055	3.643361	P	0
units:trait!R	1.0000000	NA	NA	F	0
units:trait!trait_T1:T1	1.8443112	0.3443178	5.356422	P	0
units:trait!trait_T2:T1	4.0142825	0.7412540	5.415529	P	0
units:trait!trait_T2:T2	12.4845977	2.2893355	5.453372	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
846 1772
```

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

```
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)
```

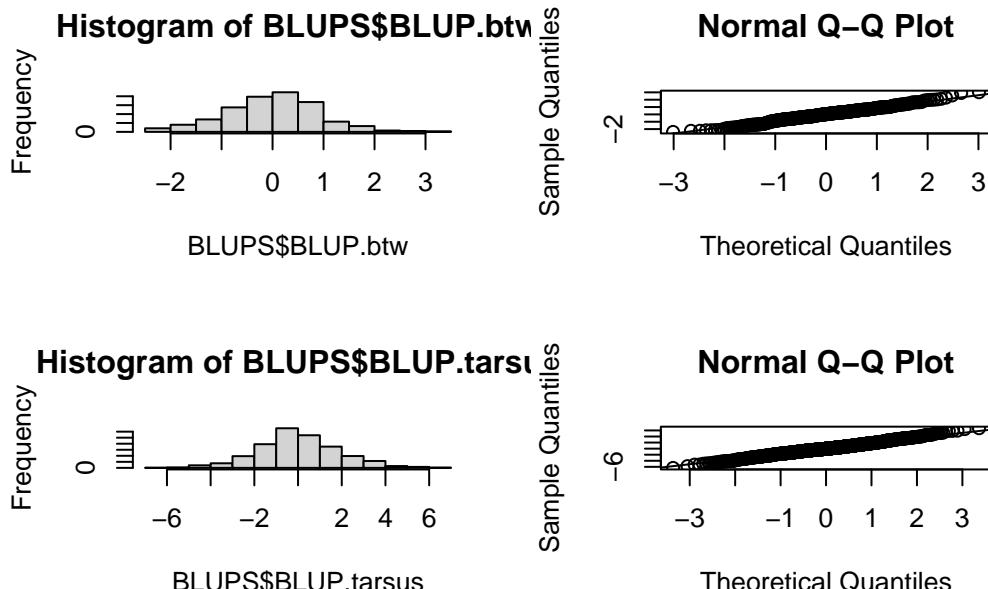
```
[1] 1310
```

```
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:1310	Min. :-2.3778	Min. :0.7494	Min. :-6.34104
Class :character	1st Qu.:-0.5797	1st Qu.:0.9993	1st Qu.:-1.14403
Mode :character	Median : 0.0350	Median :1.0223	Median :-0.02524
	Mean :-0.0082	Mean :1.0640	Mean : 0.02189
	3rd Qu.: 0.5911	3rd Qu.:1.0552	3rd Qu.: 1.17735
	Max. : 3.0123	Max. :1.4377	Max. : 6.71502
	NA's :926	NA's :926	
SE.tarsus			
Min. :1.616			
1st Qu.:2.371			
Median :2.451			
Mean :2.576			
3rd Qu.:2.810			
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)
```

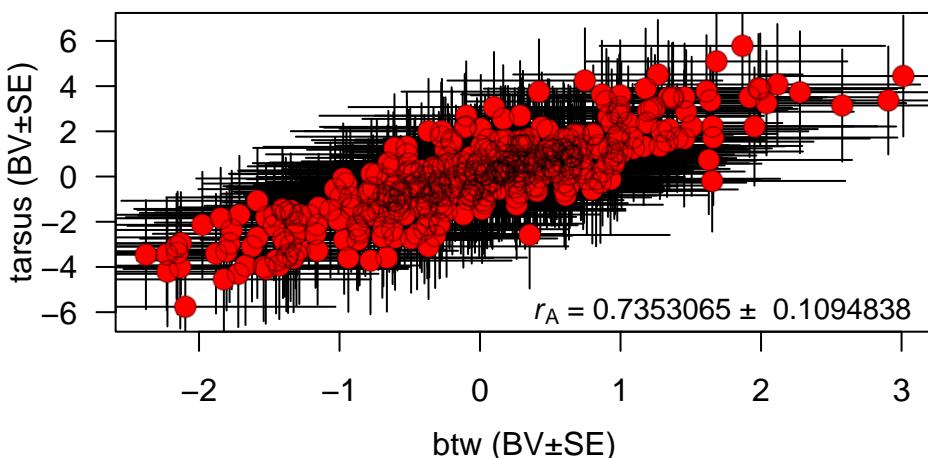
```
hist(BLUPS$BLUP.tarsus)
qqnorm(BLUPS$BLUP.tarsus)
qqline(BLUPS$BLUP.tarsus)
```



#

Here, some simple code to plot the genetic correlation.

```
plot(BLUP.tarsus ~ BLUP.btw, BLUPS, xlab = "", ylab = "", las = 1.2, bty = "o", col = "white")
arrows(x0 = BLUPS$BLUP.btw, y0 = BLUPS$BLUP.tarsus - BLUPS$SE.tarsus, x1 = BLUPS$BLUP.btw, y1 = BLUPS$SE.tarsus)
arrows(x0 = BLUPS$BLUP.btw - BLUPS$SE.btw, y0 = BLUPS$BLUP.tarsus, x1 = BLUPS$BLUP.btw + BLUPS$SE.btw, y1 = BLUPS$BLUP.tarsus)
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, adj = 0)
```



5.0.6. 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 required 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
)

```

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	LogLik	Sigma2	DF	wall
1	-2522.729	1.0	1807	11:29:10 (1 restrained)
2	-2459.512	1.0	1807	11:29:10 (3 restrained)
3	-2408.940	1.0	1807	11:29:10
4	-2392.691	1.0	1807	11:29:10

```

5      -2388.962      1.0    1807  11:29:10
6      -2388.743      1.0    1807  11:29:10
7      -2388.736      1.0    1807  11:29:10
8      -2388.736      1.0    1807  11:29:10

```

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

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

ASReml Version 4.2 08/10/2024 11:29:10

	LogLik	Sigma2	DF	wall
1	-2388.736	1.0	1807	11:29:11
2	-2388.736	1.0	1807	11:29:11

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

	component	std.error	z.ratio	bound	%ch
trait:byear!trait_bwt:bwt	0.9858478	0.2863878	3.4423530	P	0
trait:byear!trait_tarsus:bwt	0.1525063	0.4334263	0.3518622	P	0
trait:byear!trait_tarsus:tarsus	3.9981983	1.2798747	3.1238982	P	0
trait:mother!trait_bwt:bwt	1.3312734	0.2484444	5.3584371	P	0
trait:mother!trait_tarsus:bwt	-1.6174228	0.4283851	-3.7756279	P	0
trait:mother!trait_tarsus:tarsus	4.7542338	1.3546517	3.5095618	P	0
at(sex, '1'):trait:vm(animal, ainv)!trait_bwt:bwt	1.3402853	0.5670773	2.3634965	P	0
at(sex, '1'):trait:vm(animal, ainv)!trait_tarsus:bwt	2.3608392	1.1348473	2.0803144	P	0
at(sex, '1'):trait:vm(animal, ainv)!trait_tarsus:tarsus	6.0625993	3.1304394	1.9366608	P	0
at(sex, '2'):trait:vm(animal, ainv)!trait_bwt:bwt	1.8645998	0.8888206	2.0978361	P	0
at(sex, '2'):trait:vm(animal, ainv)!trait_tarsus:bwt	5.0954811	2.0684729	2.4634024	P	0
at(sex, '2'):trait:vm(animal, ainv)!trait_tarsus:tarsus	14.9771870	6.4479787	2.3227724	P	0
sex_1!R	1.0000000	NA	NA	F	0
sex_1!trait_bwt:bwt	2.3079850	0.5015651	4.6015657	P	0

	component	std.error	z.ratio	bound	%ch
sex_1!trait_tarsus:bwt	4.4287898	1.0376370	4.2681493	P	0
sex_1!trait_tarsus:tarsus	13.4857819	2.9284922	4.6050257	P	0
sex_2!R	1.0000000	NA	NA	F	0
sex_2!trait_bwt:bwt	1.7956612	0.7549779	2.3784288	P	0
sex_2!trait_tarsus:bwt	2.6340448	1.7685804	1.4893554	P	0
sex_2!trait_tarsus:tarsus	9.6094528	5.4917853	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	0.0768158	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	0.0789263

```
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	0.0917683

```
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:

	solution	std error	z.ratio
trait_bwt	6.3779149	0.2311766	27.5889321
trait_tarsus	20.5838787	0.4942649	41.6454395
at(trait, 'bwt'):sex_1	0.0000000	NA	NA
at(trait, 'bwt'):sex_2	1.9393688	0.1903239	10.1898321
at(trait, 'tarsus'):sex_1	0.0000000	NA	NA
at(trait, 'tarsus'):sex_2	-0.0554799	0.4758708	-0.1165861

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	LogLik	Sigma2	DF	wall
1	-2388.736	1.0	1807	11:29:12
2	-2388.736	1.0	1807	11:29:12

	Df	denDF	F.inc	F.con	Margin	Pr
trait	2	44.8	1.522e+03	1.522e+03		0.0000000
at(trait, 'bwt'):sex	1	137.5	2.209e+02	1.038e+02	B	0.0000000
at(trait, 'tarsus'):sex	1	138.6	1.359e-02	1.359e-02	B	0.9073748

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
)

```

ASReml Version 4.2 08/10/2024 11:29:13

	LogLik	Sigma2	DF	wall
1	-2474.972	1.0	1807	11:29:13 (3 restrained)
2	-2406.283	1.0	1807	11:29:13
3	-2394.010	1.0	1807	11:29:14
4	-2391.718	1.0	1807	11:29:14
5	-2391.480	1.0	1807	11:29:15
6	-2391.477	1.0	1807	11:29:15

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

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

ASReml Version 4.2 08/10/2024 11:29:15

	LogLik	Sigma2	DF	wall
1	-2391.476	1.0	1807	11:29:15
2	-2391.476	1.0	1807	11:29:15

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

	component	std.error	z.ratio	bound	%ch
trait:byear!trait_bwt:bwt	0.9794331	0.2848997	3.4378175	P	0
trait:byear!trait_tarsus:bwt	0.1428995	0.4322719	0.3305778	P	0
trait:byear!trait_tarsus:tarsus	4.0021595	1.2818624	3.1221444	P	0
trait:mother!trait_bwt:bwt	1.4956509	0.2568074	5.8240170	P	0
trait:mother!trait_tarsus:bwt	-1.2460057	0.4438357	-2.8073580	P	0
trait:mother!trait_tarsus:tarsus	5.3945609	1.4035705	3.8434556	P	0
at(sex, '1'):trait:vm(animal, ainv)!trait_bwt:bwt	0.5265716	0.3579555	1.4710530	P	0
at(sex, '1'):trait:vm(animal, ainv)!trait_tarsus:bwt	0.0000000	NA	NA	F	NA
at(sex, '1'):trait:vm(animal, ainv)!trait_tarsus:tarsus	1.4223969	1.9103795	0.7445625	P	0
at(sex, '2'):trait:vm(animal, ainv)!trait_bwt:bwt	1.5835813	0.8671365	1.8262193	P	0
at(sex, '2'):trait:vm(animal, ainv)!trait_tarsus:bwt	4.4288714	2.0173971	2.1953395	P	0
at(sex, '2'):trait:vm(animal, ainv)!trait_tarsus:tarsus	12.9349047	6.2946996	2.0548883	P	0
sex_1 R	1.0000000	NA	NA	F	0
sex_1!trait_bwt:bwt	2.9539767	0.4196755	7.0387165	P	0
sex_1!trait_tarsus:bwt	6.3138301	0.6802598	9.2814981	P	0
sex_1!trait_tarsus:tarsus	17.3577089	2.4730547	7.0187323	P	0
sex_2 R	1.0000000	NA	NA	F	0
sex_2!trait_bwt:bwt	1.9341439	0.7416691	2.6078261	P	0
sex_2!trait_tarsus:bwt	2.9467290	1.7370018	1.6964455	P	0
sex_2!trait_tarsus:tarsus	10.7245912	5.4025888	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.

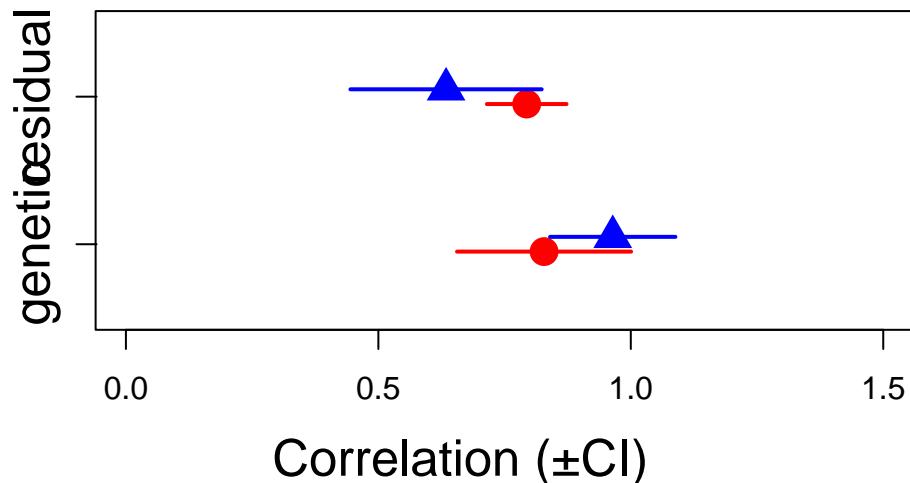
```
# code provided as an example for the moment since the model cannot run on this data
model_modif <- update.asreml(model_sex, start.values = T)
G <- model_modif$vparameters[(1:12), ]
G$fac <- factor(
  c(
    1, 2, 3, 4, 2, 6, # Additive genetic matrix 2 =5
    7, 8, 9, # byear matrix
    10, 11, 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, residual.c

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 = "", y
arrows(y0 = 0.95, x0 = cor.est[1, 1] - cor.est[1, 2], y1 = 0.95, x1 = cor.est[1, 1] + cor.est[1,
arrows(y0 = 1.05, x0 = cor.est[2, 1] - cor.est[2, 2], y1 = 1.05, x1 = cor.est[2, 1] + cor.est[2,
arrows(y0 = 1.95, x0 = cor.est[3, 1] - cor.est[3, 2], y1 = 1.95, x1 = cor.est[3, 1] + cor.est[3,
arrows(y0 = 2.05, x0 = cor.est[4, 1] - cor.est[4, 2], y1 = 2.05, x1 = cor.est[4, 1] + cor.est[4,
mtext("Correlation (\u00b1CI)", 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
)
```

ASReml Version 4.2 08/10/2024 11:29:16

	LogLik	Sigma2	DF	wall
1	-2522.729	1.0	1807	11:29:16 (2 restrained)
2	-2457.755	1.0	1807	11:29:17 (2 restrained)
3	-2407.462	1.0	1807	11:29:17 (2 restrained)
4	-2394.143	1.0	1807	11:29:18 (1 restrained)
5	-2389.368	1.0	1807	11:29:18
6	-2388.741	1.0	1807	11:29:18
7	-2388.736	1.0	1807	11:29:18

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

ASReml Version 4.2 08/10/2024 11:29:18

	LogLik	Sigma2	DF	wall
1	-2388.736	1.0	1807	11:29:19
2	-2388.736	1.0	1807	11:29:19

```
DvsS <- data.frame(
  Trait = rownames(model_sex$coefficients$random),
  BLUP = model_sex$coefficients$random,
  SE = sqrt(model_sex$vcoeff$random * model_sex$sigma2)
) %>%
  filter(grep("at\\(sex", Trait)) %>%
  mutate(
    ID = substr(Trait, 40, 44),
```

```

TRAIT = substr(Trait, 20, 21),
SEX = substr(Trait, 10, 10)
) %>%
rename(
  BLUP = "effect"
) %>%
select(BLUP:SEX)
summary(factor(DvsS$TRAIT)) # 1309 each

```

T1 T2
2618 2618

#

```

BLUPS <- reshape(DvsS, v.names = c("BLUP", "SE"), idvar = c("ID", "SEX"), timevar = "TRAIT", direc
nrow(BLUPS)

```

[1] 2618

```

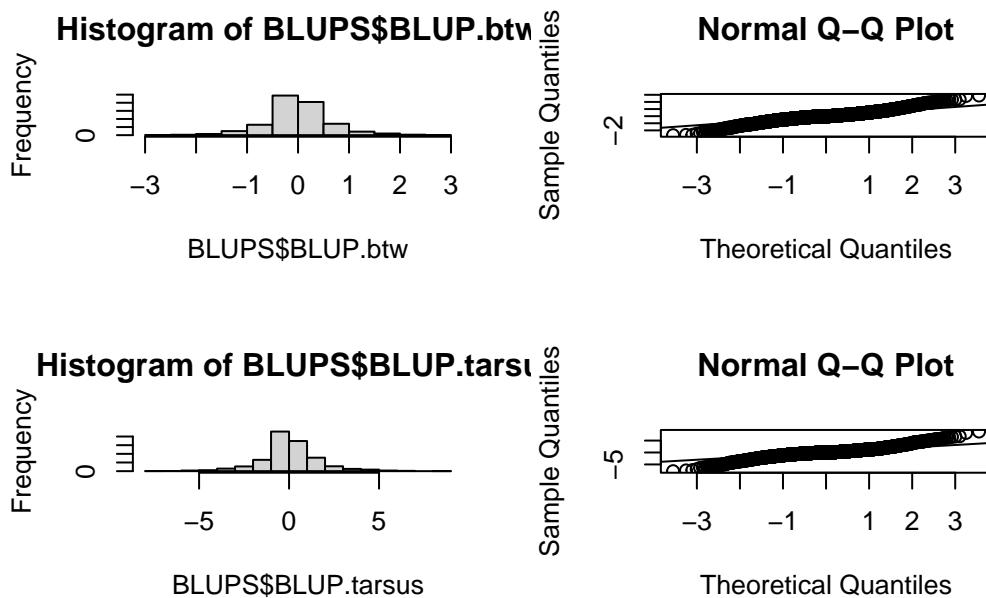
rownames(BLUPS) <- c()
colnames(BLUPS) <- c("ID", "SEX", "BLUP.btw", "SE.btw", "BLUP.tarsus", "SE.tarsus")
summary(BLUPS)

```

ID	SEX	BLUP.btw	SE.btw
Length:2618	Length:2618	Min. :-2.669649	Min. :0.8383
Class :character	Class :character	1st Qu.:-0.281979	1st Qu.:0.9366
Mode :character	Mode :character	Median : 0.000000	Median :1.1001
		Mean : 0.009574	Mean :1.0913
		3rd Qu.: 0.295795	3rd Qu.:1.1780
		Max. : 2.895393	Max. :1.4276
BLUP.tarsus	SE.tarsus		
Min. :-7.81574	Min. :1.829		
1st Qu.:-0.64388	1st Qu.:2.342		

```
Median : 0.00000 Median :2.462
Mean   : 0.03319 Mean   :2.728
3rd Qu.: 0.74473 3rd Qu.:3.329
Max.   : 8.77778 Max.   :4.038
```

```
# 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)
```



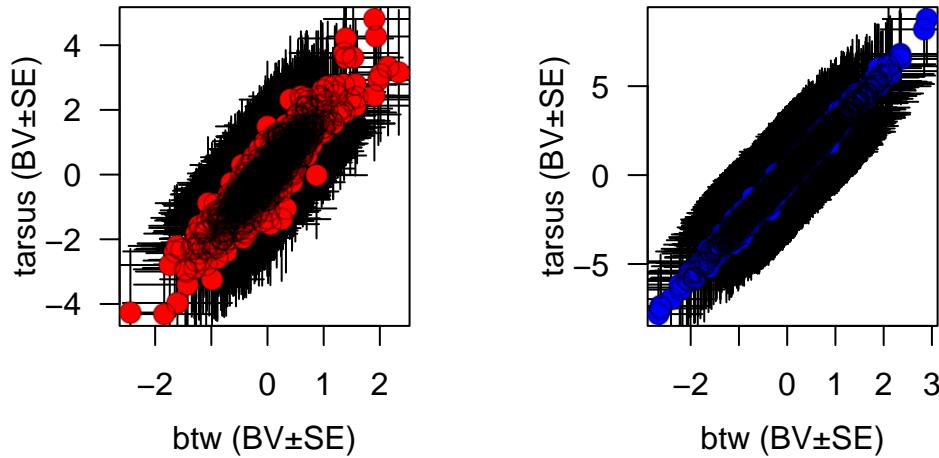
Here, some simple codes to plot the genetic correlation.

```
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 = FEM$BLUP.tarsus + FEM$SE.tarsus)
arrows(x0 = FEM$BLUP.btw - FEM$SE.btw, y0 = FEM$BLUP.tarsus, x1 = FEM$BLUP.btw + FEM$SE.btw, y1 = FEM$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±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 = MAL$BLUP.tarsus + MAL$SE.tarsus)
arrows(x0 = MAL$BLUP.btw - MAL$SE.btw, y0 = MAL$BLUP.tarsus, x1 = MAL$BLUP.btw + MAL$SE.btw, y1 = MAL$BLUP.tarsus)
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)

```



5.0.7. 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 ontogenetic 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 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
)

```

ASReml Version 4.2 08/10/2024 11:29:22

	LogLik	Sigma2	DF	wall
1	-1494.807	1.0	681	11:29:22 (1 restrained)
2	-1484.793	1.0	681	11:29:22 (1 restrained)
3	-1475.726	1.0	681	11:29:22 (1 restrained)
4	-1471.905	1.0	681	11:29:22 (1 restrained)
5	-1470.716	1.0	681	11:29:22
6	-1468.154	1.0	681	11:29:22
7	-1467.969	1.0	681	11:29:22
8	-1467.967	1.0	681	11:29:22

```

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

```

ASReml Version 4.2 08/10/2024 11:29:22

	LogLik	Sigma2	DF	wall
1	-1467.967	1.0	681	11:29:22
2	-1467.967	1.0	681	11:29:22

```

#
summary(model.BiV_Sex)$varcomp

```

	component	std.error	z.ratio	bound	%ch
trait:byear!trait_tarsus.1	3.280319	1.532909	2.1399299	U	0
trait:byear!trait_tarsus.2	4.743134	1.891252	2.5079332	U	0
trait:mother!trait_tarsus.1	1.875131	2.424092	0.7735398	U	0

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

ASReml Version 4.2 08/10/2024 11:29:23

	LogLik	Sigma2	DF	wall
1	-1494.323	1.0	681	11:29:23 (1 restrained)
2	-1482.996	1.0	681	11:29:23 (1 restrained)
3	-1472.827	1.0	681	11:29:23 (1 restrained)
4	-1468.707	1.0	681	11:29:23
5	-1467.984	1.0	681	11:29:23
6	-1467.968	1.0	681	11:29:23
7	-1467.967	1.0	681	11:29:23

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

ASReml Version 4.2 08/10/2024 11:29:23

	LogLik	Sigma2	DF	wall
1	-1467.967	1.0	681	11:29:24
2	-1467.967	1.0	681	11:29:24

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

	component	std.error	z.ratio	bound	%ch
trait:byear!trait_tarsus.1	3.2803263	1.5329224	2.1399167	U	0
trait:byear!trait_tarsus.2	4.7431679	1.8913244	2.5078553	U	0
trait:mother!trait_tarsus.1	1.8751274	2.4240942	0.7735373	U	0
trait:mother!trait_tarsus.2	4.3141262	2.7852550	1.5489160	U	0
trait:vm(animal, ainv)!trait!tarsus.2:!trait!tarsus.1.cor	0.9111864	0.4230261	2.1539720	U	0
trait:vm(animal, ainv)!trait_tarsus.1	6.5826478	3.6364929	1.8101638	U	0
trait:vm(animal, ainv)!trait_tarsus.2	12.8988848	8.0388517	1.6045681	U	0
units:trait!R	1.0000000	NA	NA	F	0
units:trait!trait!tarsus.2:!trait!tarsus.1.cor	0.0000000	NA	NA	F	NA
units:trait!trait_tarsus.1	14.8727602	3.6375549	4.0886696	P	0
units:trait!trait_tarsus.2	10.7604420	6.2948051	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)
) %>%
  filter(grep("vm\\(animal", Trait)) %>%
  mutate(
    ID = substr(Trait, 33, 36),
    TRAIT = substr(Trait, 7, 14)
) %>%
  rename(
    BLUP = "effect"
) %>%
  select(BLUP:TRAIT)

summary(factor(DvsS$TRAIT))
```

tarsus.1 tarsus.2

1309 1309

```
#
```

```
BLUPS <- reshape(DvsS, v.names = c("BLUP", "SE"), idvar = "ID", timevar = "TRAIT", direction = "w  
nrow(BLUPS)
```

```
[1] 1309
```

```
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:1309	Min. :-4.2702	Min. :1.724	Min. :-6.10276
Class :character	1st Qu.:-0.7149	1st Qu.:2.010	1st Qu.:-0.99945
Mode :character	Median : 0.0000	Median :2.127	Median : 0.00000
	Mean : 0.0718	Mean :2.198	Mean : 0.09409
	3rd Qu.: 0.8386	3rd Qu.:2.421	3rd Qu.: 1.15952
	Max. : 4.9297	Max. :2.677	Max. : 7.57246
SE.2			
Min. :2.375			
1st Qu.:2.679			
Median :3.051			
Mean :3.041			
3rd Qu.:3.375			
Max. :3.732			

```
#####
```

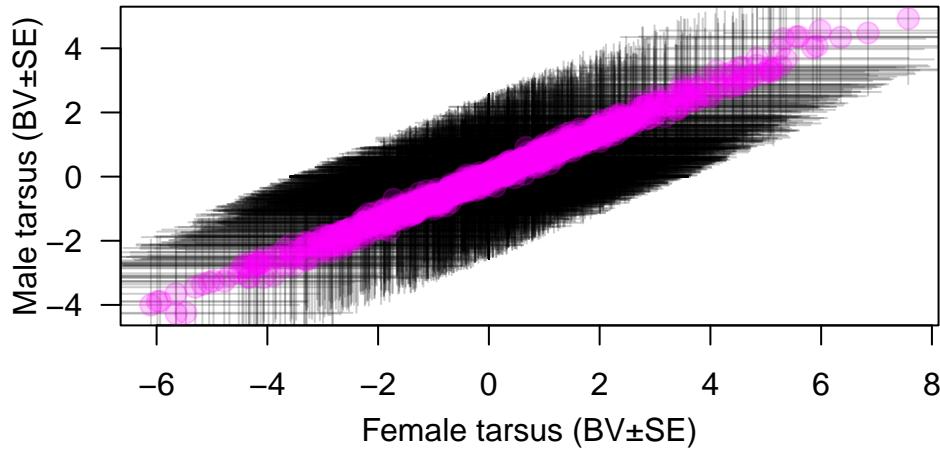
```
Y <- BLUPS$BLUP.1  
X <- BLUPS$BLUP.2  
se.Y <- BLUPS$SE.1  
se.X <- BLUPS$SE.2
```

```
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, angle = 90)
```

```

arrows(x0 = X - se.X, y0 = Y, x1 = X + se.X, y1 = Y, col = rgb(0, 0, 0, 0.2), code = 3, angle = 90)
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 difficult 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
```

Chapter 6

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)
```

Loading required package: Matrix

Attaching package: 'Matrix'

The following objects are masked from 'package:tidyR':

expand, pack, unpack

Loading required package: coda

Loading required package: ape

Attaching package: 'ape'

The following object is masked from 'package:dplyr':

where

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

6.0.1. 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: 7155.22

G-structure: ~us(trait):animal

	post.mean	l-95% CI	u-95% CI	eff.samp
traitbwt:traitbwt.animal	3.249	1.7464	4.530	147.91
traittarsus:traitbwt.animal	1.979	-0.3682	4.305	101.82
traitbwt:traittarsus.animal	1.979	-0.3682	4.305	101.82
traittarsus:traittarsus.animal	11.311	5.5498	18.810	86.94

R-structure: ~us(trait):units

	post.mean	l-95% CI	u-95% CI	eff.samp
traitbwt:traitbwt.units	3.939	2.655	5.080	159.44
traittarsus:traitbwt.units	3.685	1.695	5.647	103.97
traitbwt:traittarsus.units	3.685	1.695	5.647	103.97
traittarsus:traittarsus.units	18.659	12.927	24.404	99.97

Location effects: cbind(bwt, tarsus) ~ trait - 1

	post.mean	l-95% CI	u-95% CI	eff.samp	pMCMC
traitbwt	7.479	7.199	7.769	1000	<0.001 ***
traittarsus	20.433	19.916	21.077	1000	<0.001 ***
<hr/>					

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

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

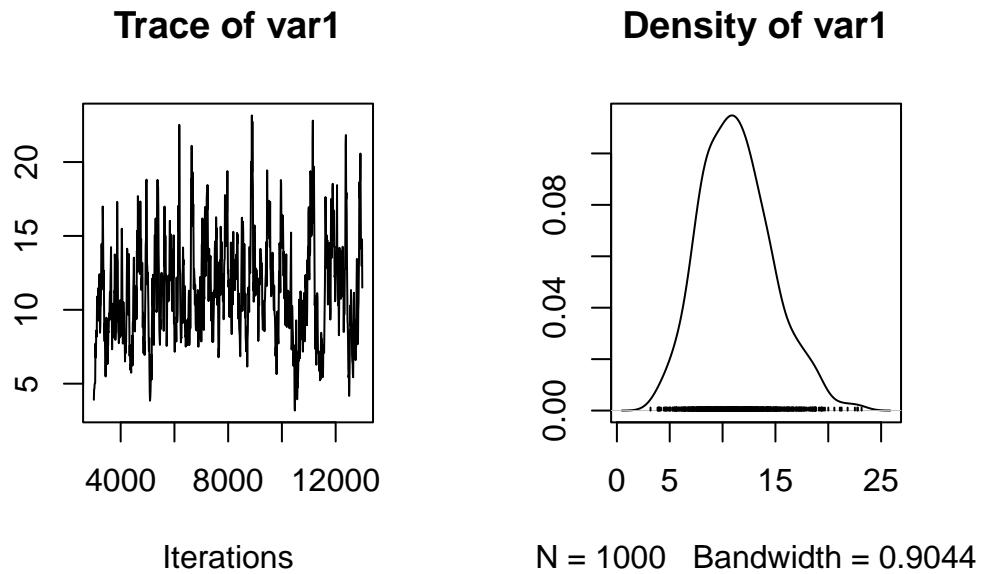


Figure 6.1.: The posterior distribution of the additive genetic effect for tarsus length in a MCMCglmm run with default values

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

```
Lag 10
0.8398828
```

We have constructed the prior similarly to 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 see the vignette of the MCMCglmm package (Hadfield 2010) 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 than 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 0.8398828 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
0.3501744
```

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
            3.471888              2.949939
  traitbwt:traittarsus.animal traittarsus:traittarsus.animal
            2.949939              12.012766
  traitbwt:traitbwt.units      traittarsus:traitbwt.units
            3.953930              3.876887
  traitbwt:traittarsus.units   traittarsus:traittarsus.units
            3.876887              19.604460
```

```
heritability.bwt2.1 <- model2.1$VCV[, "traitbwt:traitbwt.animal"] / (model2.1$VCV[, "traitbwt:tra
```

```
posterior.mode(heritability.bwt2.1)
```

```
var1
```

```
0.4999336
```

```
heritability.tarsus2.1 <- model2.1$VCV[, "trai
```

```
ttarsus:trai
```

```
ttarsus.animal"] / (model2.1$VCV[, "tra
```

```
posterior.mode(heritability.tarsus2.1)
```

```
var1
```

```
0.3719549
```

```
genetic.correlation2.1 <- model2.1$VCV[, "traitbwt:trai
```

```
ttarsus.animal"] / sqrt(model2.1$VCV[, "trai
```

```
posterior.mode(genetic.correlation2.1)
```

```
var1
```

```
0.4041642
```

6.0.2. 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
traiittarsus:traitbwt.animal	2.290	0.3241	4.264	274.8
traitbwt:traiittarsus.animal	2.290	0.3241	4.264	274.8
traiittarsus:traiittarsus.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
traiittarsus:traitbwt.byear	0.07332	-0.8100	0.9791	1000
traitbwt:traiittarsus.byear	0.07332	-0.8100	0.9791	1000

```
traiittarsus:traiittarsus.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
traiittarsus:traitbwt.mother	-1.508	-2.1667	-0.8288	648.6
traitbwt:traiittarsus.mother	-1.508	-2.1667	-0.8288	648.6
traiittarsus:traiittarsus.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
traiittarsus:traitbwt.units	4.81	3.111	6.568	414.7
traitbwt:traiittarsus.units	4.81	3.111	6.568	414.7
traiittarsus:traiittarsus.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 ***
traiittarsus	20.3985	19.4021	21.4106	1000	<0.001 ***
traitbwt:sex2	2.0354	1.7347	2.3529	1000	<0.001 ***
traiittarsus: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) [, , "traiittarsus:traiittarsus.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)
```

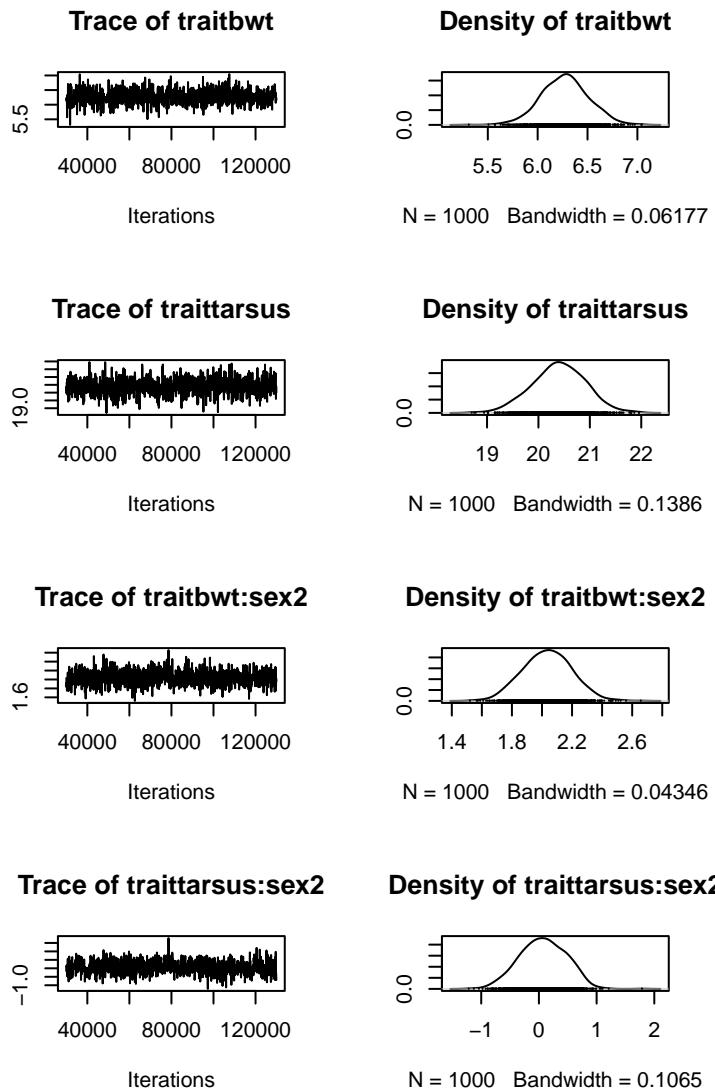


Figure 6.2.: Posterior trace and distribution for the fixed effects in model 2.2

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$VCV[, "traitbwt:traittarsus.animal"] / sqrt(model2.2$VCV[, "tr
maternal.correlation2.2 <- model2.2$VCV[, "traitbwt:traittarsus.mother"] / sqrt(model2.2$VCV[, "t
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 of these posterior distributions overlaps zero, so we can consider them both statistically supported.

6.0.3. 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)  
  )  
)  
  
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 + idh(trait),  
  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:

```

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"):traiittarsus:at.level(sex, "1"):traitbwt.animal	1.127
at.level(sex, "1"):traitbwt:at.level(sex, "1"):traiittarsus.animal	1.127
at.level(sex, "1"):traiittarsus:at.level(sex, "1"):traiittarsus.animal	3.379
	l-95% CI
at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.animal	0.1602
at.level(sex, "1"):traiittarsus:at.level(sex, "1"):traitbwt.animal	-0.6531
at.level(sex, "1"):traitbwt:at.level(sex, "1"):traiittarsus.animal	-0.6531
at.level(sex, "1"):traiittarsus:at.level(sex, "1"):traiittarsus.animal	0.1844
	u-95% CI
at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.animal	2.359
at.level(sex, "1"):traiittarsus:at.level(sex, "1"):traitbwt.animal	3.496
at.level(sex, "1"):traitbwt:at.level(sex, "1"):traiittarsus.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		
 	1-95% 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	1-95% CI	u-95% CI	eff.samp

traitbwt.byear	0.9309	0.4614	1.463	1000
traiittarsus.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
traiittarsus.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"):traiittarsus:at.level(sex, "1"):traitbwt.units	4.533
at.level(sex, "1"):traitbwt:at.level(sex, "1"):traiittarsus.units	4.533
at.level(sex, "1"):traiittarsus:at.level(sex, "1"):traiittarsus.units	14.113

	l-95% CI
at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.units	0.9958
at.level(sex, "1"):traiittarsus:at.level(sex, "1"):traitbwt.units	2.4185
at.level(sex, "1"):traitbwt:at.level(sex, "1"):traiittarsus.units	2.4185
at.level(sex, "1"):traiittarsus:at.level(sex, "1"):traiittarsus.units	8.1848

	u-95% CI
at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.units	3.128
at.level(sex, "1"):traiittarsus:at.level(sex, "1"):traitbwt.units	6.875
at.level(sex, "1"):traitbwt:at.level(sex, "1"):traiittarsus.units	6.875
at.level(sex, "1"):traiittarsus:at.level(sex, "1"):traiittarsus.units	18.935

	eff.samp
at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.units	207.2
at.level(sex, "1"):traiittarsus:at.level(sex, "1"):traitbwt.units	168.4
at.level(sex, "1"):traitbwt:at.level(sex, "1"):traiittarsus.units	168.4
at.level(sex, "1"):traiittarsus:at.level(sex, "1"):traiittarsus.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
	1-95% 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	1-95% 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

```
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"):traiittarsus: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"):traiittarsus.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"):traiittarsus:at.level(sex, "1"):traiittarsus.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

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"):traiittarsus.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"):traiittarsus:at.level(sex, "1"):traiittarsus.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"):traiittarsus: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"):traiittarsus.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"):traiittarsus:at.level(sex, "2"):traiittarsus.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
Lag 100	-0.043720033	0.03483594	-0.0765923141
Lag 500	-0.052466217	0.02987272	-0.0662772868
Lag 1000	-0.001034192	0.03110963	-0.0728720391
Lag 5000	-0.034160786	0.05472996	0.0008533055
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"):traiittarsus:at.level(sex, "1"):traiittarsus.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"):traiittarsus:at.level(sex, "2"):traiittarsus.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"):traiittarsus.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"):traiittarsus:at.level(sex, "2"):traiittarsus.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"):traiittarsus: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
Lag 100	-0.03261563	0.04790144	0.03175029
Lag 500	-0.02904559	0.05050843	0.04377317
Lag 1000	-0.03811545	0.05361475	0.07019878
Lag 5000	0.04062218	0.04654678	0.03310770
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"):traiittarsus.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"):traiittarsus: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"):traiittarsus.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"):traiittarsus:at.level(sex, "1"):traiittarsus.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
Lag 100	-0.03261563	0.04790144	0.03175029
Lag 500	-0.02904559	0.05050843	0.04377317
Lag 1000	-0.03811545	0.05361475	0.07019878
Lag 5000	0.04062218	0.04654678	0.03310770
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"):traiittarsus.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"):traiittarsus:at.level(sex, "2"):traiittarsus.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"):traiittarsus: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"):traiittarsus.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		

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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"):traiittarsus.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"):traiittarsus:at.level(sex, "2"):traiittarsus.animal			
Lag 0		0.04924110		
Lag 100		0.04492689		
Lag 500		0.02422838		
Lag 1000		-0.04034312		
Lag 5000		-0.03784851		
	traitbwt.byear traiittarsus.byear traitbwt.mother traiittarsus.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"):traiittarsus: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"):traiittarsus.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"):traiittarsus:at.level(sex, "2"):traiittarsus.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"):traiittarsus: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"):traiittarsus.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"):traiittarsus:at.level(sex, "1"):traiittarsus.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		1.0000000000		

```

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"):traiittarsus.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"):traiittarsus:at.level(sex, "2"):traiittarsus.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"):traiittarsus: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"):traiittarsus: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"):traiittarsus.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"):traiittarsus.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"):traiittarsus:at.level(sex, "1"):traiittarsus.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"):traiittarsus: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"):traiittarsus.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"):traiittarsus:at.level(sex, "2"):traiittarsus.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"):traiittarsus:at.level(sex, "1"):traiittarsus.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"):traiittarsus: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"):traiittarsus.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"):traiittarsus:at.level(sex, "2"):traiittarsus.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

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```

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

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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"):traiittarsus.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"):traiittarsus:at.level(sex, "2"):traiittarsus.animal
Lag 0                                -0.7532567
Lag 100                             -0.7106727
Lag 500                             -0.5497772
Lag 1000                            -0.3502307
Lag 5000                            0.1338020
                                         traitbwt.byear traiittarsus.byear traitbwt.mother traiittarsus.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"):traiittarsus: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"):trai	tarsus.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"):trai	tarsus:at.level(sex, "1"):trai	tarsus.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"):trai	tarsus:at.level(sex, "2"):trai	tarsus.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"):trai	tarsus.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"):trai	tarsus:at.level(sex, "2"):trai	tarsus.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$VCV[, "at.level(sex, \"1\"):traittarsus:at.level(sex, \"1\")"]  
residual.correlation2.4.F <- model2.4$VCV[, "at.level(sex, \"1\"):traittarsus:at.level(sex, \"1\")"]  
genetic.correlation2.4.M <- model2.4$VCV[, "at.level(sex, \"2\"):traittarsus:at.level(sex, \"2\")"]  
residual.correlation2.4.M <- model2.4$VCV[, "at.level(sex, \"2\"):traittarsus:at.level(sex, \"2\")"]  
#  
posterior.mode(genetic.correlation2.4.F)
```

```
var1  
0.7852385
```

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

```
var1  
0.8738073
```

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

```
var1  
0.9166822
```

```
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:

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

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

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

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

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

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

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

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

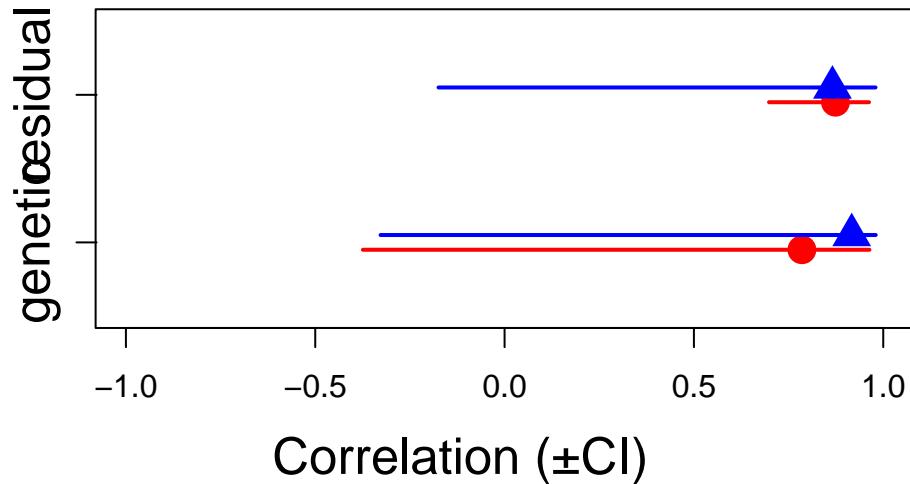
Here a plot to visualize the overlaps of covariances.

```
cor.est <- rbind(
  cbind(posterior.mode(genetic.correlation2.4.F, ), HPDinterval(genetic.correlation2.4.F, , 0.95),
  cbind(posterior.mode(genetic.correlation2.4.M), HPDinterval(genetic.correlation2.4.M, 0.95)),
  cbind(posterior.mode(residual.correlation2.4.F, ), HPDinterval(residual.correlation2.4.F, , 0.95),
  cbind(posterior.mode(residual.correlation2.4.M), HPDinterval(residual.correlation2.4.M, 0.95))
)
```

```

plot(c(0.95, 1.05, 1.95, 2.05) ~ cor.est[, 1], xlim = c(-1, 1), ylim = c(0.5, 2.5), xlab = "", yl
arrows(y0 = 0.95, x0 = cor.est[1, 2], y1 = 0.95, x1 = cor.est[1, 3], code = 3, angle = 90, length
arrows(y0 = 1.05, x0 = cor.est[2, 2], y1 = 1.05, x1 = cor.est[2, 3], code = 3, angle = 90, length
arrows(y0 = 1.95, x0 = cor.est[3, 2], y1 = 1.95, x1 = cor.est[3, 3], code = 3, angle = 90, length
arrows(y0 = 2.05, x0 = cor.est[4, 2], y1 = 2.05, x1 = cor.est[4, 3], code = 3, angle = 90, length
mtext("Correlation ( $\pm$ 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.

6.0.4. 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 ontogenetic 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 == i)]
}
#
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 == i)]
}

#
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
traiittarsus.1:traiittarsus.1.animal	6.632	2.136	12.69	85.74
traiittarsus.2:traiittarsus.1.animal	8.043	2.389	13.54	117.04
traiittarsus.1:traiittarsus.2.animal	8.043	2.389	13.54	117.04
traiittarsus.2:traiittarsus.2.animal	16.145	3.128	28.93	21.81

~idh(trait):byear

	post.mean	l-95% CI	u-95% CI	eff.samp
traiittarsus.1.byear	3.184	0.505	6.515	357.4
traiittarsus.2.byear	4.576	1.346	8.476	442.5

```

~idh(trait):mother

post.mean l-95% CI u-95% CI eff.samp
traiittarsus.1.mother     1.777  0.07858    4.714   299.68
traiittarsus.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
traiittarsus.1:traiittarsus.1.units   15.455   8.998   21.84  104.923
traiittarsus.2:traiittarsus.1.units  -1.497  -15.500   15.53   8.767
traiittarsus.1:traiittarsus.2.units  -1.497  -15.500   15.53   8.767
traiittarsus.2:traiittarsus.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
traiittarsus.1      20.48    19.62    21.48    703.9 <0.001 ***
traiittarsus.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)

, , traiittarsus.1:traiittarsus.1.animal

traiittarsus.1:traiittarsus.1.animal traiittarsus.2:traiittarsus.1.animal
Lag 0                  1.000000000 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

traiittarsus.1:traiittarsus.2.animal traiittarsus.2:traiittarsus.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
traiittarsus.1.byear traiittarsus.2.byear traiittarsus.1.mother		
Lag 0	0.05650214	-0.059474225
Lag 100	0.03805347	-0.063250151
Lag 500	0.03353186	-0.031583736
Lag 1000	0.02971111	0.032191172
Lag 5000	0.04021796	-0.001198619
traiittarsus.2.mother traiittarsus.1:traiittarsus.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
traiittarsus.2:traiittarsus.1.units traiittarsus.1:traiittarsus.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
traiittarsus.2:traiittarsus.2.units		
Lag 0	0.24444681	
Lag 100	0.28630940	
Lag 500	0.28676382	
Lag 1000	0.25016902	
Lag 5000	-0.01889626	
, , traiittarsus.2:traiittarsus.1.animal		
traiittarsus.1:traiittarsus.1.animal traiittarsus.2:traiittarsus.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
traiittarsus.1:traiittarsus.2.animal traiittarsus.2:traiittarsus.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
traiittarsus.1.byear traiittarsus.2.byear traiittarsus.1.mother		
Lag 0	-0.028123268	0.068035501
Lag 100	-0.036441213	0.058376180
Lag 500	-0.017206400	-0.002869166
Lag 1000	-0.004346341	-0.017320527
Lag 5000	-0.044798021	-0.083350187
traiittarsus.2.mother traiittarsus.1:traiittarsus.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
traiittarsus.2:traiittarsus.1.units traiittarsus.1:traiittarsus.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
traiittarsus.2:traiittarsus.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	0.068035501
Lag 100	-0.036441213	0.058376180
Lag 500	-0.017206400	-0.002869166
Lag 1000	-0.004346341	-0.017320527
Lag 5000	-0.044798021	-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
traiittarsus.2:traiittarsus.2.units		
Lag 0	-0.3304177	
Lag 100	-0.2624116	
Lag 500	-0.1893048	
Lag 1000	-0.2045441	
Lag 5000	-0.1580773	
 , , traiittarsus.2:traiittarsus.2.animal		
traiittarsus.1:traiittarsus.1.animal traiittarsus.2:traiittarsus.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
 traiittarsus.1:traiittarsus.2.animal traiittarsus.2:traiittarsus.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
 traiittarsus.1.byear traiittarsus.2.byear traiittarsus.1.mother		
Lag 0	-0.020084226	0.007263224
Lag 100	-0.015303798	0.013922907
Lag 500	-0.009604004	-0.022794079
Lag 1000	-0.036443873	0.038406389
Lag 5000	-0.046131641	-0.012187074
 traiittarsus.2.mother traiittarsus.1:traiittarsus.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
traiittarsus.2:traiittarsus.1.units traiittarsus.1:traiittarsus.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
traiittarsus.2:traiittarsus.2.units		
Lag 0	-0.90778147	
Lag 100	-0.84400702	
Lag 500	-0.70957533	
Lag 1000	-0.62450980	
Lag 5000	-0.06262314	
, , traiittarsus.1.byear		
traiittarsus.1:traiittarsus.1.animal traiittarsus.2:traiittarsus.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
traiittarsus.1:traiittarsus.2.animal traiittarsus.2:traiittarsus.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
traiittarsus.1.byear traiittarsus.2.byear traiittarsus.1.mother		
Lag 0	1.00000000	-0.008840935
Lag 100	0.23201455	-0.040849216
Lag 500	0.10173419	0.018677216
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
Lag 100	0.003895756	0.15813110
Lag 500	-0.028206511	0.02861588
Lag 1000	-0.022327614	0.02577769
Lag 5000	0.054519302	-0.01863939
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
traiittarsus.1:traiittarsus.2.animal traiittarsus.2:traiittarsus.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
traiittarsus.1.byear traiittarsus.2.byear traiittarsus.1.mother		
Lag 0	-0.034026465	0.019871390
Lag 100	-0.044009625	-0.022642909
Lag 500	0.033149894	-0.058758981
Lag 1000	-0.034811076	-0.041691079
Lag 5000	0.003520887	-0.007417182
traiittarsus.2.mother traiittarsus.1:traiittarsus.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
traiittarsus.2:traiittarsus.1.units traiittarsus.1:traiittarsus.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
traiittarsus.2:traiittarsus.2.units		
Lag 0	0.02429791	
Lag 100	0.01285473	
Lag 500	0.02017728	
Lag 1000	0.06093906	
Lag 5000	0.10720949	
, , traiittarsus.2.mother		

	trai	tarsus.1:trai	tarsus.1.animal	trai	tarsus.2:trai	tarsus.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	
	trai	tarsus.1:trai	tarsus.2.animal	trai	tarsus.2:trai	tarsus.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	
	trai	tarsus.1.byear	trai	tarsus.2.byear	trai	tarsus.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
	trai	tarsus.2.mother	trai	tarsus.1:trai	tarsus.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	
	trai	tarsus.2:trai	tarsus.1.units	trai	tarsus.1:trai	tarsus.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	
	trai	tarsus.2:trai	tarsus.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
traiittarsus.2:traiittarsus.2.units		
Lag 0	-0.2610614	
Lag 100	-0.3079509	
Lag 500	-0.2969894	
Lag 1000	-0.2847495	
Lag 5000	-0.0427216	
, , traiittarsus.2:traiittarsus.1.units		
traiittarsus.1:traiittarsus.1.animal traiittarsus.2:traiittarsus.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
traiittarsus.1:traiittarsus.2.animal traiittarsus.2:traiittarsus.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
traiittarsus.1.byear traiittarsus.2.byear traiittarsus.1.mother		
Lag 0	0.06264243	0.02138992
Lag 100	0.06751797	0.02085557
Lag 500	0.06731777	0.05500122
Lag 1000	0.06629827	0.10333723
Lag 5000	0.08927471	0.06016204
traiittarsus.2.mother traiittarsus.1:traiittarsus.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
 traiittarsus.2:traiittarsus.1.units traiittarsus.1:traiittarsus.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
 traiittarsus.2:traiittarsus.2.units		
Lag 0	-0.04275237	
Lag 100	-0.06227874	
Lag 500	-0.06672641	
Lag 1000	-0.04382724	
Lag 5000	0.03699475	
 , , traiittarsus.1:traiittarsus.2.units		
 traiittarsus.1:traiittarsus.1.animal traiittarsus.2:traiittarsus.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
 traiittarsus.1:traiittarsus.2.animal traiittarsus.2:traiittarsus.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
 traiittarsus.1.byear traiittarsus.2.byear traiittarsus.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 td="" traittarsus.1:traittarsus.1.units<=""><td data-kind="ghost"></td><td data-kind="ghost"></td><td data-kind="ghost"></td></traittarsus.2.mother>			
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 td="" traittarsus.1:traittarsus.2.units<=""><td data-kind="ghost"></td><td data-kind="ghost"></td><td data-kind="ghost"></td></traittarsus.2:traittarsus.1.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< td=""><td data-kind="ghost"></td><td data-kind="ghost"></td><td data-kind="ghost"></td></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 td="" traittarsus.2:traittarsus.1.animal<=""><td data-kind="ghost"></td><td data-kind="ghost"></td><td data-kind="ghost"></td></traittarsus.1: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 td="" traittarsus.2:traittarsus.2.animal<=""><td data-kind="ghost"></td><td data-kind="ghost"></td><td data-kind="ghost"></td></traittarsus.1: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
traiittarsus.1.byear traiittarsus.2.byear traiittarsus.1.mother		
Lag 0	0.01382634	-0.056471508
Lag 100	0.01730830	-0.030701856
Lag 500	0.03968933	0.004065694
Lag 1000	0.03341332	-0.048898719
Lag 5000	0.05219060	-0.013503372
traiittarsus.2.mother traiittarsus.1:traiittarsus.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
traiittarsus.2:traiittarsus.1.units traiittarsus.1:traiittarsus.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
traiittarsus.2:traiittarsus.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[, "traittarsus.1:traittarsus.2.animal"])
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))
) %>%
  filter(grepl("animal", Trait))

DvsS$ID <- substr(DvsS$Trait, 22, 26)
DvsS$TRAIT <- substr(DvsS$Trait, 6, 13)
summary(factor(DvsS$TRAIT))
```

```
tarsus.1 tarsus.2
```

```
1309      1309
```

```
DvsS$Trait <- NULL
```

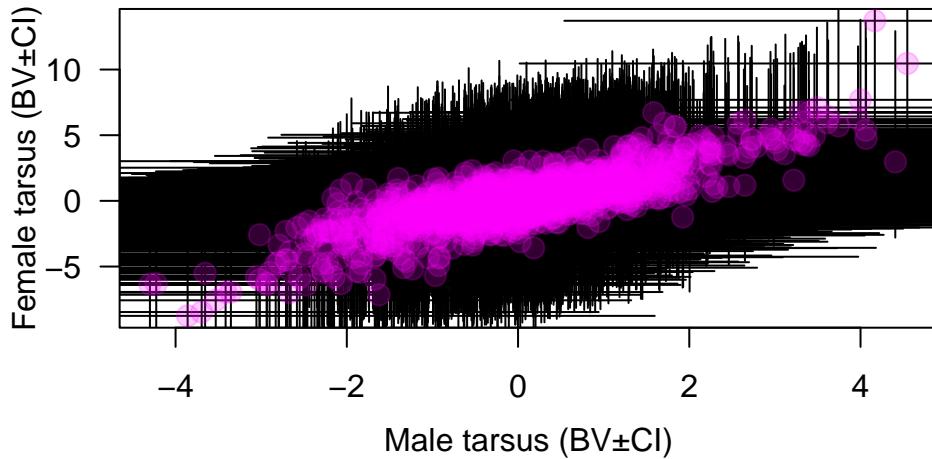
```
BLUPS <- reshape(DvsS, v.names = c("BLUP", "CI.lower", "CI.upper"), idvar = "ID", timevar = "TRAIT")
nrow(BLUPS)
```

```
[1] 1309
```

```
rownames(BLUPS) <- c()
colnames(BLUPS) <- c("ID", "BLUP.btw", "CI.L.btw", "CI.U.btw", "BLUP.tarsus", "CI.L.tarsus", "CI.U.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 : 0.024560	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.: -1.07251	1st Qu.: -8.156	1st Qu.: 4.9947	
Median : 0.07087	Median : -6.720	Median : 6.8749	
Mean : 0.07139	Mean : -6.464	Mean : 6.6127	
3rd Qu.: 1.17195	3rd Qu.: -4.869	3rd Qu.: 8.3021	
Max. : 13.71503	Max. : 1.264	Max. : 16.7611	

```
plot(BLUP.tarsus ~ BLUP.btw, BLUPS, xlab = "", ylab = "", las = 1.2, bty = "o", col = "white")
arrows(x0 = BLUPS$BLUP.btw, y0 = BLUPS$CI.L.tarsus, x1 = BLUPS$BLUP.btw, y1 = BLUPS$CI.U.tarsus,
arrows(x0 = BLUPS$CI.L.btw, y0 = BLUPS$BLUP.tarsus, x1 = BLUPS$CI.U.btw, y1 = BLUPS$BLUP.tarsus,
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,
  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:

```
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
traiittarsus.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
traiittarsus.1	20.424	19.488	21.324	484.6	<0.001 ***
traitbwt.1	6.143	5.686	6.550	596.7	<0.001 ***
traiittarsus.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

```
autocorr(model.MultivSex$VCV)
```

```
, , traiittarsus.1:traiittarsus.1.animal
```

	traiittarsus.1:traiittarsus.1.animal	traitbwt.1:traiittarsus.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

	traiittarsus.2:traiittarsus.1.animal	traitbwt.2:traiittarsus.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

	traiittarsus.1:traitbwt.1.animal	traitbwt.1:traiittarsus.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
traiittarsus.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
traiittarsus.1:traiittarsus.2.units traitbwt.1:traiittarsus.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
traiittarsus.2:traiittarsus.2.units traitbwt.2:traiittarsus.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
traiittarsus.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
traiittarsus.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
Lag 100	0.05744185	-0.04365919
Lag 500	0.04182580	-0.01683610
Lag 1000	0.08409670	0.04075709
Lag 5000	0.07211397	0.04755605
traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother		
Lag 0	-0.026101857	0.015326642
Lag 100	-0.026229006	0.004791955
Lag 500	-0.004795139	0.018197593
Lag 1000	-0.025567829	-0.014419690
Lag 5000	-0.011401634	-0.003782365
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
 traiittarsus.1:traiittarsus.1.units traitbwt.1:traiittarsus.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
 traiittarsus.2:traiittarsus.1.units traitbwt.2:traiittarsus.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
 traiittarsus.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
 traiittarsus.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
 traiittarsus.1:traiittarsus.2.units traitbwt.1:traiittarsus.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
 traiittarsus.2:traiittarsus.2.units traitbwt.2:traiittarsus.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

traiittarsus.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

traiittarsus.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

, , traiittarsus.2:traiittarsus.1.animal

traiittarsus.1:traiittarsus.1.animal traitbwt.1:traiittarsus.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

traiittarsus.2:traiittarsus.1.animal traitbwt.2:traiittarsus.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

traiittarsus.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
traiittarsus.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
traiittarsus.1:traiittarsus.2.animal traitbwt.1:traiittarsus.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
traiittarsus.2:traiittarsus.2.animal traitbwt.2:traiittarsus.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
traiittarsus.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
traiittarsus.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
traiittarsus.1.byear traitbwt.1.byear traiittarsus.2.byear		
Lag 0	0.01620495	0.04295234
Lag 100	0.02029711	0.05648775
Lag 500	0.04765917	0.03285861
Lag 1000	0.03767470	0.07587887
Lag 5000	-0.02249363	0.05599353
traitbwt.2.byear traiittarsus.1.mother traitbwt.1.mother		
Lag 0	-0.04161269	-0.102952660
Lag 100	-0.05474586	-0.077407539
Lag 500	-0.01536913	-0.009985327
Lag 1000	-0.02242552	-0.016880479
Lag 5000	0.05382429	0.093039192
traiittarsus.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
traiittarsus.1:traiittarsus.1.units traitbwt.1:traiittarsus.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
traiittarsus.2:traiittarsus.1.units traitbwt.2:traiittarsus.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
traiittarsus.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
traiittarsus.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
traiittarsus.1:traiittarsus.2.units traitbwt.1:traiittarsus.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
traiittarsus.2:traiittarsus.2.units traitbwt.2:traiittarsus.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
traiittarsus.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
traiittarsus.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	
Lag 5000	-0.006519724	0.08285167	
traiittarsus.2:traiittarsus.2.animal traitbwt.2:traiittarsus.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	
traiittarsus.1:traitbwt.2.animal traitbwt.1:traitbwt.2.animal			
Lag 0	1.0000000	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	
traiittarsus.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	
traiittarsus.1.byear traitbwt.1.byear traiittarsus.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 traiittarsus.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
traiittarsus.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

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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

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Lag 1000	0.2351271	0.3004179
Lag 5000	0.1671396	0.1589172
traiittarsus.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
traiittarsus.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
traiittarsus.1:traiittarsus.2.animal traitbwt.1:traiittarsus.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
traiittarsus.2:traiittarsus.2.animal traitbwt.2:traiittarsus.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
traiittarsus.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
traiittarsus.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
traiittarsus.1.byear traitbwt.1.byear traiittarsus.2.byear		
Lag 0	0.06781216	-0.04857154
Lag 100	0.05744185	-0.04365919
Lag 500	0.04182580	-0.01683610
Lag 1000	0.08409670	0.04075709
Lag 5000	0.07211397	0.04755605
traitbwt.2.byear traiittarsus.1.mother traitbwt.1.mother		
Lag 0	-0.026101857	0.015326642
Lag 100	-0.026229006	0.004791955
Lag 500	-0.004795139	0.018197593
Lag 1000	-0.025567829	-0.014419690
Lag 5000	-0.011401634	-0.003782365
traiittarsus.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
traiittarsus.1:traiittarsus.1.units traitbwt.1:traiittarsus.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
traiittarsus.2:traiittarsus.1.units traitbwt.2:traiittarsus.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
traiittarsus.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
traiittarsus.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
traiittarsus.1:traiittarsus.2.units traitbwt.1:traiittarsus.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
traiittarsus.2:traiittarsus.2.units traitbwt.2:traiittarsus.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
traiittarsus.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
traiittarsus.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

traiittarsus.1:traiittarsus.1.animal traitbwt.1:traiittarsus.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

traiittarsus.2:traiittarsus.1.animal traitbwt.2:traiittarsus.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

traiittarsus.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

traiittarsus.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

traiittarsus.1:traiittarsus.2.animal traitbwt.1:traiittarsus.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
Lag 100	0.038096586	-0.064724456
Lag 500	-0.002027739	0.020824115
Lag 1000	0.057546907	0.008429484
Lag 5000	0.105389029	0.003598701
traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother		
Lag 0	-0.02489988	0.063535708
Lag 100	-0.02027214	0.044670327
Lag 500	-0.01893478	0.000885945

Lag 1000	-0.01593842	-0.053672083	-0.098869582
Lag 5000	-0.06322669	0.022199101	0.007755258
traiittarsus.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	
traiittarsus.1:traiittarsus.1.units traitbwt.1:traiittarsus.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
traiittarsus.2:traiittarsus.1.units traitbwt.2:traiittarsus.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
traiittarsus.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
traiittarsus.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
traiittarsus.1:traiittarsus.2.units traitbwt.1:traiittarsus.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
traiittarsus.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
traiittarsus.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
traiittarsus.1:traiittarsus.2.animal traitbwt.1:traiittarsus.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
traiittarsus.2:traiittarsus.2.animal traitbwt.2:traiittarsus.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
traiittarsus.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
Lag 100	0.024425366	0.01320865
Lag 500	0.050837464	0.03060238
Lag 1000	0.065685010	0.04013922
Lag 5000	-0.006279369	0.01390888
traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother		
Lag 0	-0.06566102	0.010266822
Lag 100	-0.05957647	0.001133316
Lag 500	-0.03310752	-0.035302602
Lag 1000	-0.01325750	-0.005132729
Lag 5000	0.07737072	0.051936326
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
traiittarsus.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
traiittarsus.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
traiittarsus.1:traiittarsus.2.units traitbwt.1:traiittarsus.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
traiittarsus.2:traiittarsus.2.units traitbwt.2:traiittarsus.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
traiittarsus.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
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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		
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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 td="" traitbwt.2:traittarsus.1.animal<=""><td data-kind="ghost"></td><td data-kind="ghost"></td></traittarsus.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 td="" traitbwt.1:traitbwt.1.animal<=""><td data-kind="ghost"></td><td data-kind="ghost"></td></traittarsus.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 td="" traitbwt.2:traitbwt.1.animal<=""><td data-kind="ghost"></td><td data-kind="ghost"></td></traittarsus.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
traiittarsus.1:traiittarsus.2.animal traitbwt.1:traiittarsus.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
traiittarsus.2:traiittarsus.2.animal traitbwt.2:traiittarsus.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
traiittarsus.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
traiittarsus.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
traiittarsus.1.byear traitbwt.1.byear traiittarsus.2.byear		
Lag 0	0.034800266	0.007431509
Lag 100	0.051936557	-0.001493245
Lag 500	0.071129943	0.067797207
Lag 1000	0.103624443	0.063225351
Lag 5000	-0.000397122	0.008471637
traitbwt.2.byear traiittarsus.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
traiittarsus.1:traiittarsus.2.units traitbwt.1:traiittarsus.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
traiittarsus.2:traiittarsus.2.units traitbwt.2:traiittarsus.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
traiittarsus.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
traiittarsus.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
, , traiittarsus.1:traiittarsus.2.animal		
traiittarsus.1:traiittarsus.1.animal traitbwt.1:traiittarsus.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
Lag 100	0.02029711	0.05648775
Lag 500	0.04765917	0.03285861
Lag 1000	0.03767470	0.07587887
Lag 5000	-0.02249363	0.05599353
traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother		
Lag 0	-0.04161269	-0.102952660
Lag 100	-0.05474586	-0.077407539
Lag 500	-0.01536913	-0.009985327
Lag 1000	-0.02242552	-0.016880479
Lag 5000	0.05382429	0.093039192
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
traiittarsus.2:traiittarsus.1.units traitbwt.2:traiittarsus.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
traiittarsus.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
traiittarsus.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
traiittarsus.1:traiittarsus.2.units traitbwt.1:traiittarsus.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
traiittarsus.2:traiittarsus.2.units traitbwt.2:traiittarsus.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
traiittarsus.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
 traiittarsus.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:traiittarsus.2.animal		
 traiittarsus.1:traiittarsus.1.animal traitbwt.1:traiittarsus.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
 traiittarsus.2:traiittarsus.1.animal traitbwt.2:traiittarsus.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
 traiittarsus.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
 traiittarsus.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
Lag 100	0.024425366	0.01320865
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
traiittarsus.2:traiittarsus.1.animal traitbwt.2:traiittarsus.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
traiittarsus.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
traiittarsus.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
traiittarsus.1:traiittarsus.2.animal traitbwt.1:traiittarsus.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
traiittarsus.2:traiittarsus.2.animal traitbwt.2:traiittarsus.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
Lag 100	0.026817555	-0.002104493
Lag 500	0.008446146	-0.011130916
Lag 1000	0.029054326	0.040567400
Lag 5000	-0.032575030	0.020439004
traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother		
Lag 0	-0.08333086	0.04651404
Lag 100	-0.08053153	0.06577446
Lag 500	-0.03847864	0.11200938
Lag 1000	-0.04249559	0.08134977
Lag 5000	0.07016400	0.02226530
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
traiittarsus.2:traiittarsus.1.units traitbwt.2:traiittarsus.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
traiittarsus.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
traiittarsus.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
traiittarsus.1:traiittarsus.2.units traitbwt.1:traiittarsus.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
traiittarsus.2:traiittarsus.2.units traitbwt.2:traiittarsus.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
traiittarsus.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
traiittarsus.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:traiittarsus.2.animal		
traiittarsus.1:traiittarsus.1.animal traitbwt.1:traiittarsus.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
traiittarsus.2:traiittarsus.1.animal traitbwt.2:traiittarsus.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
traiittarsus.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
traiittarsus.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
traiittarsus.1:traiittarsus.2.animal traitbwt.1:traiittarsus.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
traiittarsus.2:traiittarsus.2.animal traitbwt.2:traiittarsus.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
traiittarsus.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
traiittarsus.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
traiittarsus.1.byear traitbwt.1.byear traiittarsus.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
Lag 100		-0.1156256	-0.12366939
Lag 500		-0.1042741	-0.12078005

Lag 1000	-0.1076860	-0.15700540
Lag 5000	0.0712461	0.01799705
traiittarsus.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
traiittarsus.1:traiittarsus.2.units traitbwt.1:traiittarsus.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
traiittarsus.2:traiittarsus.2.units traitbwt.2:traiittarsus.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
traiittarsus.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
traiittarsus.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
traiittarsus.1:traitbwt.2.animal traitbwt.1:traitbwt.2.animal		
Lag 0	1.0000000	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
traiittarsus.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
traiittarsus.1.byear traitbwt.1.byear traiittarsus.2.byear		
Lag 0	0.063463728	0.02730871
Lag 100	0.066558472	0.03961464
Lag 500	0.076728186	0.05374642
Lag 1000	0.100842393	0.09752083
Lag 5000	-0.006751012	0.04984406
traitbwt.2.byear traiittarsus.1.mother traitbwt.1.mother		
Lag 0	-0.09337461	0.02006907
Lag 100	-0.09001277	0.02763705
Lag 500	-0.04869538	0.02000750
Lag 1000	-0.05831890	0.02560894
Lag 5000	0.04246982	0.06392166
traiittarsus.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
traiittarsus.1:traiittarsus.1.units traitbwt.1:traiittarsus.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
traiittarsus.2:traiittarsus.1.units traitbwt.2:traiittarsus.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
traiittarsus.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
traiittarsus.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
traiittarsus.1:traiittarsus.2.units traitbwt.1:traiittarsus.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
traiittarsus.2:traiittarsus.2.units traitbwt.2:traiittarsus.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
 traiittarsus.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
 traiittarsus.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		
 traiittarsus.1:traiittarsus.1.animal traitbwt.1:traiittarsus.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
 traiittarsus.2:traiittarsus.1.animal traitbwt.2:traiittarsus.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
 traiittarsus.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
traiittarsus.1.byear traitbwt.1.byear traiittarsus.2.byear		
Lag 0	0.034800266	0.007431509
Lag 100	0.051936557	-0.001493245
Lag 500	0.071129943	0.067797207
Lag 1000	0.103624443	0.063225351
Lag 5000	-0.000397122	0.008471637
traitbwt.2.byear traiittarsus.1.mother traitbwt.1.mother		
Lag 0	-0.08333568	0.100888337
Lag 100	-0.07762909	0.079323546
Lag 500	-0.03825641	-0.007478373
Lag 1000	-0.02784742	0.017077993
Lag 5000	0.04558001	0.022598106
traiittarsus.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
traiittarsus.1:traiittarsus.1.units traitbwt.1:traiittarsus.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
traiittarsus.2:traiittarsus.1.units traitbwt.2:traiittarsus.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
traiittarsus.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
traiittarsus.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
traiittarsus.1:traiittarsus.2.units traitbwt.1:traiittarsus.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
traiittarsus.2:traiittarsus.2.units traitbwt.2:traiittarsus.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
traiittarsus.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
traiittarsus.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
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
Lag 100	0.04921037	0.008930910
Lag 500	0.03899327	0.015514352
Lag 1000	0.06406637	0.051682789
Lag 5000	-0.01137788	0.015052216
traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother		
Lag 0	-0.12402916	0.08639137
Lag 100	-0.10713277	0.09204331
Lag 500	-0.07124572	0.09145340
Lag 1000	-0.06554488	0.09437629
Lag 5000	0.06888625	0.02727995
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
traiittarsus.1:traiittarsus.1.units traitbwt.1:traiittarsus.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
traiittarsus.2:traiittarsus.1.units traitbwt.2:traiittarsus.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
traiittarsus.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
traiittarsus.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
traiittarsus.1:traiittarsus.2.units traitbwt.1:traiittarsus.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
, , 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
 traiittarsus.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
 traiittarsus.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
 traiittarsus.1:traiittarsus.2.animal traitbwt.1:traiittarsus.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
 traiittarsus.2:traiittarsus.2.animal traitbwt.2:traiittarsus.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
Lag 5000	0.0305572	-0.02000725
 traiittarsus.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
 traiittarsus.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
traiittarsus.1.byear traitbwt.1.byear traiittarsus.2.byear		
Lag 0	0.05353374	0.007606345
Lag 100	0.05915538	0.016873424
Lag 500	0.05495199	0.034153584
Lag 1000	0.08867289	0.063336260
Lag 5000	0.01157646	0.010648297
traitbwt.2.byear traiittarsus.1.mother traitbwt.1.mother		
Lag 0	-0.11303991	0.128729447
Lag 100	-0.10682241	0.132664466
Lag 500	-0.06622430	0.082749840
Lag 1000	-0.06796661	0.092840268
Lag 5000	0.07422776	0.007625067
traiittarsus.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
traiittarsus.1:traiittarsus.1.units traitbwt.1:traiittarsus.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
traiittarsus.2:traiittarsus.1.units traitbwt.2:traiittarsus.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
traiittarsus.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
traiittarsus.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
traiittarsus.1:traiittarsus.2.units traitbwt.1:traiittarsus.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
traiittarsus.2:traiittarsus.2.units traitbwt.2:traiittarsus.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
traiittarsus.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
traiittarsus.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
traiittarsus.2:traiittarsus.2.animal traitbwt.2:traiittarsus.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
traiittarsus.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
traiittarsus.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
traiittarsus.1.byear traitbwt.1.byear traiittarsus.2.byear		
Lag 0	1.00000000	-0.011500754
Lag 100	0.29498964	0.032775932
Lag 500	0.01534486	-0.007063004
Lag 1000	-0.00531817	0.074940752
Lag 5000	-0.04617778	-0.015458692
traitbwt.2.byear traiittarsus.1.mother traitbwt.1.mother		
Lag 0	-0.0081906518	0.107143639
Lag 100	-0.0458427594	0.096733446
Lag 500	0.0004877642	0.068025342

Lag 1000	0.0105349484	-0.002189929	-0.01019378
Lag 5000	-0.0644916207	-0.020934152	0.04368155
traiittarsus.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	
traiittarsus.1:traiittarsus.1.units traitbwt.1:traiittarsus.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
traiittarsus.2:traiittarsus.1.units traitbwt.2:traiittarsus.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
traiittarsus.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
traiittarsus.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
traiittarsus.1:traiittarsus.2.units traitbwt.1:traiittarsus.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
 traiittarsus.2:traiittarsus.2.units traitbwt.2:traiittarsus.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
 traiittarsus.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
Lag 1000	-0.01855463	0.00885959
Lag 5000	0.01037899	0.01362772
 traiittarsus.2:traitbwt.2.units traitbwt.2:traiittarsus.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		
 traiittarsus.1:traiittarsus.1.animal traitbwt.1:traiittarsus.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
 traiittarsus.2:traiittarsus.1.animal traitbwt.2:traiittarsus.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
traiittarsus.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
traiittarsus.1.byear traitbwt.1.byear traiittarsus.2.byear		
Lag 0	-0.011500754	1.00000000
Lag 100	-0.008778968	0.12997956
Lag 500	-0.004505343	0.03863671
Lag 1000	0.025463698	-0.01655625
Lag 5000	0.001254535	-0.04239004
traitbwt.2.byear traiittarsus.1.mother traitbwt.1.mother		
Lag 0	-0.039257246	-0.02879748
Lag 100	0.015007558	-0.03208555
Lag 500	-0.005393351	0.03210587
Lag 1000	0.043913747	0.05551756
Lag 5000	-0.026820593	0.05843803
traiittarsus.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
traiittarsus.1:traiittarsus.1.units traitbwt.1:traiittarsus.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
traiittarsus.2:traiittarsus.1.units traitbwt.2:traiittarsus.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
traiittarsus.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
traiittarsus.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
traiittarsus.1:traiittarsus.2.units traitbwt.1:traiittarsus.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
traiittarsus.2:traiittarsus.2.units traitbwt.2:traiittarsus.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
traiittarsus.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		
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
Lag 100	0.004989327	0.01606065
Lag 500	0.044052804	0.03428138
Lag 1000	-0.001440518	0.01039861
Lag 5000	0.022958892	-0.01931981
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
traiittarsus.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	
traiittarsus.1:traiittarsus.1.units traitbwt.1:traiittarsus.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
traiittarsus.2:traiittarsus.1.units traitbwt.2:traiittarsus.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
traiittarsus.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
traiittarsus.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
traiittarsus.1:traiittarsus.2.units traitbwt.1:traiittarsus.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
traiittarsus.2:traiittarsus.2.units traitbwt.2:traiittarsus.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
traiittarsus.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
traiittarsus.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		
traiittarsus.1:traiittarsus.1.animal traitbwt.1:traiittarsus.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
traiittarsus.2:traiittarsus.1.animal traitbwt.2:traiittarsus.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
traiittarsus.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
traiittarsus.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
traiittarsus.1:traiittarsus.2.animal traitbwt.1:traiittarsus.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
traiittarsus.2:traiittarsus.2.animal traitbwt.2:traiittarsus.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
traiittarsus.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	0.03963537
Lag 100	-0.031080960	0.00903900
Lag 500	0.006051004	-0.06809153
Lag 1000	0.018314138	-0.02323337
Lag 5000	-0.026798307	-0.01177870
traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother		
Lag 0	1.000000000	0.019595061
Lag 100	0.148773685	0.013805361
Lag 500	0.023071337	0.001042167
Lag 1000	0.001235911	0.034032045
Lag 5000	-0.035993191	-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
traiittarsus.2:traiittarsus.1.units traitbwt.2:traiittarsus.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
traiittarsus.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
traiittarsus.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
traiittarsus.1:traiittarsus.2.units traitbwt.1:traiittarsus.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
traiittarsus.2:traiittarsus.2.units traitbwt.2:traiittarsus.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
traiittarsus.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
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
traiittarsus.1:traiittarsus.2.animal traitbwt.1:traiittarsus.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
traiittarsus.2:traiittarsus.2.animal traitbwt.2:traiittarsus.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
traiittarsus.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
traiittarsus.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
traiittarsus.1.byear traitbwt.1.byear traiittarsus.2.byear		
Lag 0	0.10714364	-0.028797482
Lag 100	0.12475726	-0.002859105
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			
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
traiittarsus.1:traitbwt.2.animal traitbwt.1:traitbwt.2.animal		
Lag 0	-0.06942502	-0.21005355
Lag 100	-0.06694784	-0.17453411
Lag 500	-0.04628001	-0.13167639
Lag 1000	-0.02832344	-0.06743430
Lag 5000	0.06116511	0.06036364
traiittarsus.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
traiittarsus.1.byear traitbwt.1.byear traiittarsus.2.byear		
Lag 0	-0.06029833	0.065880688
Lag 100	-0.06060175	0.002155759
Lag 500	0.02852613	-0.001260087
Lag 1000	-0.02910626	0.001290157
Lag 5000	-0.01024266	0.050399045
traitbwt.2.byear traiittarsus.1.mother traitbwt.1.mother		
Lag 0	0.0195950614	-0.2712137958
Lag 100	-0.0008933777	-0.1720110752
Lag 500	0.0366638614	-0.0393624856
Lag 1000	-0.0151426446	0.0476618317
Lag 5000	0.0123140414	0.0001252644
traiittarsus.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
traiittarsus.1:traiittarsus.1.units traitbwt.1:traiittarsus.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
traiittarsus.2:traiittarsus.1.units traitbwt.2:traiittarsus.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
traiittarsus.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
traiittarsus.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
traiittarsus.1:traiittarsus.2.units traitbwt.1:traiittarsus.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
traiittarsus.2:traiittarsus.2.units traitbwt.2:traiittarsus.2.units		
Lag 0	0.08205572	0.11704839
Lag 100	0.07607819	0.11403531
Lag 500	0.10265484	0.14762922

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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

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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
traiittarsus.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
traiittarsus.1:traiittarsus.2.units traitbwt.1:traiittarsus.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
traiittarsus.2:traiittarsus.2.units traitbwt.2:traiittarsus.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
traiittarsus.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
traiittarsus.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
Lag 100	-0.01583481	0.05520016
Lag 500	0.03917478	0.01148328
Lag 1000	-0.03694049	0.02504159
Lag 5000	-0.06196001	0.02957462
traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother		
Lag 0	-0.007859673	-0.05622667
Lag 100	0.010189964	-0.05585546
Lag 500	0.007357905	0.02124383
Lag 1000	0.029340288	0.06934074
Lag 5000	0.011164278	0.01230641
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
traiittarsus.1:traiittarsus.1.units traitbwt.1:traiittarsus.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
traiittarsus.2:traiittarsus.1.units traitbwt.2:traiittarsus.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
traiittarsus.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
traiittarsus.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
traiittarsus.1:traiittarsus.2.units traitbwt.1:traiittarsus.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
traiittarsus.2:traiittarsus.2.units traitbwt.2:traiittarsus.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
traiittarsus.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
traiittarsus.1:traiittarsus.2.animal traitbwt.1:traiittarsus.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
traiittarsus.2:traiittarsus.2.animal traitbwt.2:traiittarsus.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
traiittarsus.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
traiittarsus.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
traiittarsus.1.byear traitbwt.1.byear traiittarsus.2.byear		
Lag 0	-0.14506604	-0.043558650
Lag 100	-0.12498034	-0.053994536
Lag 500	-0.05225308	-0.005205432
Lag 1000	-0.05643316	-0.037921140
Lag 5000	-0.01904738	-0.070857345
traitbwt.2.byear traiittarsus.1.mother traitbwt.1.mother		
Lag 0	0.01051817	-0.28511353
Lag 100	0.03224747	-0.21849925
Lag 500	0.03546917	-0.12897815
Lag 1000	0.01230618	-0.03335119
Lag 5000	0.02825979	-0.05125552
traiittarsus.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
traiittarsus.1:traiittarsus.1.units traitbwt.1:traiittarsus.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
traiittarsus.2:traiittarsus.1.units traitbwt.2:traiittarsus.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
traiittarsus.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
traiittarsus.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
traiittarsus.1:traiittarsus.2.units traitbwt.1:traiittarsus.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
traiittarsus.2:traiittarsus.2.units traitbwt.2:traiittarsus.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
traiittarsus.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
traiittarsus.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	
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
traiittarsus.1:traiittarsus.1.units traitbwt.1:traiittarsus.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
traiittarsus.2:traiittarsus.1.units traitbwt.2:traiittarsus.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
traiittarsus.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
traiittarsus.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
traiittarsus.1:traiittarsus.2.units traitbwt.1:traiittarsus.2.units		
Lag 0	-0.1706739	-0.1666030
Lag 100	-0.1802375	-0.1812316
Lag 500	-0.2103921	-0.2194596

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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

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Lag 1000	0.2243627	0.17422740
Lag 5000	0.1612708	0.09845918
traiittarsus.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
traiittarsus.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
traiittarsus.1:traiittarsus.2.animal traitbwt.1:traiittarsus.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
traiittarsus.2:traiittarsus.2.animal traitbwt.2:traiittarsus.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
traiittarsus.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
traiittarsus.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
traiittarsus.1.byear traitbwt.1.byear traiittarsus.2.byear		
Lag 0	-0.03847015	0.05293519
Lag 100	-0.03144044	0.04956734
Lag 500	-0.01780154	0.05591029
Lag 1000	-0.02643841	0.04337011
Lag 5000	-0.01140358	0.03031863
traitbwt.2.byear traiittarsus.1.mother traitbwt.1.mother		
Lag 0	-0.041798551	0.1697424
Lag 100	-0.034073821	0.1688986
Lag 500	-0.048890409	0.1720568
Lag 1000	-0.040999443	0.1790535
Lag 5000	-0.002784642	0.1836021
traiittarsus.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
traiittarsus.1:traiittarsus.1.units traitbwt.1:traiittarsus.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
traiittarsus.2:traiittarsus.1.units traitbwt.2:traiittarsus.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
traiittarsus.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
traiittarsus.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
traiittarsus.1:traiittarsus.2.units traitbwt.1:traiittarsus.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
traiittarsus.2:traiittarsus.2.units traitbwt.2:traiittarsus.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
traiittarsus.1:traitbwt.2.units traitbwt.1:traitbwt.2.units		
Lag 0	0.9603400	0.9034487
Lag 100	0.94444274	0.8893146
Lag 500	0.90544416	0.8539291
Lag 1000	0.8617258	0.8157349
Lag 5000	0.6022291	0.5773694
traiittarsus.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.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
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
Lag 100	-0.031641858	0.05864059
Lag 500	-0.001530924	0.04503326
Lag 1000	-0.016005519	0.03161375
Lag 5000	0.010619935	0.01730446
traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother		
Lag 0	-0.032356483	0.1703875
Lag 100	-0.034654911	0.1647608
Lag 500	-0.052597308	0.1600416
		0.005553001

Lag 1000	-0.039591608	0.1872703	-0.009042770
Lag 5000	0.004455343	0.1972374	-0.027185781
traiittarsus.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	
traiittarsus.1:traiittarsus.1.units traitbwt.1:traiittarsus.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
traiittarsus.2:traiittarsus.1.units traitbwt.2:traiittarsus.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
traiittarsus.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
traiittarsus.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
traiittarsus.1:traiittarsus.2.units traitbwt.1:traiittarsus.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
traiittarsus.2:traiittarsus.2.units traitbwt.2:traiittarsus.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
traiittarsus.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
traiittarsus.2:traitbwt.2.units traitbwt.2:traiittarsus.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
, , traiittarsus.1:traitbwt.1.units		
traiittarsus.1:traiittarsus.1.animal traitbwt.1:traiittarsus.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
traiittarsus.2:traiittarsus.1.animal traitbwt.2:traiittarsus.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
traiittarsus.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
traiittarsus.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
traiittarsus.1:traiittarsus.2.animal traitbwt.1:traiittarsus.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
traiittarsus.2:traiittarsus.2.animal traitbwt.2:traiittarsus.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
traiittarsus.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
traiittarsus.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
traiittarsus.1.byear traitbwt.1.byear traiittarsus.2.byear		
Lag 0	-0.10471675	0.01021951
Lag 100	-0.08194667	0.01380504
Lag 500	-0.01278894	0.03290932
Lag 1000	-0.06407190	-0.02170329
Lag 5000	-0.07516029	-0.06130238
traitbwt.2.byear traiittarsus.1.mother traitbwt.1.mother		
Lag 0	0.02175859	-0.039522955
Lag 100	0.03477326	-0.019056605
Lag 500	-0.01973469	-0.002626844
Lag 1000	0.04003712	0.003169525
Lag 5000	0.02550062	-0.010727363
traiittarsus.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
traiittarsus.1:traiittarsus.1.units traitbwt.1:traiittarsus.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
traiittarsus.2:traiittarsus.1.units traitbwt.2:traiittarsus.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
traiittarsus.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
traiittarsus.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
traiittarsus.1:traiittarsus.2.units traitbwt.1:traiittarsus.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
traiittarsus.2:traiittarsus.2.units traitbwt.2:traiittarsus.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
traiittarsus.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	
traiittarsus.1:traiittarsus.2.animal traitbwt.1:traiittarsus.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	
traiittarsus.2:traiittarsus.2.animal traitbwt.2:traiittarsus.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	
traiittarsus.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	
traiittarsus.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	
traiittarsus.1.byear traitbwt.1.byear traiittarsus.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 traiittarsus.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
traiittarsus.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	
traiittarsus.1:traiittarsus.1.units traitbwt.1:traiittarsus.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
traiittarsus.2:traiittarsus.1.units traitbwt.2:traiittarsus.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
traiittarsus.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
traiittarsus.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
Lag 5000	-0.1444361	-0.1252641
traiittarsus.1:traiittarsus.2.units traitbwt.1:traiittarsus.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
traiittarsus.2:traiittarsus.2.units traitbwt.2:traiittarsus.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
traiittarsus.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
traiittarsus.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
, , traiittarsus.2:traitbwt.1.units		
traiittarsus.1:traiittarsus.1.animal traitbwt.1:traiittarsus.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 td="" traitbwt.2:traittarsus.1.animal<=""><td data-kind="ghost"></td><td data-kind="ghost"></td></traittarsus.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 td="" traitbwt.1:traitbwt.1.animal<=""><td data-kind="ghost"></td><td data-kind="ghost"></td></traittarsus.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 td="" traitbwt.2:traitbwt.1.animal<=""><td data-kind="ghost"></td><td data-kind="ghost"></td></traittarsus.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 td="" traitbwt.1:traittarsus.2.animal<=""><td data-kind="ghost"></td><td data-kind="ghost"></td></traittarsus.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
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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
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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
Lag 100	-0.023937020	0.05747431
Lag 500	-0.009997799	0.05757848
Lag 1000	-0.028336813	0.03932991
Lag 5000	-0.028421868	0.02850733
traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother		
Lag 0	-0.0558751650	0.1570314
Lag 100	-0.0390036691	0.1577619
Lag 500	-0.0604361094	0.1762753
Lag 1000	-0.0544777158	0.1711484
Lag 5000	0.0009703848	0.1611550
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
traiittarsus.2:traiittarsus.1.units traitbwt.2:traiittarsus.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
traiittarsus.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
traiittarsus.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
traiittarsus.1:traiittarsus.2.units traitbwt.1:traiittarsus.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
traiittarsus.2:traiittarsus.2.units traitbwt.2:traiittarsus.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
traiittarsus.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
 traiittarsus.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		
 traiittarsus.1:traiittarsus.1.animal traitbwt.1:traiittarsus.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
 traiittarsus.2:traiittarsus.1.animal traitbwt.2:traiittarsus.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
 traiittarsus.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
 traiittarsus.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
Lag 100	-0.021944414	0.05837761
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
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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
traiittarsus.2:traiittarsus.1.animal traitbwt.2:traiittarsus.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
traiittarsus.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
traiittarsus.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
traiittarsus.1:traiittarsus.2.animal traitbwt.1:traiittarsus.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
traiittarsus.2:traiittarsus.2.animal traitbwt.2:traiittarsus.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
Lag 100	-0.03144044	0.04956734
Lag 500	-0.01780154	0.05591029
Lag 1000	-0.02643841	0.04337011
Lag 5000	-0.01140358	0.03031863
traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother		
Lag 0	-0.041798551	0.1697424
Lag 100	-0.034073821	0.1688986
Lag 500	-0.048890409	0.1720568
Lag 1000	-0.040999443	0.1790535
Lag 5000	-0.002784642	0.1836021
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
traiittarsus.2:traiittarsus.1.units traitbwt.2:traiittarsus.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
traiittarsus.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
traiittarsus.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
traiittarsus.1:traiittarsus.2.units traitbwt.1:traiittarsus.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
traiittarsus.2:traiittarsus.2.units traitbwt.2:traiittarsus.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
traiittarsus.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
traiittarsus.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:traiittarsus.2.units		
traiittarsus.1:traiittarsus.1.animal traitbwt.1:traiittarsus.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
traiittarsus.2:traiittarsus.1.animal traitbwt.2:traiittarsus.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
traiittarsus.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
traiittarsus.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
traiittarsus.1:traiittarsus.2.animal traitbwt.1:traiittarsus.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
traiittarsus.2:traiittarsus.2.animal traitbwt.2:traiittarsus.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
traiittarsus.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
traiittarsus.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
traiittarsus.1.byear traitbwt.1.byear traiittarsus.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
traiittarsus.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
traiittarsus.1:traiittarsus.2.units traitbwt.1:traiittarsus.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
traiittarsus.2:traiittarsus.2.units traitbwt.2:traiittarsus.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
traiittarsus.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
traiittarsus.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	
traiittarsus.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	
traiittarsus.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	
traiittarsus.1.byear traitbwt.1.byear traiittarsus.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 traiittarsus.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
traiittarsus.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
traiittarsus.1:traiittarsus.1.units traitbwt.1:traiittarsus.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
traiittarsus.2:traiittarsus.1.units traitbwt.2:traiittarsus.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
traiittarsus.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
traiittarsus.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
traiittarsus.1:traiittarsus.2.units traitbwt.1:traiittarsus.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
traiittarsus.2:traiittarsus.2.units traitbwt.2:traiittarsus.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
 traiittarsus.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
 traiittarsus.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:traiittarsus.2.units		
 traiittarsus.1:traiittarsus.1.animal traitbwt.1:traiittarsus.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
 traiittarsus.2:traiittarsus.1.animal traitbwt.2:traiittarsus.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
 traiittarsus.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
traiittarsus.1.byear traitbwt.1.byear traiittarsus.2.byear		
Lag 0	-0.04533921	-0.001638125
Lag 100	-0.04526568	0.002752216
Lag 500	-0.02361959	-0.010266769
Lag 1000	-0.08661480	-0.055915794
Lag 5000	0.02028860	-0.015718402
traitbwt.2.byear traiittarsus.1.mother traitbwt.1.mother		
Lag 0	0.09224924	-0.08507034
Lag 100	0.09712475	-0.09090158
Lag 500	0.06704383	-0.06950074
Lag 1000	0.06946025	-0.09719184
Lag 5000	-0.05957284	-0.01506617
traiittarsus.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
traiittarsus.1:traiittarsus.1.units traitbwt.1:traiittarsus.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
traiittarsus.2:traiittarsus.1.units traitbwt.2:traiittarsus.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
traiittarsus.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
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
traiittarsus.2:traiittarsus.2.animal traitbwt.2:traiittarsus.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
traiittarsus.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
traiittarsus.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
traiittarsus.1.byear traitbwt.1.byear traiittarsus.2.byear		
Lag 0	-0.032369970	0.05768879
Lag 100	-0.031641858	0.05864059
Lag 500	-0.001530924	0.04503326
Lag 1000	-0.016005519	0.03161375
Lag 5000	0.010619935	0.01730446
traitbwt.2.byear traiittarsus.1.mother traitbwt.1.mother		
Lag 0	-0.032356483	0.1703875
Lag 100	-0.034654911	0.1647608
Lag 500	-0.052597308	0.1600416
Lag 1000	-0.039591608	0.1872703
Lag 5000	0.004455343	0.1972374
traiittarsus.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
traiittarsus.1:traiittarsus.1.units traitbwt.1:traiittarsus.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
traiittarsus.2:traiittarsus.1.units traitbwt.2:traiittarsus.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
traiittarsus.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
traiittarsus.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
traiittarsus.1:traiittarsus.2.units traitbwt.1:traiittarsus.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
traiittarsus.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
traiittarsus.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
traiittarsus.1:traiittarsus.2.animal traitbwt.1:traiittarsus.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
traiittarsus.2:traiittarsus.2.animal traitbwt.2:traiittarsus.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
traiittarsus.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
traiittarsus.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
Lag 100	-0.021944414	0.05837761
Lag 500	-0.004019018	0.04124133
Lag 1000	-0.014592442	0.02897141
Lag 5000	-0.001455363	0.01713092
traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother		
Lag 0	-0.03458419	0.1501420
Lag 100	-0.02882752	0.1495980
Lag 500	-0.05044049	0.1542703
Lag 1000	-0.04326520	0.1753867
Lag 5000	0.01976572	0.1700994
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
traiittarsus.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
traiittarsus.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
traiittarsus.1:traiittarsus.2.units traitbwt.1:traiittarsus.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
traiittarsus.2:traiittarsus.2.units traitbwt.2:traiittarsus.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
traiittarsus.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
traiittarsus.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
traiittarsus.2:traiittarsus.2.animal traitbwt.2:traiittarsus.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
traiittarsus.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
traiittarsus.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
traiittarsus.1.byear traitbwt.1.byear traiittarsus.2.byear		
Lag 0	-0.04533921	-0.001638125
Lag 100	-0.04526568	0.002752216
Lag 500	-0.02361959	-0.010266769
Lag 1000	-0.08661480	-0.055915794
Lag 5000	0.02028860	-0.015718402
traitbwt.2.byear traiittarsus.1.mother traitbwt.1.mother		
Lag 0	0.09224924	-0.08507034
Lag 100	0.09712475	-0.09090158
Lag 500	0.06704383	-0.06950074
		0.093258667

Lag 1000	0.06946025	-0.09719184	0.091569829
Lag 5000	-0.05957284	-0.01506617	-0.004965446
traiittarsus.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	
traiittarsus.1:traiittarsus.1.units traitbwt.1:traiittarsus.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
traiittarsus.2:traiittarsus.1.units traitbwt.2:traiittarsus.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
traiittarsus.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
traiittarsus.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
traiittarsus.1:traiittarsus.2.units traitbwt.1:traiittarsus.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
 traiittarsus.2:traiittarsus.2.units traitbwt.2:traiittarsus.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
 traiittarsus.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
 traiittarsus.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		
 traiittarsus.1:traiittarsus.1.animal traitbwt.1:traiittarsus.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
 traiittarsus.2:traiittarsus.1.animal traitbwt.2:traiittarsus.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
traiittarsus.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
traiittarsus.1.byear traitbwt.1.byear traiittarsus.2.byear		
Lag 0	-0.044815839	-0.007601342
Lag 100	-0.046632422	-0.009618828
Lag 500	-0.039749429	-0.026455434
Lag 1000	-0.096232932	-0.063248471
Lag 5000	-0.007307801	-0.011838332
traitbwt.2.byear traiittarsus.1.mother traitbwt.1.mother		
Lag 0	0.07926090	-0.11755479
Lag 100	0.09525987	-0.11193096
Lag 500	0.05998165	-0.06092327
Lag 1000	0.06572238	-0.09798980
Lag 5000	-0.05632018	-0.00703712
traiittarsus.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
traiittarsus.1:traiittarsus.1.units traitbwt.1:traiittarsus.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
traiittarsus.2:traiittarsus.1.units traitbwt.2:traiittarsus.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
traiittarsus.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
traiittarsus.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
traiittarsus.1:traiittarsus.2.units traitbwt.1:traiittarsus.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
traiittarsus.2:traiittarsus.2.units traitbwt.2:traiittarsus.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
traiittarsus.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
traiittarsus.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

Chapter 7

brms

First load brms:

```
library(brms)
```

Loading required package: Rcpp

Loading 'brms' package (version 2.21.0). Useful instructions
can be found by typing `help('brms')`. A more detailed introduction
to the package is available through `vignette('brms_overview')`.

Attaching package: 'brms'

The following object is masked from 'package:stats':

ar

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

7.0.1. 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
```

Multilevel Hyperparameters:

~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			

Regression Coefficients:

	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

Further Distributional Parameters:

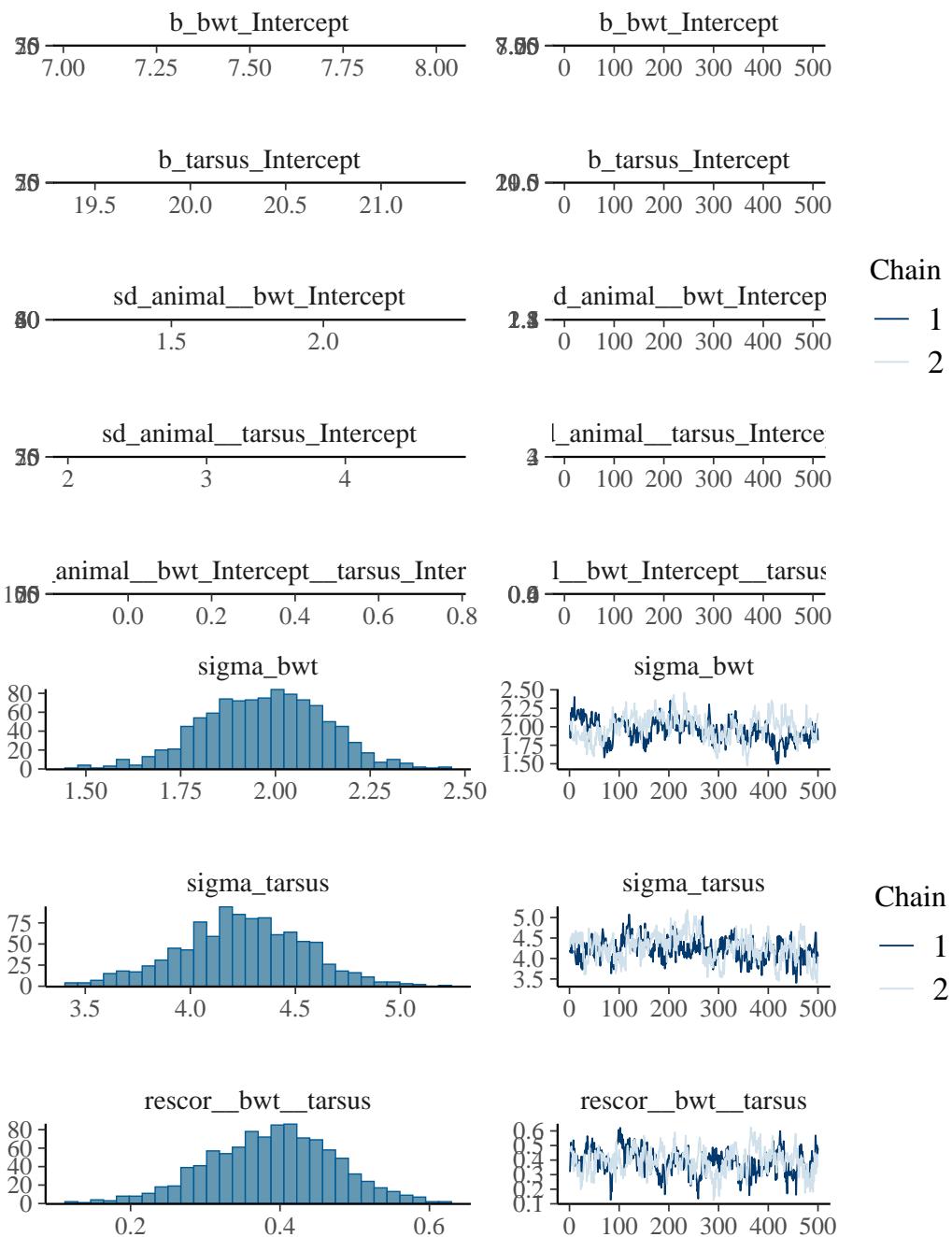
	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sigma_bwt	1.97	0.16	1.66	2.28	1.06	27	172
sigma_tarsus	4.24	0.30	3.63	4.82	1.04	72	162

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).

```
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 1.00000000
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 1.00000000

$animal$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 0.0000000 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 0.0000000 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[, 2] / (v_animal[, 2] + v_r[, 2]))  
  
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

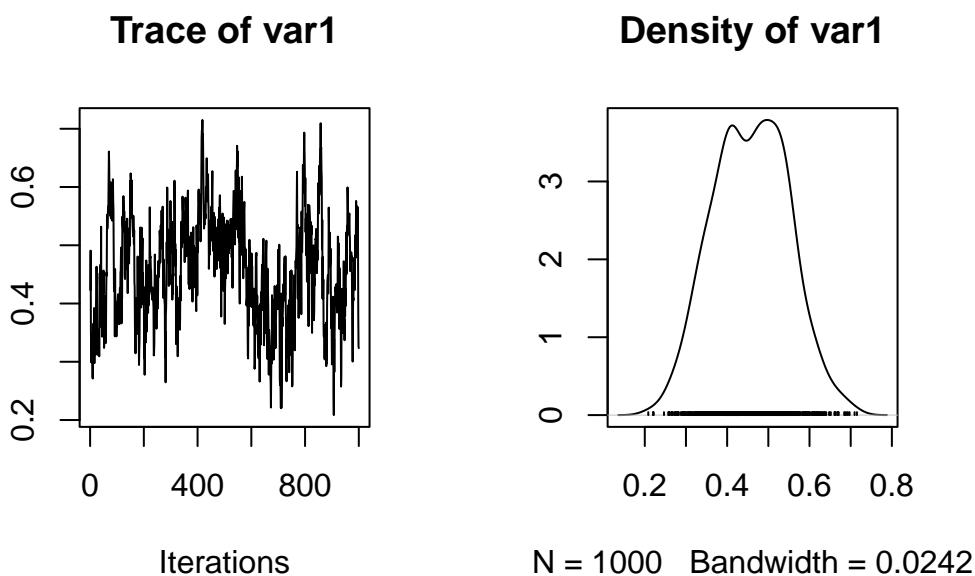
1. Empirical mean and standard deviation for each variable,
plus standard error of the mean:

Mean	SD	Naive SE	Time-series SE
0.397237	0.087350	0.002762	0.009971

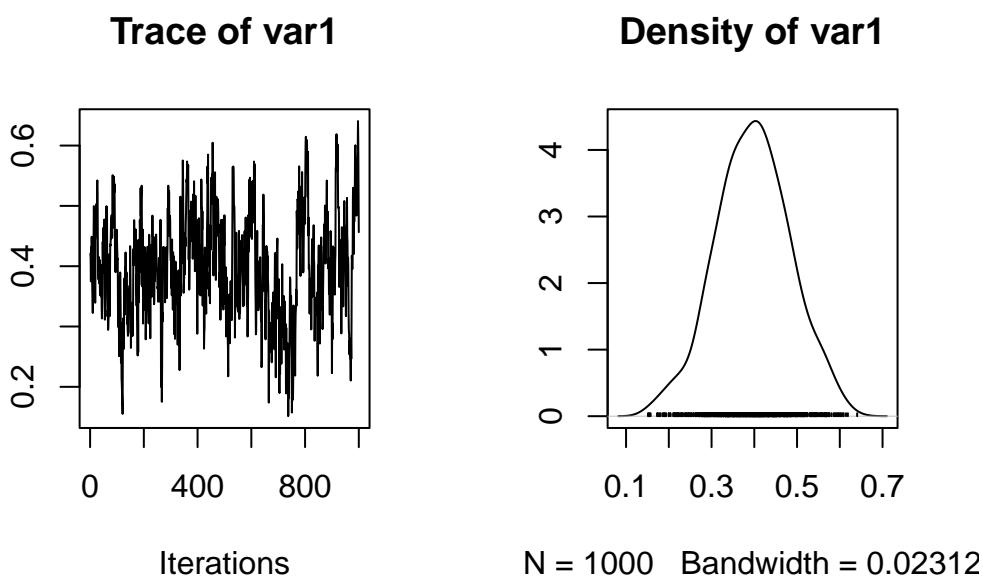
2. Quantiles for each variable:

2.5% 25% 50% 75% 97.5%
0.2174 0.3390 0.3982 0.4553 0.5682

```
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

```
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,

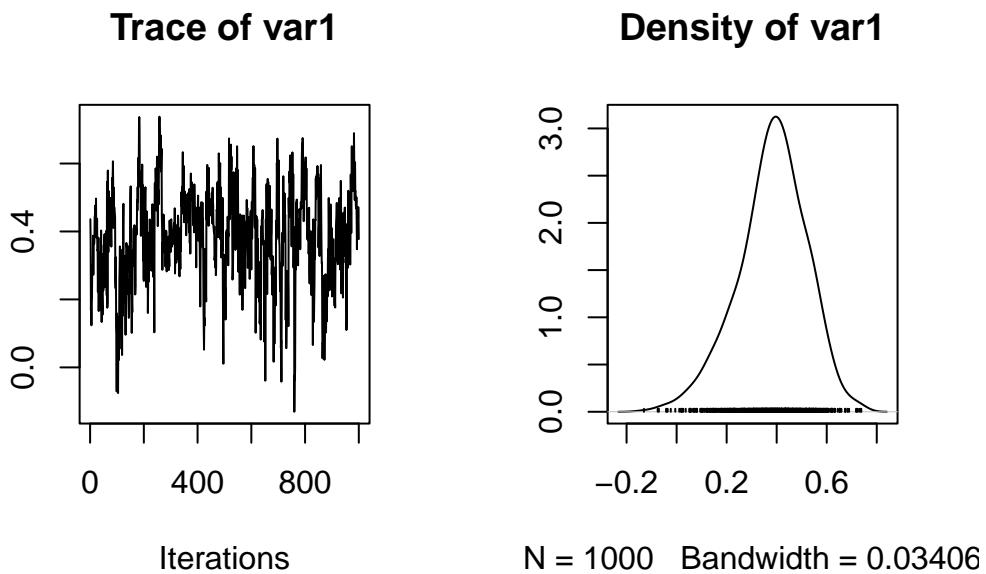
plus standard error of the mean:

Mean	SD	Naive SE	Time-series SE
0.388875	0.085105	0.002691	0.009215

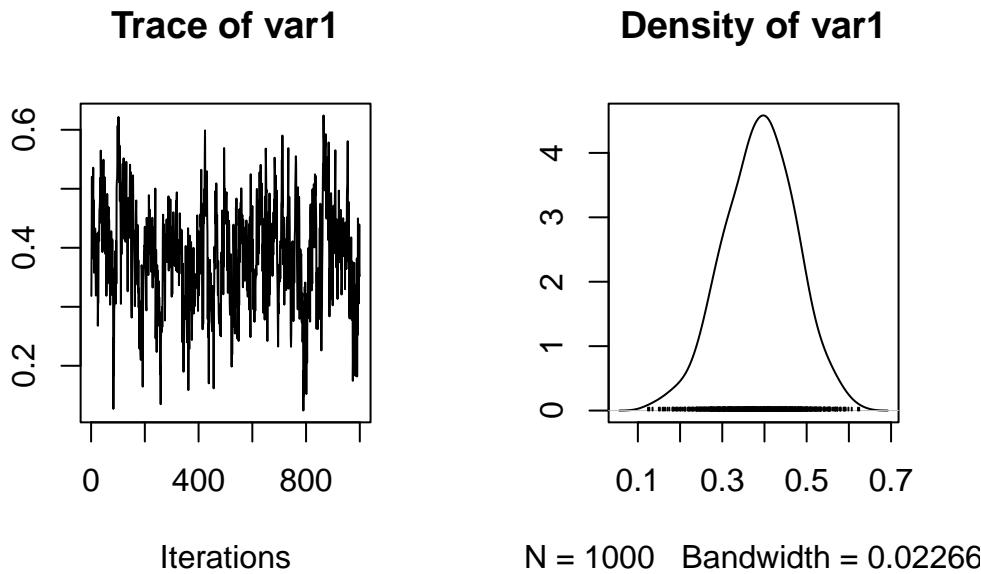
2. Quantiles for each variable:

2.5% 25% 50% 75% 97.5%
0.2128 0.3319 0.3913 0.4484 0.5527

```
plot(cor_g)
```



```
plot(cor_res)
```



Here we can plot the genetic correlation by extraction the breeding values or BLUP.

```
bls_m2.1 <- ranef(brms_m2.1)$animal
bl_m2.1 <- as.data.frame(abind::abind(lapply(1:dim(bls_m2.1)[[3]], function(x) bls_m2.1[, c(1, 3,
colnames(bl_m2.1) <- paste0(rep(dimnames(bls_m2.1)[[3]], each = 3), c("", "_lo", "_up"))
bl_m2.1$id <- rownames(bl_m2.1)
```

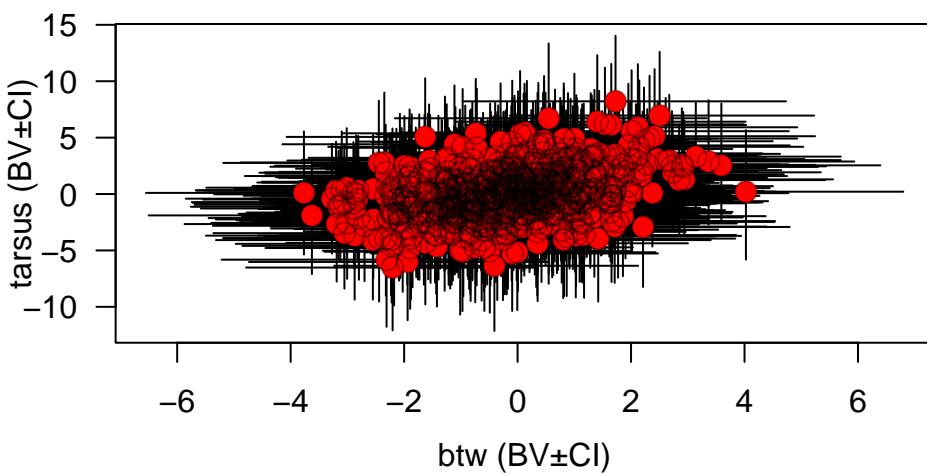
Here, some simple code to plot the genetic correlation.

```
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 = c(1.5))
mtext("btw (BV±CI)", side = 1, line = 2.4)
mtext("tarsus (BV±CI)", side = 2, line = 2, las = 3)

```



7.0.2. 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 | moth
bf_tarsus_2 <- bf(tarsus ~ 1 + sex + (1 | a | gr(animal, cov = Amat)) + (1 | b | byear) + (1 | c | moth

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 | mother)
          tarsus ~ 1 + sex + (1 | a | gr(animal, cov = Amat)) + (1 | b | byear) + (1 | c | mother)
Data: gryphon (Number of observations: 683)
Draws: 2 chains, each with iter = 1000; warmup = 500; thin = 1;
       total post-warmup draws = 1000
```

Multilevel Hyperparameters:

~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					
 Regression Coefficients:							
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

Further Distributional 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

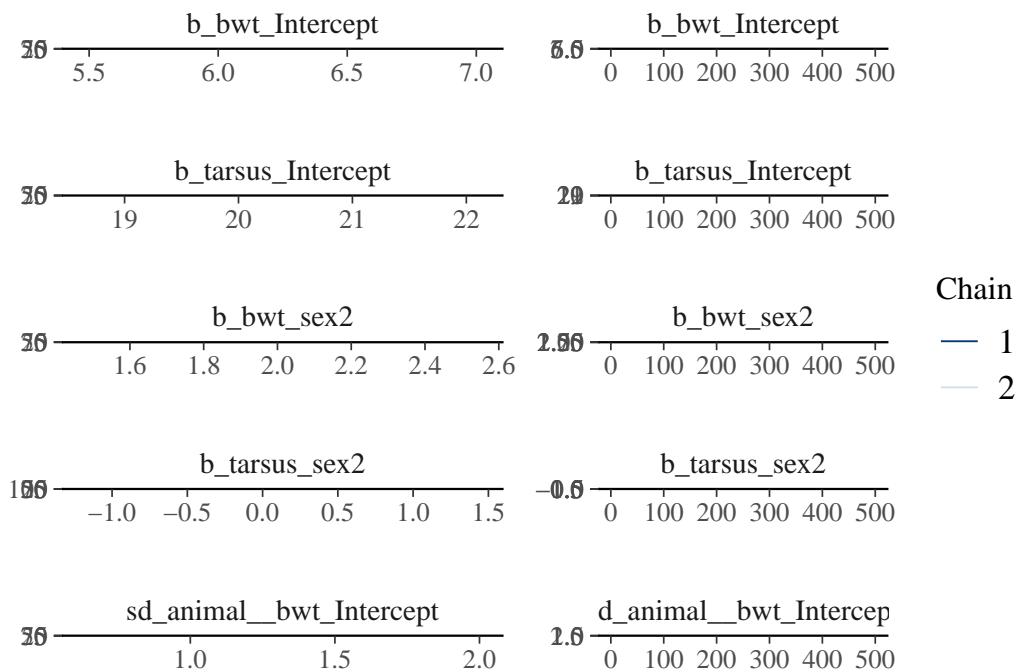
```
sigma_tarsus      3.73      0.32      3.14      4.32 1.00      55      176
```

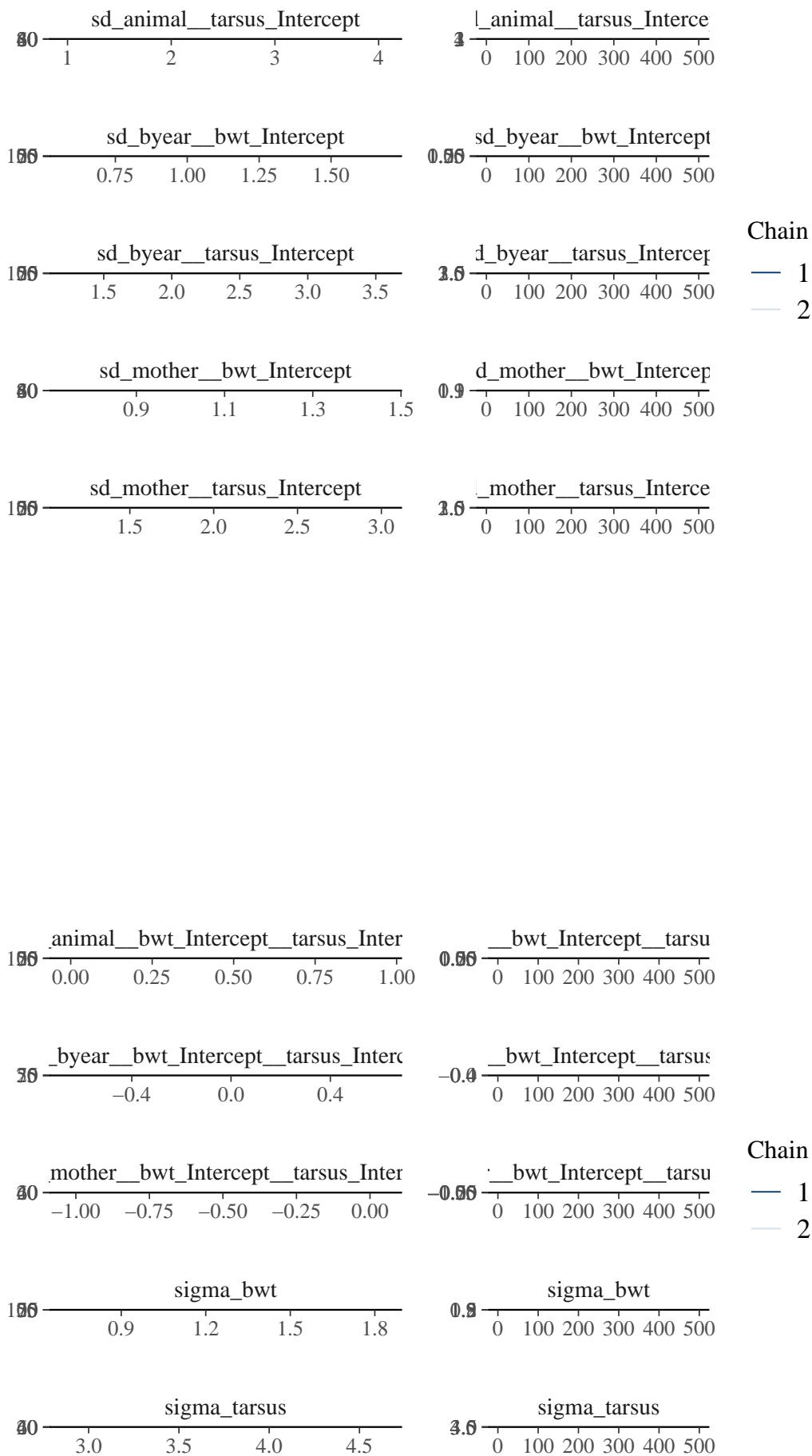
Residual Correlations:

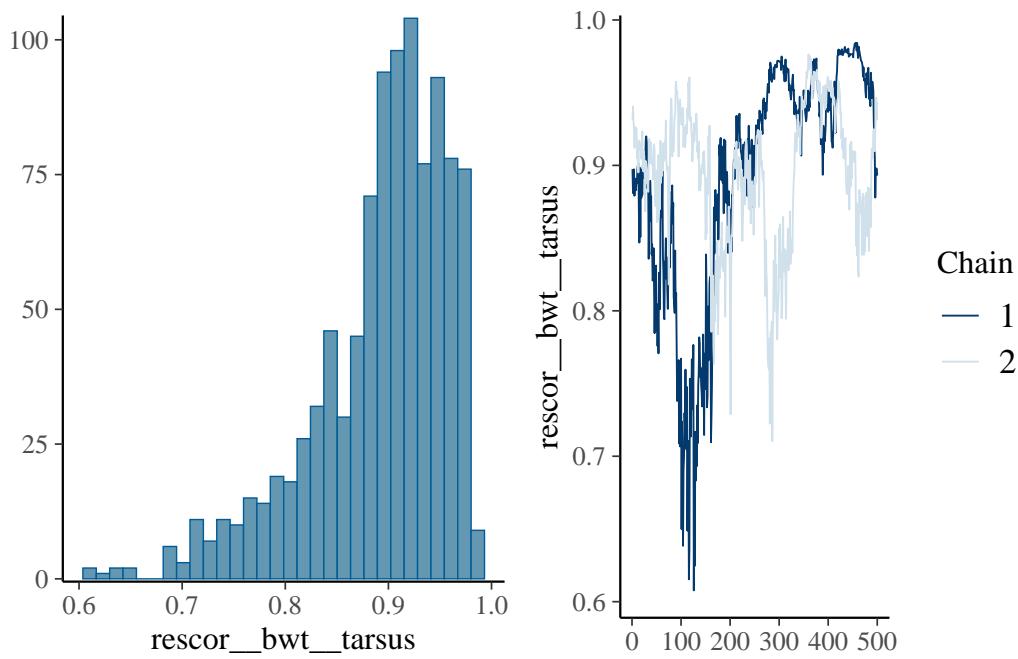
	Estimate	Est.Error	l-95%	CI	u-95%	CI	Rhat	Bulk_ESS	Tail_ESS
rescor(bwt,tarsus)	0.89	0.07	0.72	0.98	1.50		4	24	

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).

```
plot(brms_m2.2, ask = FALSE)
```







```
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 1.0000000 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
```

```
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

```
summary(cor_res)
```

Iterations = 1:1000
Thinning interval = 1
Number of chains = 1
Sample size per chain = 1000

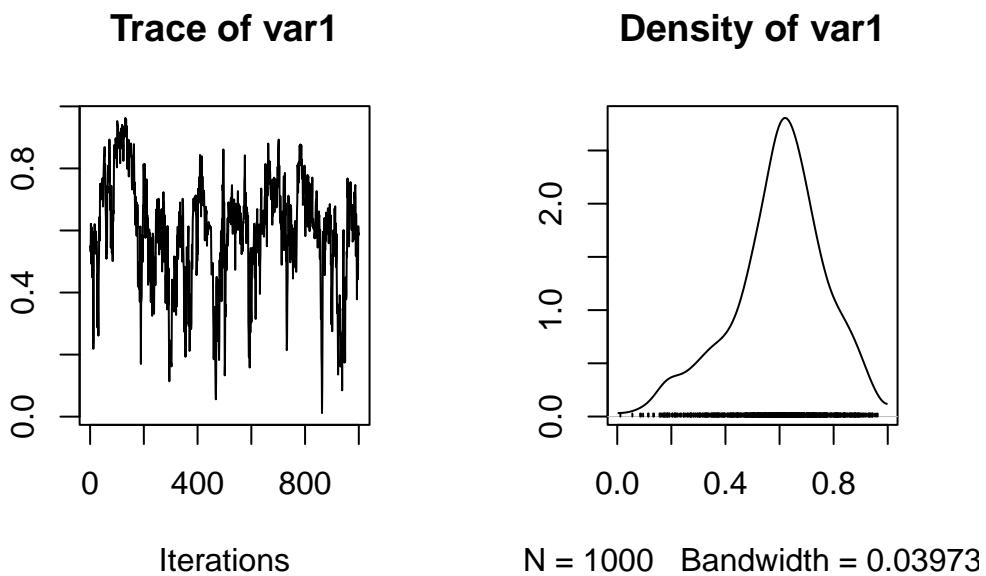
1. Empirical mean and standard deviation for each variable,
plus standard error of the mean:

Mean	SD	Naive SE	Time-series SE
0.892512	0.067229	0.002126	0.026496

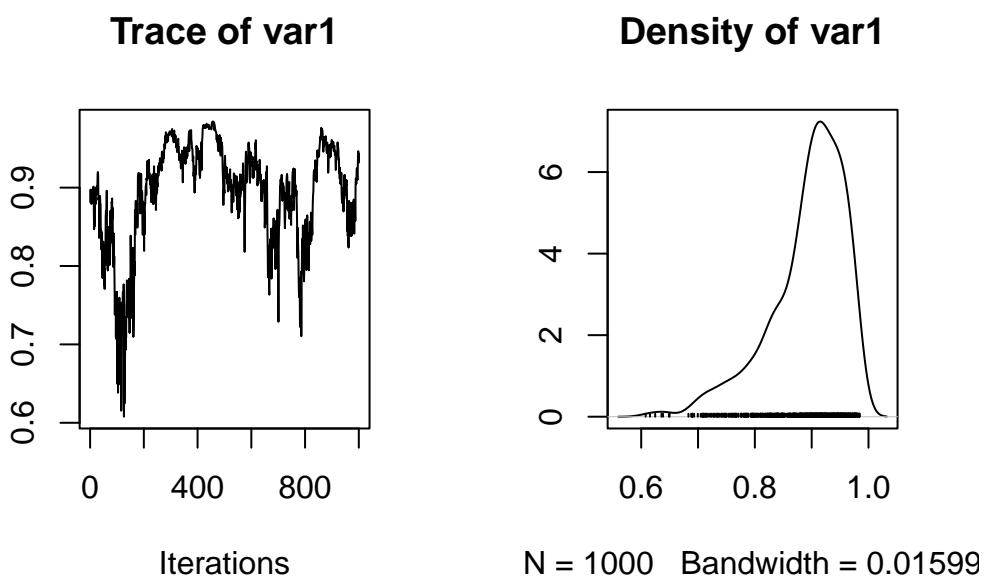
2. Quantiles for each variable:

2.5% 25% 50% 75% 97.5%
0.7168 0.8620 0.9069 0.9425 0.9775

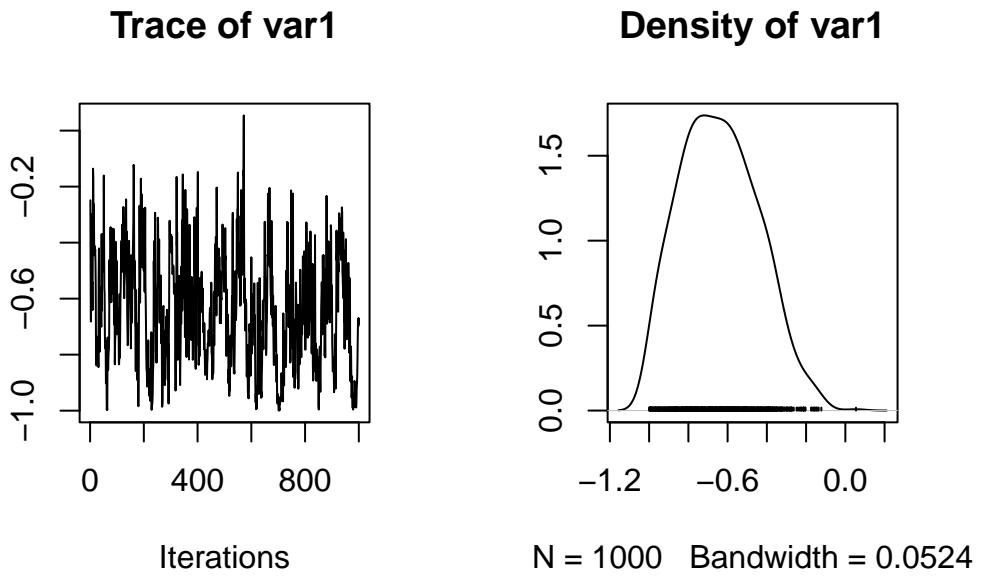
```
plot(cor_g)
```



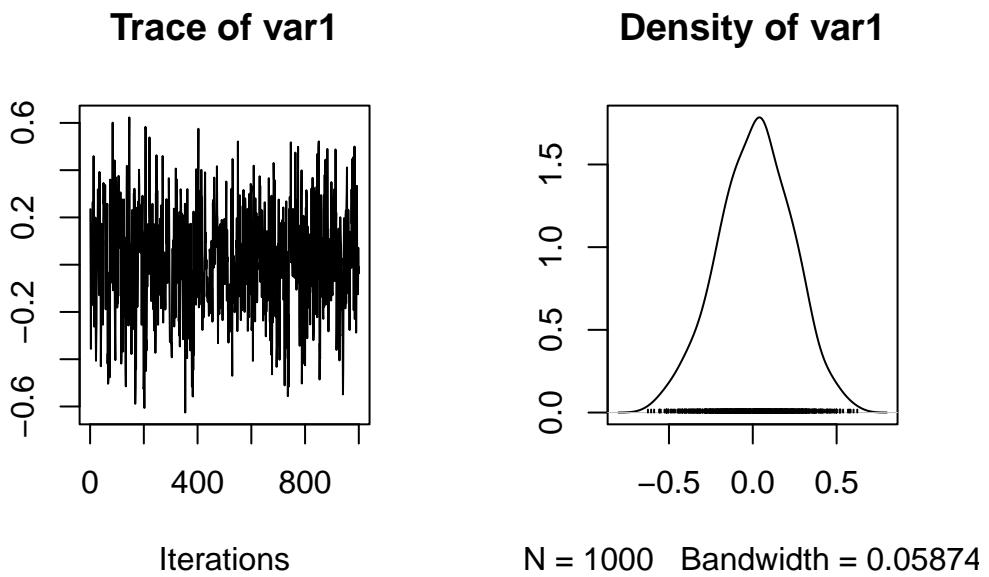
```
plot(cor_res)
```



```
plot(cor_mother)
```



```
plot(cor_byear)
```



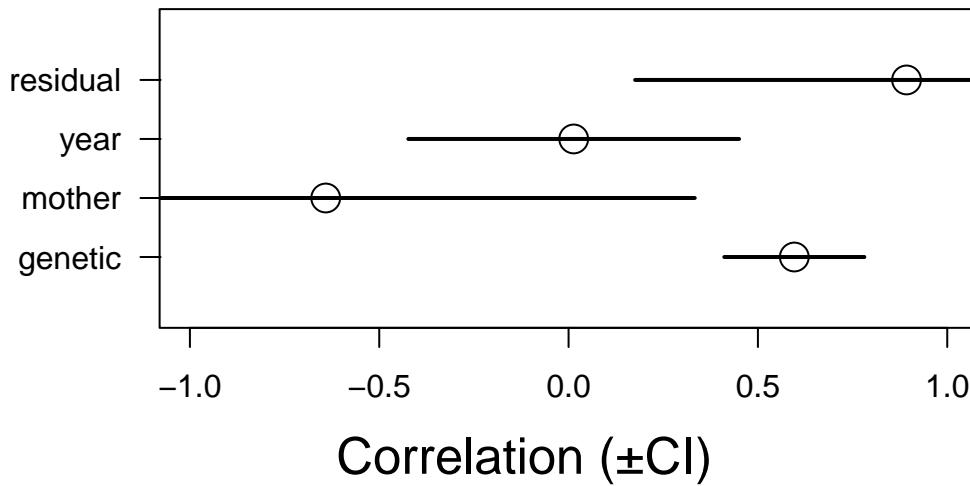
Neither of these posterior distributions overlaps zero, so we can consider them both statistically supported.

```
cor.est <- rbind(
  cbind(summary(cor_g)$statistics[1], summary(cor_g)$quantiles[1], summary(cor_g)$quantiles[5]),
  cbind(summary(cor_mother)$statistics[1], summary(cor_mother)$quantiles[1], summary(cor_mother)$quantiles[5]),
  cbind(summary(cor_byear)$statistics[1], summary(cor_byear)$quantiles[1], summary(cor_byear)$quantiles[5]),
  cbind(summary(cor_res)$statistics[1], summary(cor_res)$quantiles[1], summary(cor_res)$quantiles[5])
)
```

```

plot(c(1, 2, 3, 4) ~ cor.est[, 1], xlim = c(-1, 1), ylim = c(0, 5), xlab = "", ylab = "", cex = 2)
segments(y0 = 1, x0 = cor.est[1, 1] - cor.est[1, 2], y1 = 1, x1 = cor.est[1, 1] + cor.est[1, 2],
segments(y0 = 2, x0 = cor.est[2, 1] - cor.est[2, 2], y1 = 2, x1 = cor.est[2, 1] + cor.est[2, 2],
segments(y0 = 3, x0 = cor.est[3, 1] - cor.est[3, 2], y1 = 3, x1 = cor.est[3, 1] + cor.est[3, 2],
segments(y0 = 4, x0 = cor.est[4, 1] - cor.est[4, 2], y1 = 4, x1 = cor.est[4, 1] + cor.est[4, 2],
mtext("Correlation (\u00b1CI)", 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

```
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:

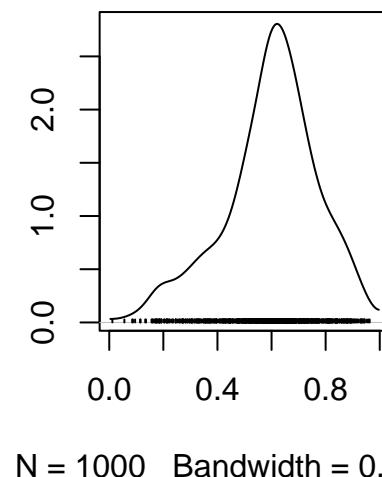
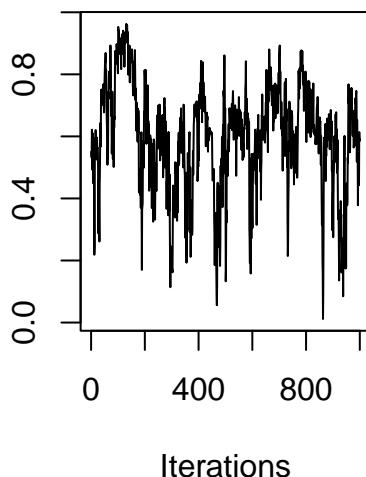
Mean	SD	Naive SE	Time-series SE
0.892512	0.067229	0.002126	0.026496

2. Quantiles for each variable:

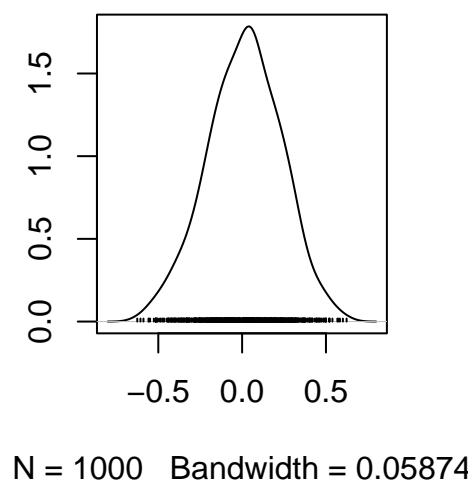
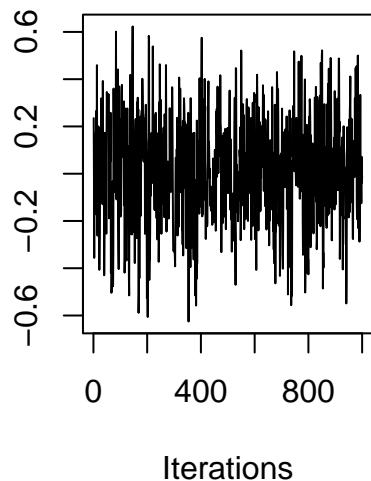
2.5% 25% 50% 75% 97.5%
0.7168 0.8620 0.9069 0.9425 0.9775

```
plot(cor_g_2)
```

Trace of sd_animal_bwt_Intensity of sd_animal_bwt_Intensity



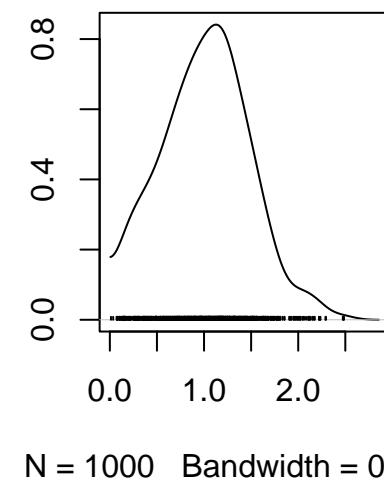
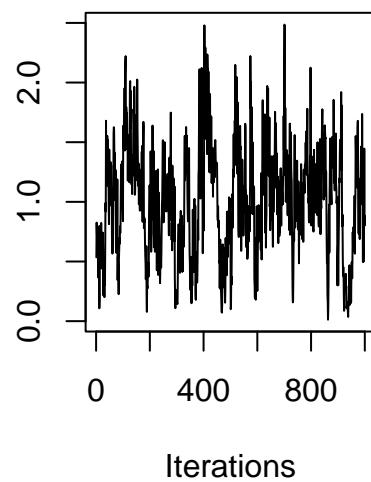
```
plot(cor_byear_2)
```

Trace of sd_byear_bwt_Inter

Iterations

N = 1000 Bandwidth = 0.05874

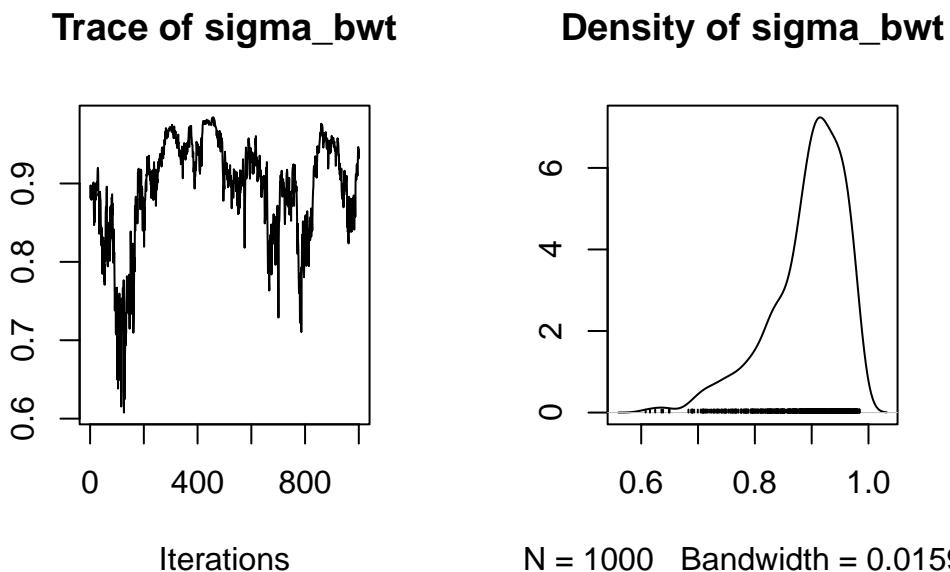
```
plot(cor_mother_2)
```

Trace of sd_mother_bwt_Inter

Iterations

N = 1000 Bandwidth = 0.1234

```
plot(cor_res_2)
```



7.0.3. 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 | byear) +
bf_tarsus_3 <- bf(tarsus ~ 1 + sex + (1 | a | gr(animal, cov = Amat, by = sex)) + (1 | b | byear)

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) + (1 | c
 tarsus ~ 1 + sex + (1 | a | gr(animal, cov = Amat, by = sex)) + (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

Multilevel Hyperparameters:

~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			

Regression Coefficients:

	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

Further Distributional Parameters:

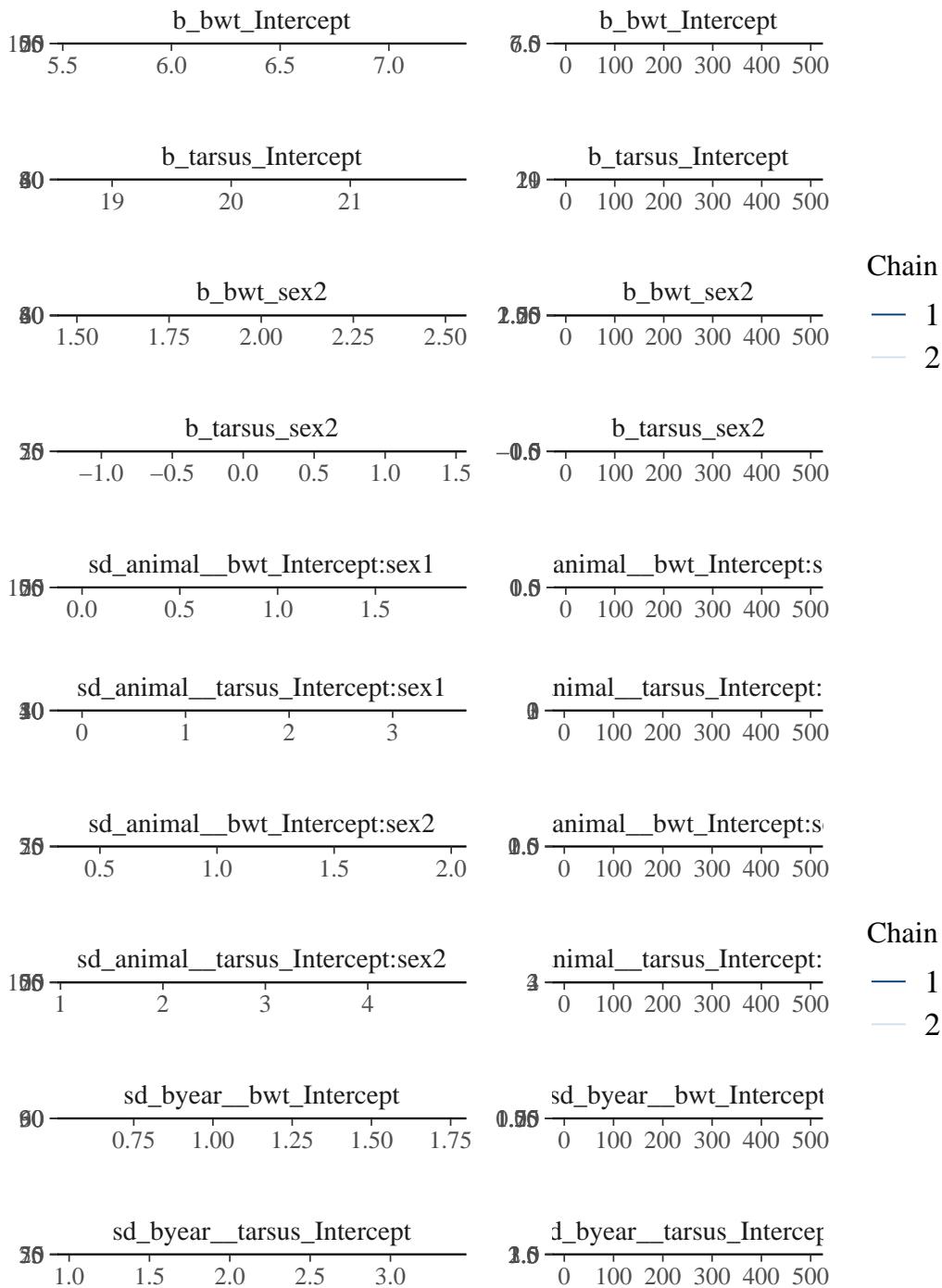
	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sigma_bwt	1.49	0.15	1.16	1.74	1.33	5	81
sigma_tarsus	3.88	0.27	3.27	4.35	1.04	42	85

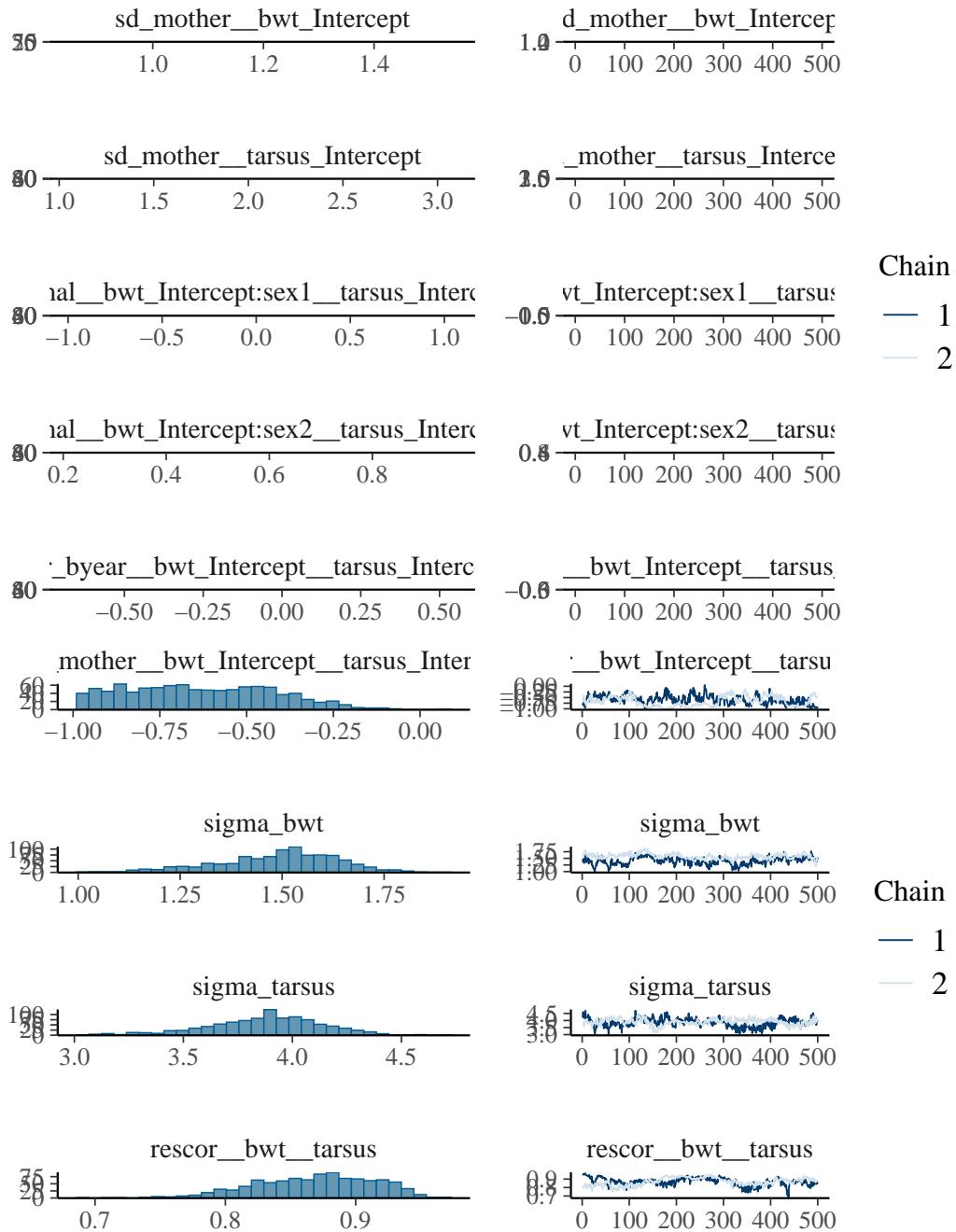
Residual Correlations:

	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)
```





`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	0.0000000
tarsus_Intercept:sex2	0.0000000	0.0000000	0.0000000	0.0000000

```
, , tarsus_Intercept:sex1
```

	Estimate	Est.Error	Q2.5	Q97.5
bwt_Intercept:sex1	0.7957577	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	0.0000000
tarsus_Intercept:sex2	0.0000000	0.0000000	0.00000000	0.0000000

```
, , 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	0.0000000	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	0.0000000	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 essential group-specific partitioning (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 partition 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.

```

bf_bwt_4 <- bf(bwt ~ 1 + sex + ((1 | a | gr(animal, cov = Amat, by = sex))) + (1 | b | byear) +
bf_tarsus_4 <- bf(tarsus ~ 1 + sex + (1 | a | gr(animal, cov = Amat, by = sex)) + (1 | b | byear)

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:

```

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) + (1 | c  
       sigma ~ sex - 1  
       tarsus ~ 1 + sex + (1 | a | gr(animal, cov = Amat, by = sex)) + (1 | b | byear) + (1 | c  
       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
```

Multilevel Hyperparameters:

~animal (Number of levels: 683)

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(bwt_Intercept:sex1)	0.86	0.35	0.14	1.48	1.00	59	101
sd(tarsus_Intercept:sex1)	1.40	0.82	0.10	3.00	1.07	45	111
sd(bwt_Intercept:sex2)	1.40	0.23	0.94	1.83	1.04	42	40
sd(tarsus_Intercept:sex2)	3.49	0.72	1.96	4.62	1.22	8	50
cor(bwt_Intercept:sex1,tarsus_Intercept:sex1)	0.28	0.51	-0.85	0.94	1.05	60	287
cor(bwt_Intercept:sex2,tarsus_Intercept:sex2)	0.78	0.10	0.56	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			

Regression Coefficients:

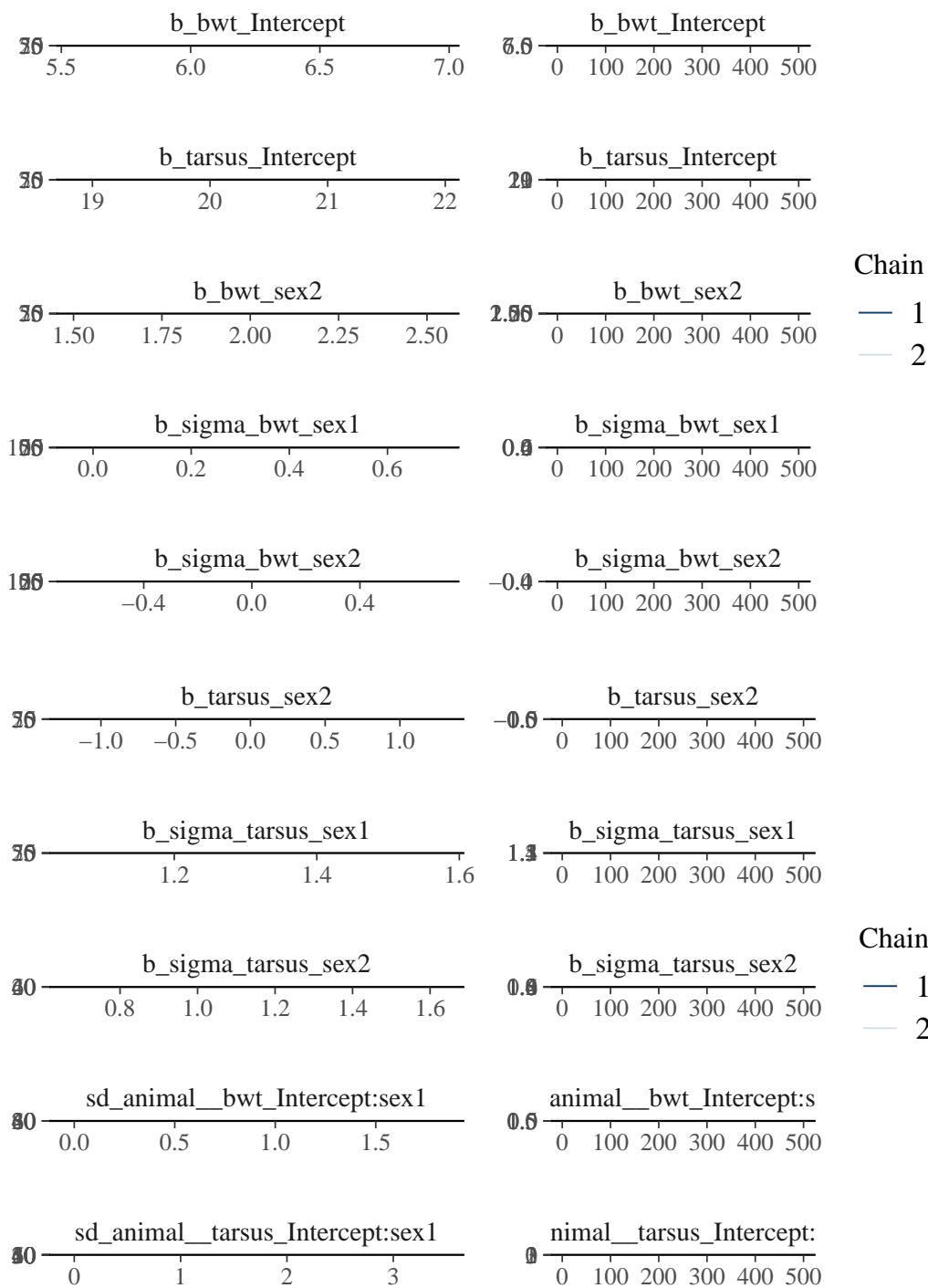
	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
bwt_Intercept	6.27	0.23	5.82	6.73	1.01	336	556
tarsus_Intercept	20.39	0.49	19.42	21.37	1.00	384	509
bwt_sex2	2.04	0.17	1.70	2.38	1.00	483	507
sigma_bwt_sex1	0.45	0.12	0.18	0.63	1.00	68	128
sigma_bwt_sex2	0.26	0.17	-0.17	0.52	1.06	38	33
tarsus_sex2	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

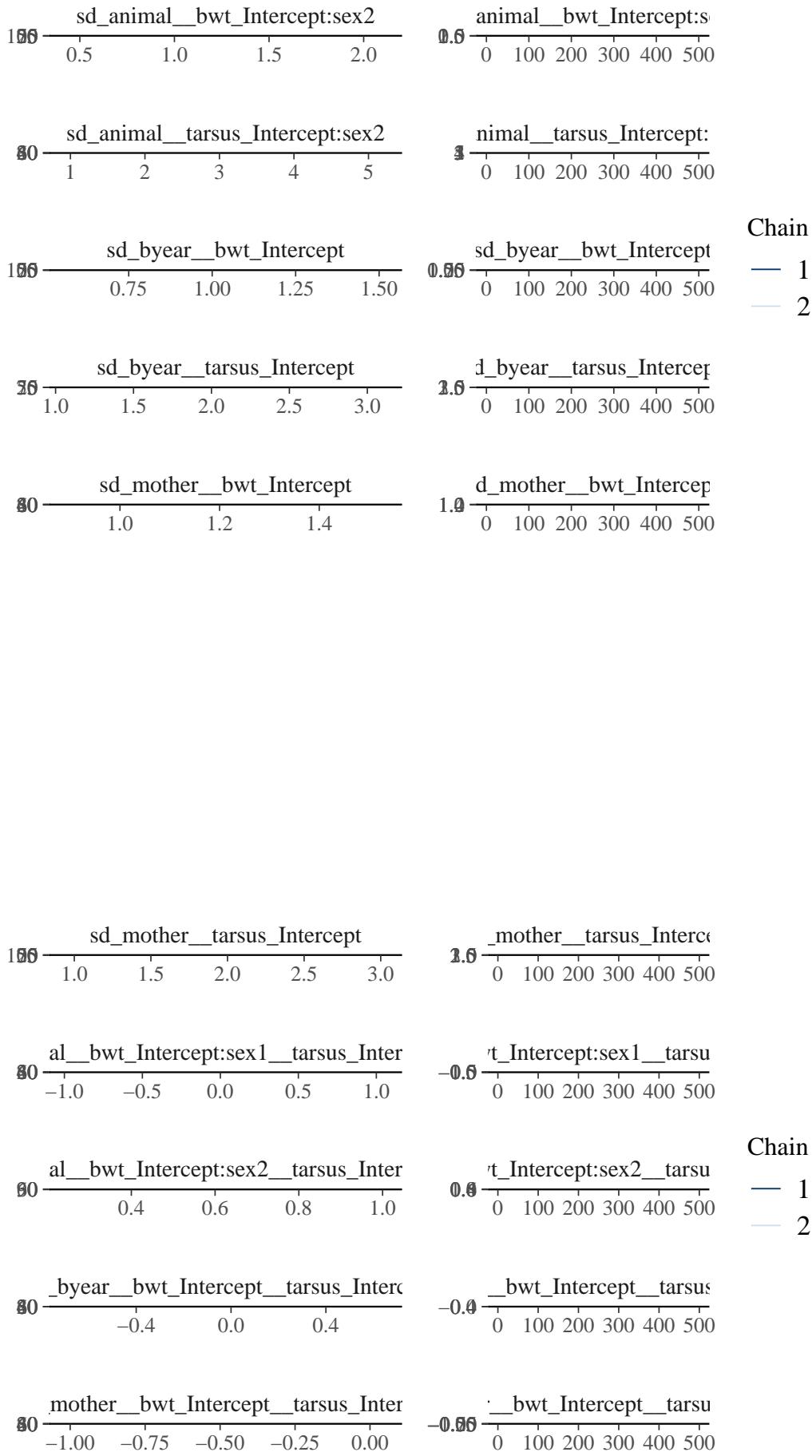
Residual Correlations:

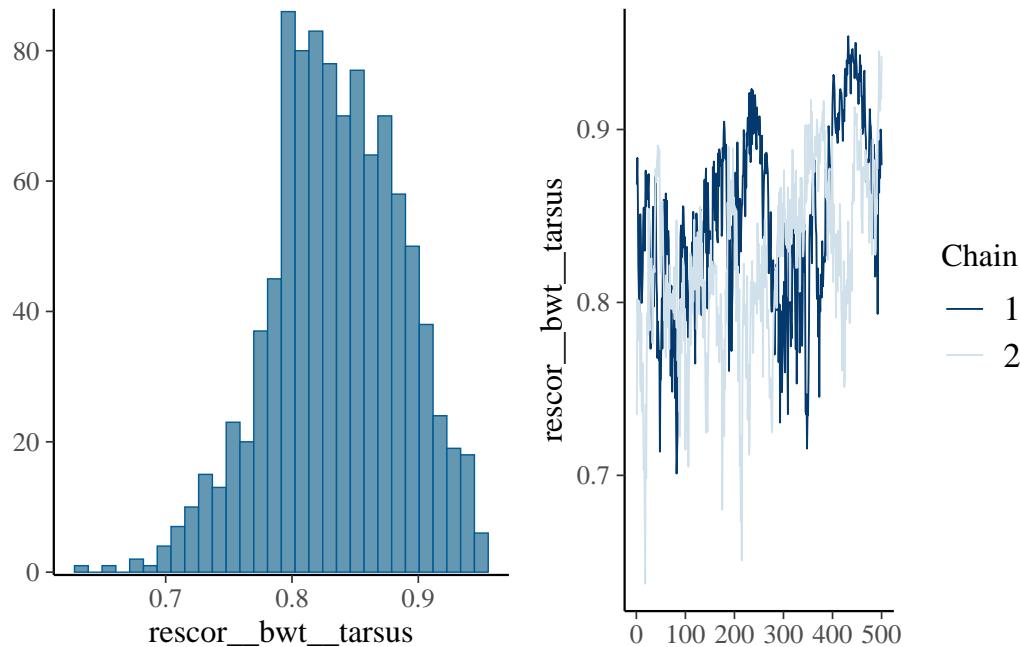
	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
rescor(bwt,tarsus)	0.84	0.05	0.73	0.93	1.15	11	29

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)
```







```
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	0.0000000	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	0.7781659	0.09850178	0.564036	0.9699765
, , 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	0.7781659	0.09850178	0.564036	0.9699765
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	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	0.0000000
tarsus_Intercept:sex2	0.0000000	0.0000000	0.0000000	0.0000000
, , tarsus_Intercept:sex1				

	Estimate	Est.Error	Q2.5	Q97.5
bwt_Intercept:sex1	0.6483841	0.914370	-0.448120294	2.989048
tarsus_Intercept:sex1	2.6216677	2.500989	0.009954235	9.015666
bwt_Intercept:sex2	0.0000000	0.000000	0.0000000000	0.000000
tarsus_Intercept:sex2	0.0000000	0.000000	0.0000000000	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

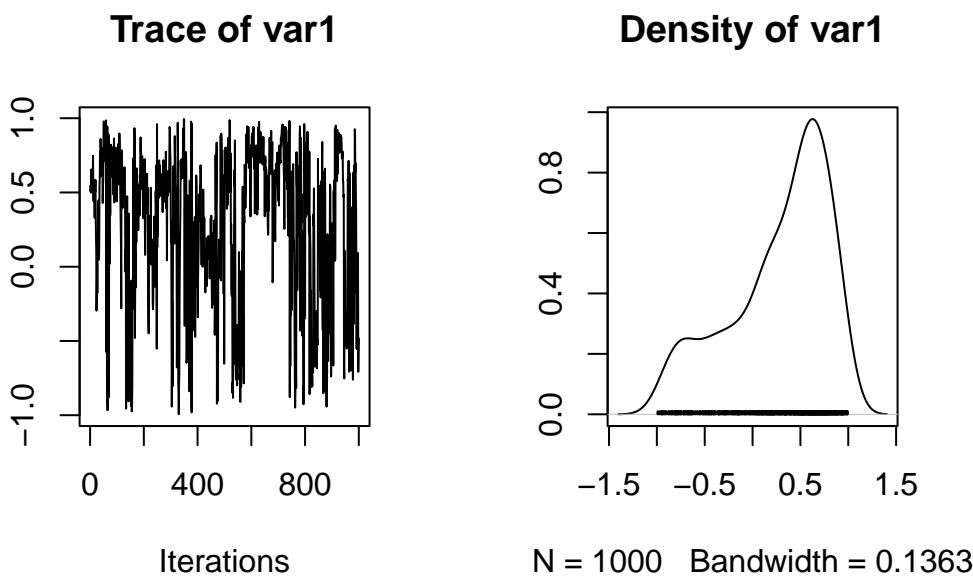
1. Empirical mean and standard deviation for each variable,
plus standard error of the mean:

Mean	SD	Naive SE	Time-series SE
0.778166	0.098502	0.003115	0.013827

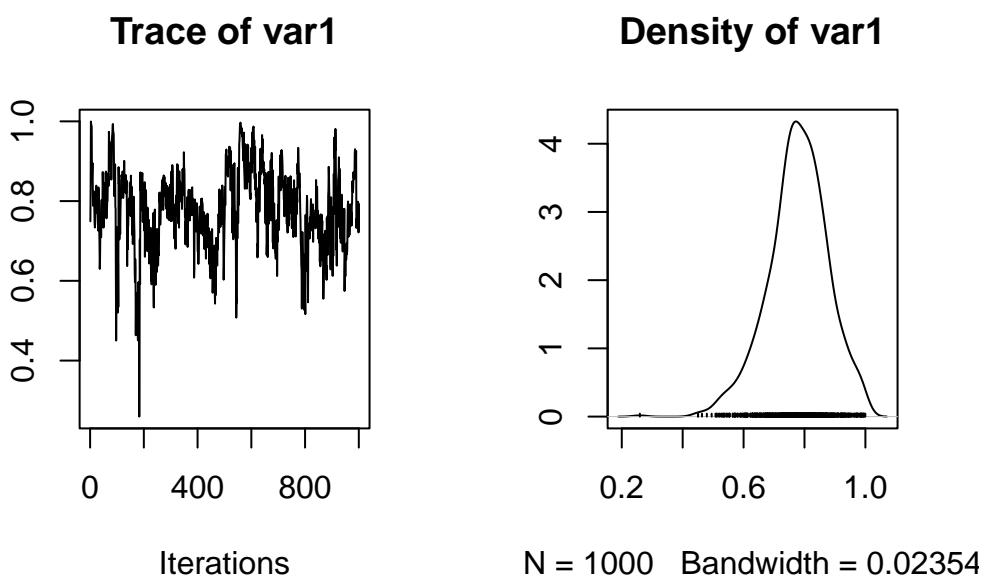
2. Quantiles for each variable:

2.5% 25% 50% 75% 97.5%
0.5640 0.7240 0.7805 0.8424 0.9700

```
plot(cor_g_F)
```



```
plot(cor_g_M)
```



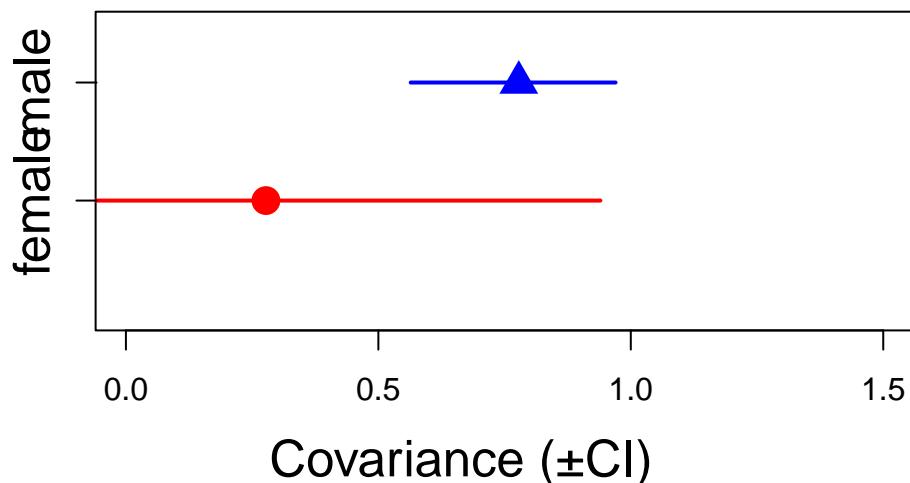
Here a plot to visualize the overlaps of covariances.

```

cor.est <- rbind(
  cbind(summary(cor_g_F)$statistics[1], summary(cor_g_F)$quantiles[1], summary(cor_g_F)$quantiles[2]),
  cbind(summary(cor_g_M)$statistics[1], summary(cor_g_M)$quantiles[1], summary(cor_g_M)$quantiles[2])
)

plot(c(1, 2) ~ cor.est[, 1], xlim = c(0, 1.5), ylim = c(0, 2.5), xlab = "", ylab = "", col = c("red", "blue"))
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 ( $\pm$ 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)$animal
bl_m2.4 <- as.data.frame(abind::abind(lapply(1:dim(bls_m2.4)[3], function(x) bls_m2.4[, c(1, 3, 4)]),
  colnames(bl_m2.4) <- paste0(rep(dimnames(bls_m2.4)[[3]], each = 3), c("", "_lo", "_up")))
bl_m2.4$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")

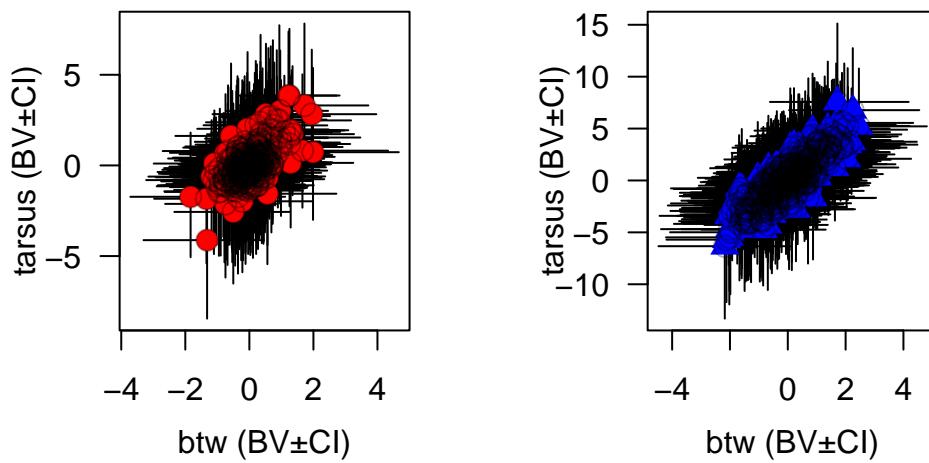
```

```
#  
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(1.5))  
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(1.5))
mtext("btw (BV±CI)", side = 1, line = 2.4)
mtext("tarsus (BV±CI)", side = 2, line = 2, las = 3)

```



7.0.4. 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 ontogenetic 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 partitioning variance per sex is a bit different than 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 + sex | c
  sigma ~ sex - 1

```

```
)  
bf_tarsus_5 <- bf(  
  tarsus ~ 1 + sex + (0 + sex | a | gr(animal, cov = Amat)) + (0 + sex | b | mother) + (0 + sex |  
  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) + (0 +  
  sigma ~ sex - 1  
  tarsus ~ 1 + sex + (0 + sex | a | gr(animal, cov = Amat)) + (0 + sex | b | mother) + (0  
  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

Multilevel Hyperparameters:

~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	1-95% 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

Regression Coefficients:

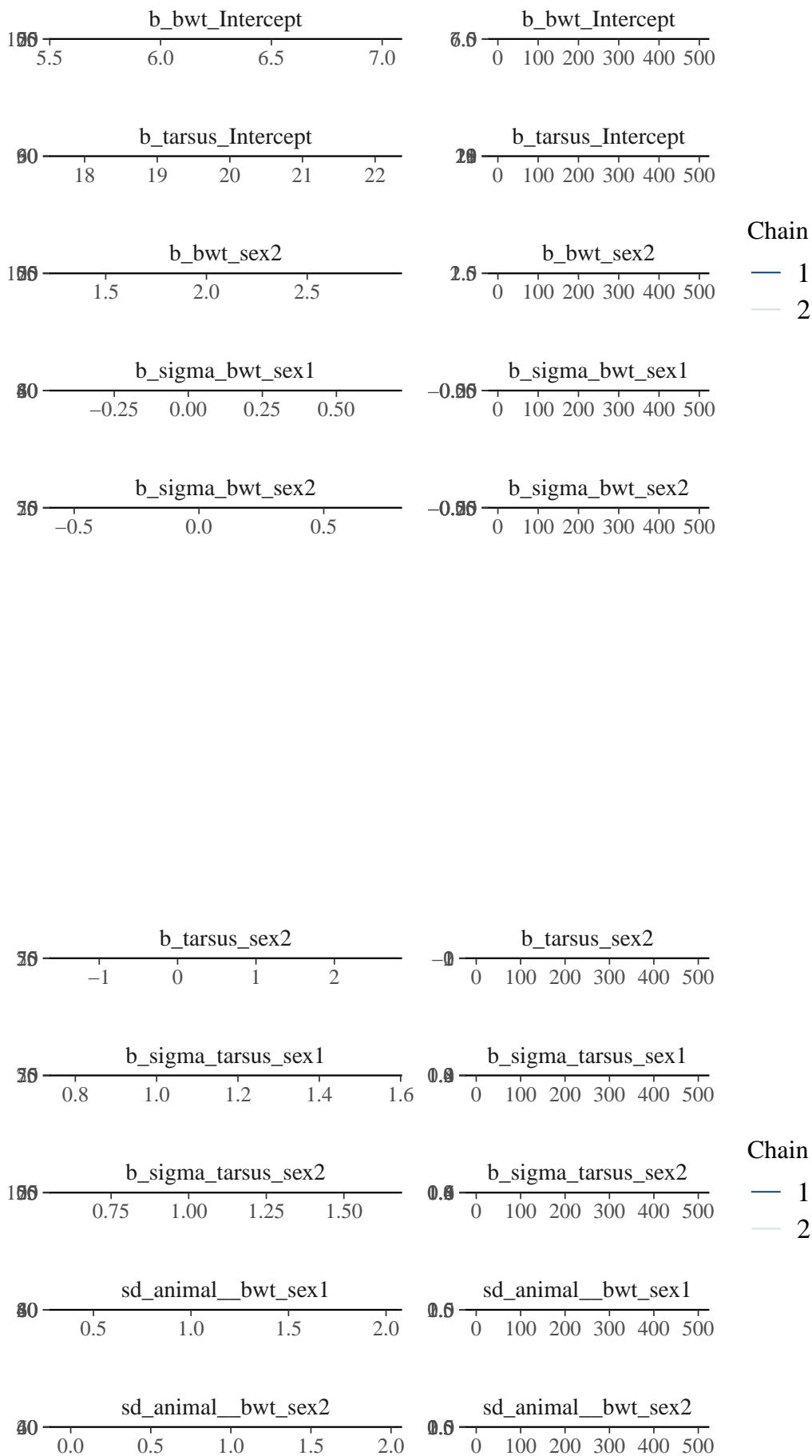
	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
bwt_Intercept	6.18	0.22	5.81	6.66	1.01	421	413
tarsus_Intercept	20.24	0.55	19.12	21.25	1.01	497	527
bwt_sex2	2.11	0.24	1.61	2.57	1.01	541	569
sigma_bwt_sex1	0.27	0.20	-0.16	0.56	1.08	18	66
sigma_bwt_sex2	0.31	0.23	-0.35	0.59	1.11	18	22
tarsus_sex2	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

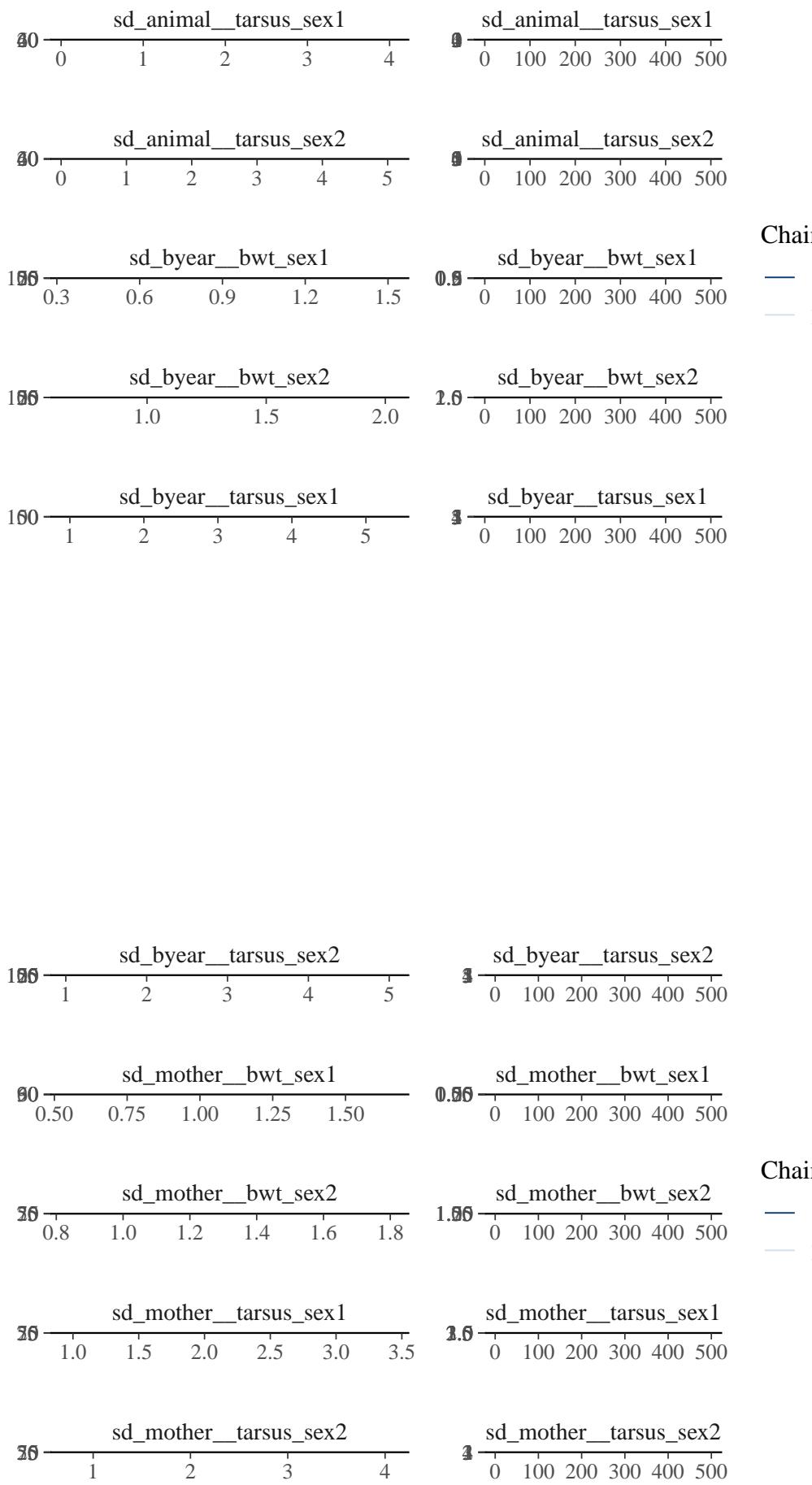
Residual Correlations:

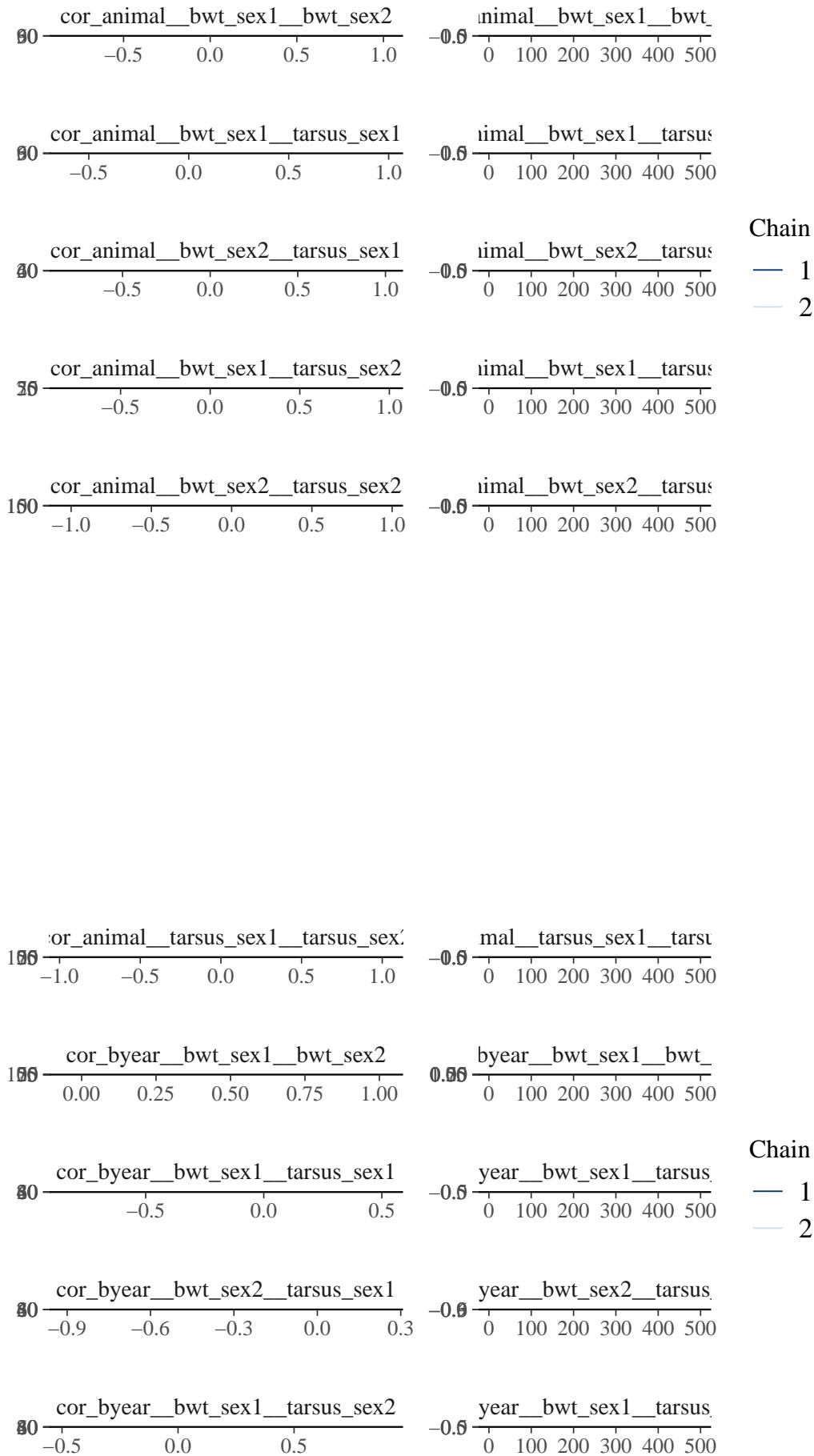
	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
rescor(bwt,tarsus)	0.88	0.05	0.71	0.95	1.32	5	33

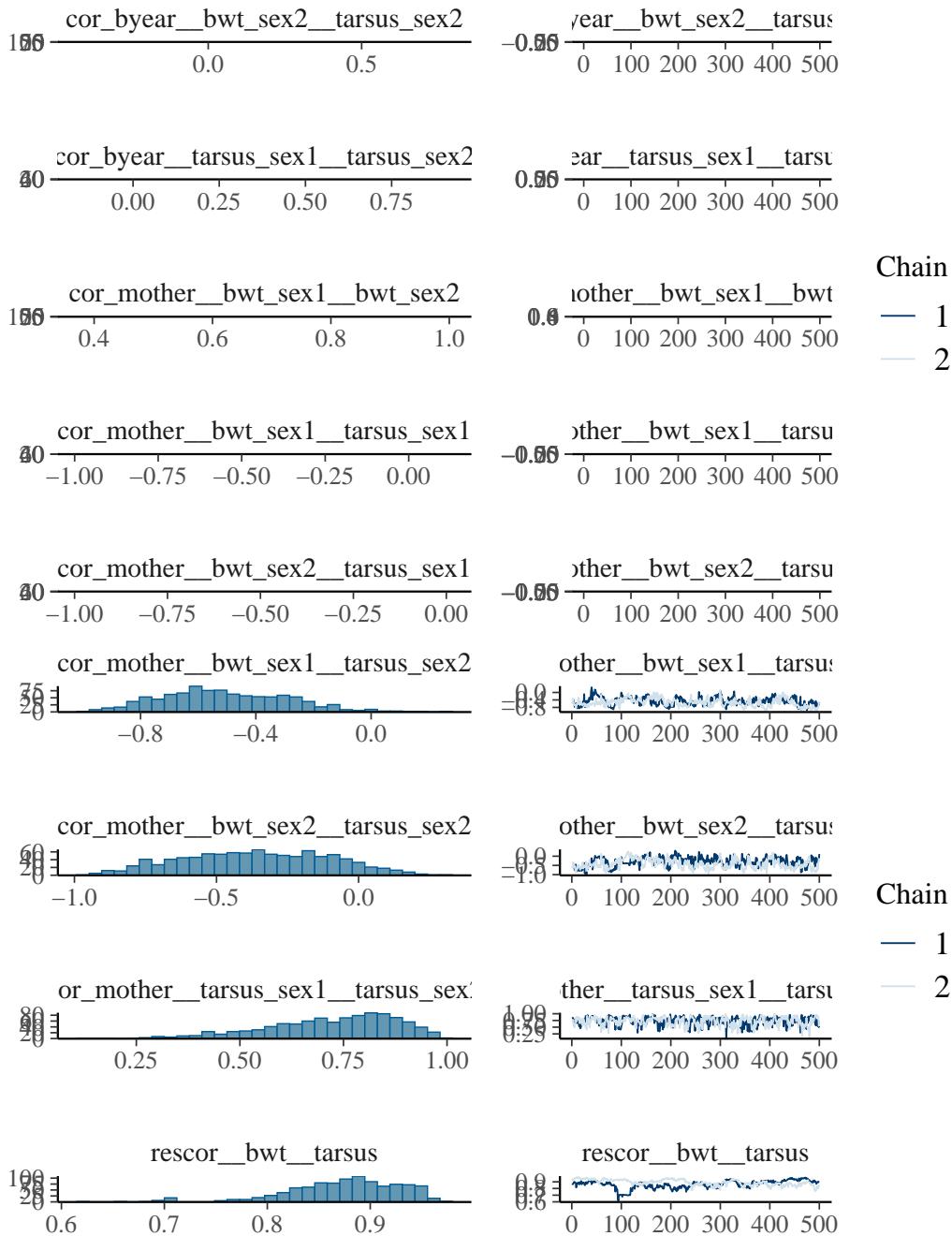
Draws were sampled using sampling(NUTS). For each parameter, Bulk_ESS and Tail_ESS are effective sample size measures, and Rhat is the potential scale reduction factor on split chains (at convergence, Rhat = 1).

```
plot(brms_m2.5, ask = FALSE)
```









`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	1.0000000	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	1.0000000	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	1.0000000000
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	1.0000000

```
$mother$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 common 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:

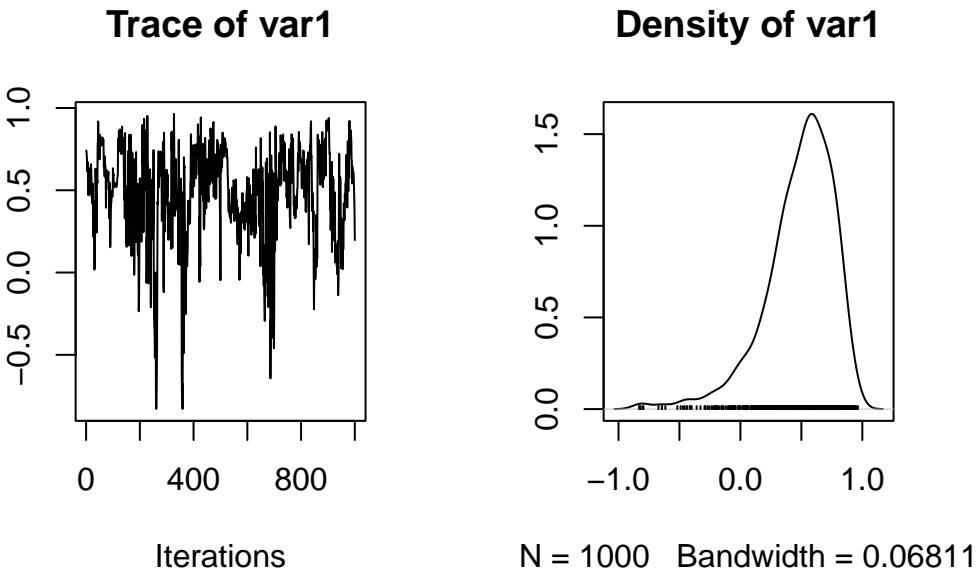
Mean	SD	Naive SE	Time-series SE
0.440143	0.292918	0.009263	0.048863

2. Quantiles for each variable:

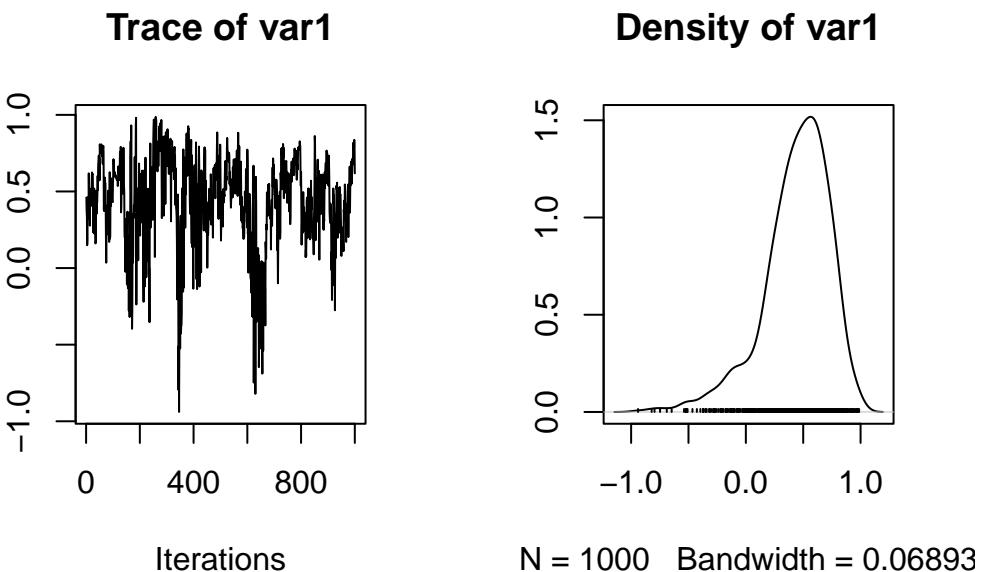
2.5%	25%	50%	75%	97.5%
------	-----	-----	-----	-------

```
-0.2962  0.2950  0.4846  0.6419  0.8720
```

```
plot(cross_sex.cor.btw)
```



```
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, col = "black"))
with(bl_m2.5, segments(x0 = bwt_sex1_lo, y0 = bwt_sex2, x1 = bwt_sex1_up, y1 = bwt_sex2, col = "black"))

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))

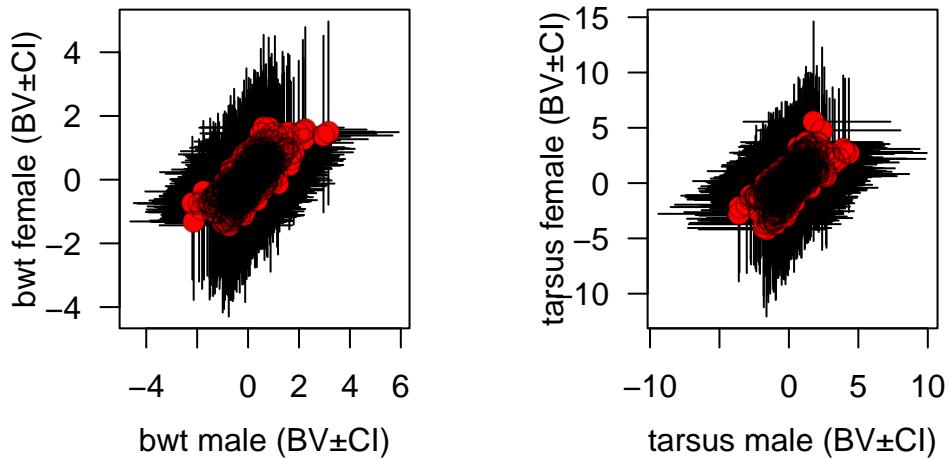
mtext("bwt male (BV±CI)", side = 1, line = 2.4)
mtext("bwt female (BV±CI)", side = 2, line = 2, las = 3)

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 = tarsus_sex2_up, col = "black"))
with(bl_m2.5, segments(x0 = tarsus_sex1_lo, y0 = tarsus_sex2, x1 = tarsus_sex1_up, y1 = tarsus_sex2, col = "black"))

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 access 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.

Part III.

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.

Scenario and data

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.

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 ...
```

```
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			

```
head(gryphonRM)
```

	animal	byear	age	year	laydate
	1	990	2	992	19
	1	990	3	993	23
	1	990	4	994	24
	1	990	5	995	23
	1	990	6	996	29
	2	990	2	992	21

Chapter 8

Asreml-R

First we need to load the `asreml` library:

```
library(asreml)
```

```
Loading required package: Matrix
```

```
Online License checked out Tue Oct  8 11:38:12 2024
```

```
Loading ASReml-R version 4.2
```

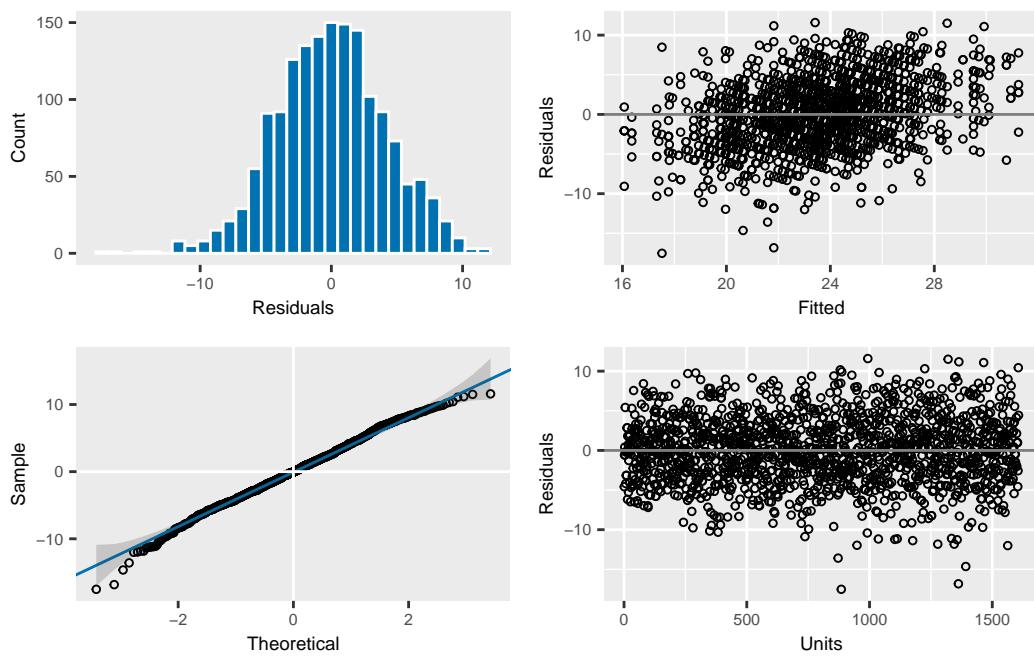
8.0.1. Estimating repeatability

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} ; $R = V_{ind}/V_P = V_{ind}/(V_{ind} + V_R)$.

```
modelv <- asreml(
  fixed = laydate ~ 1,
  random = ~animal,
  residual = ~ idv(units),
  data = gryphonRM,
  na.action = na.method(x = "omit", y = "omit")
)
```

	LogLik	Sigma2	DF	wall
1	-10182.83	1.0	1606	11:38:12
2	-8266.097	1.0	1606	11:38:12
3	-6145.012	1.0	1606	11:38:12
4	-4651.572	1.0	1606	11:38:12
5	-3819.309	1.0	1606	11:38:12
6	-3554.215	1.0	1606	11:38:12
7	-3501.557	1.0	1606	11:38:12
8	-3497.576	1.0	1606	11:38:12
9	-3497.536	1.0	1606	11:38:12
10	-3497.536	1.0	1606	11:38:12

```
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	23.938799	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")
)
```

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	LogLik	Sigma2	DF	wall
1	-8402.968	1.0	1602	11:38:14
2	-6912.361	1.0	1602	11:38:14
3	-5274.379	1.0	1602	11:38:14
4	-4143.634	1.0	1602	11:38:14
5	-3541.895	1.0	1602	11:38:14
6	-3372.909	1.0	1602	11:38:14
7	-3347.670	1.0	1602	11:38:14
8	-3346.655	1.0	1602	11:38:14
9	-3346.652	1.0	1602	11:38:14

```
summary(modelw)$varcomp
```

	component	std.error	z.ratio	bound	%ch
animal	12.28982	1.156116	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.

```
      solution std.error   z.ratio
(Intercept) 20.305073 0.2899515 70.029214
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
```

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```
      LogLik      Sigma2     DF    wall
1 -3346.652      1.0  1602 11:38:14
2 -3346.652      1.0  1602 11:38:14
```

	Df	denDF	F.inc	F.con	Margin	Pr
(Intercept)	1	460.2	14880.00	14880.00		0
age	4	1225.3	88.73	88.73	A	0

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.

8.0.2. 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")
)

```

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	LogLik	Sigma2	DF	wall
1	-8751.390	1.0	1602	11:38:14
2	-7169.205	1.0	1602	11:38:14
3	-5427.604	1.0	1602	11:38:14
4	-4219.598	1.0	1602	11:38:14
5	-3569.815	1.0	1602	11:38:14
6	-3382.341	1.0	1602	11:38:14
7	-3352.867	1.0	1602	11:38:14

```

8      -3351.565      1.0    1602  11:38:14
9      -3351.560      1.0    1602  11:38:14

```

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	1.156116	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")
)
```

	LogLik	Sigma2	DF	wall
1	-7731.394	1.0	1602	11:38:14
2	-6426.548	1.0	1602	11:38:14
3	-4997.252	1.0	1602	11:38:14
4	-4018.486	1.0	1602	11:38:14
5	-3504.988	1.0	1602	11:38:14
6	-3363.160	1.0	1602	11:38:14
7	-3341.611	1.0	1602	11:38:14
8	-3340.682	1.0	1602	11:38:14
9	-3340.679	1.0	1602	11:38:14

```
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:

```
vpredict(modely, h2 ~ V1 / (V1 + V2 + V3))
```

	Estimate	SE
h2	0.1701523	0.0607397

```
vpredict(modely, repeatability ~ (V1 + V2) / (V1 + V2 + V3))
```

	Estimate	SE
repeatability	0.4284108	0.027416

8.0.3. 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.

```
modelz <- asreml(
  fixed = laydate ~ age,
  random = ~ vm(animal, ainv) + ide(animal) +
    year + byear,
  residual = ~ idv(units),
  data = gryphonRM,
  na.action = na.method(x = "omit", y = "omit")
)
```

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	LogLik	Sigma2	DF	wall
1	-4650.748	1.0	1602	11:38:14
2	-4088.264	1.0	1602	11:38:14
3	-3494.147	1.0	1602	11:38:14
4	-3127.161	1.0	1602	11:38:14 (1 restrained)
5	-2976.449	1.0	1602	11:38:14 (1 restrained)
6	-2955.785	1.0	1602	11:38:14 (1 restrained)
7	-2955.097	1.0	1602	11:38:14 (1 restrained)
8	-2955.095	1.0	1602	11:38:14 (1 restrained)
9	-2955.095	1.0	1602	11:38:14

```
summary(modelz)$varcomp
```

	component	std.error	z.ratio	bound	%ch
byear	0.0000002	NA	NA	B	NA
year	7.9385763	1.9344619	4.103765	P	0
vm(animal, ainv)	4.8151355	1.6682351	2.886365	P	0
ide(animal)	8.4333254	1.5495778	5.442337	P	0
units!units	7.7955597	0.3324411	23.449443	P	0

	component	std.error	z.ratio	bound	%ch
units!R	1.0000000	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.

```
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")
)
```

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	LogLik	Sigma2	DF	wall
1	-4665.606	1.0	1602	11:38:15
2	-4097.928	1.0	1602	11:38:15
3	-3498.611	1.0	1602	11:38:15
4	-3128.789	1.0	1602	11:38:15
5	-2976.883	1.0	1602	11:38:15
6	-2955.806	1.0	1602	11:38:15
7	-2955.096	1.0	1602	11:38:15
8	-2955.095	1.0	1602	11:38:15

```
summary(modelz_2)$varcomp
```

	component	std.error	z.ratio	bound	%ch
year	7.938576	1.9344829	4.103720	P	0

	component	std.error	z.ratio	bound	%ch
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] 0.9990453

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")
)
```

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LogLik	Sigma2	DF	wall
--------	--------	----	------

1	-4623.985	1.0	1569	11:38:15
2	-4063.535	1.0	1569	11:38:15
3	-3471.618	1.0	1569	11:38:15
4	-3105.972	1.0	1569	11:38:15
5	-2955.436	1.0	1569	11:38:15
6	-2934.435	1.0	1569	11:38:15
7	-2933.721	1.0	1569	11:38:15
8	-2933.720	1.0	1569	11:38:15

```
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

	solution	std	error	z.ratio
(Intercept)	20.305073	0.2899515	70.029214	
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	

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	LogLik	Sigma2	DF	wall
1	-2933.720	1.0	1569	11:38:15
2	-2933.720	1.0	1569	11:38:15

	Df	denDF	F.inc	F.con	Margin	Pr
(Intercept)	1	55.3	1894.0000	1894.0000		0.0000000
age	4	845.2	152.7000	132.9000	A	0.0000000
byear	33	466.5	0.7722	0.7722	A	0.8164617

Chapter 9

MCMCglmm

9.0.1. 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 uninformative 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)
```

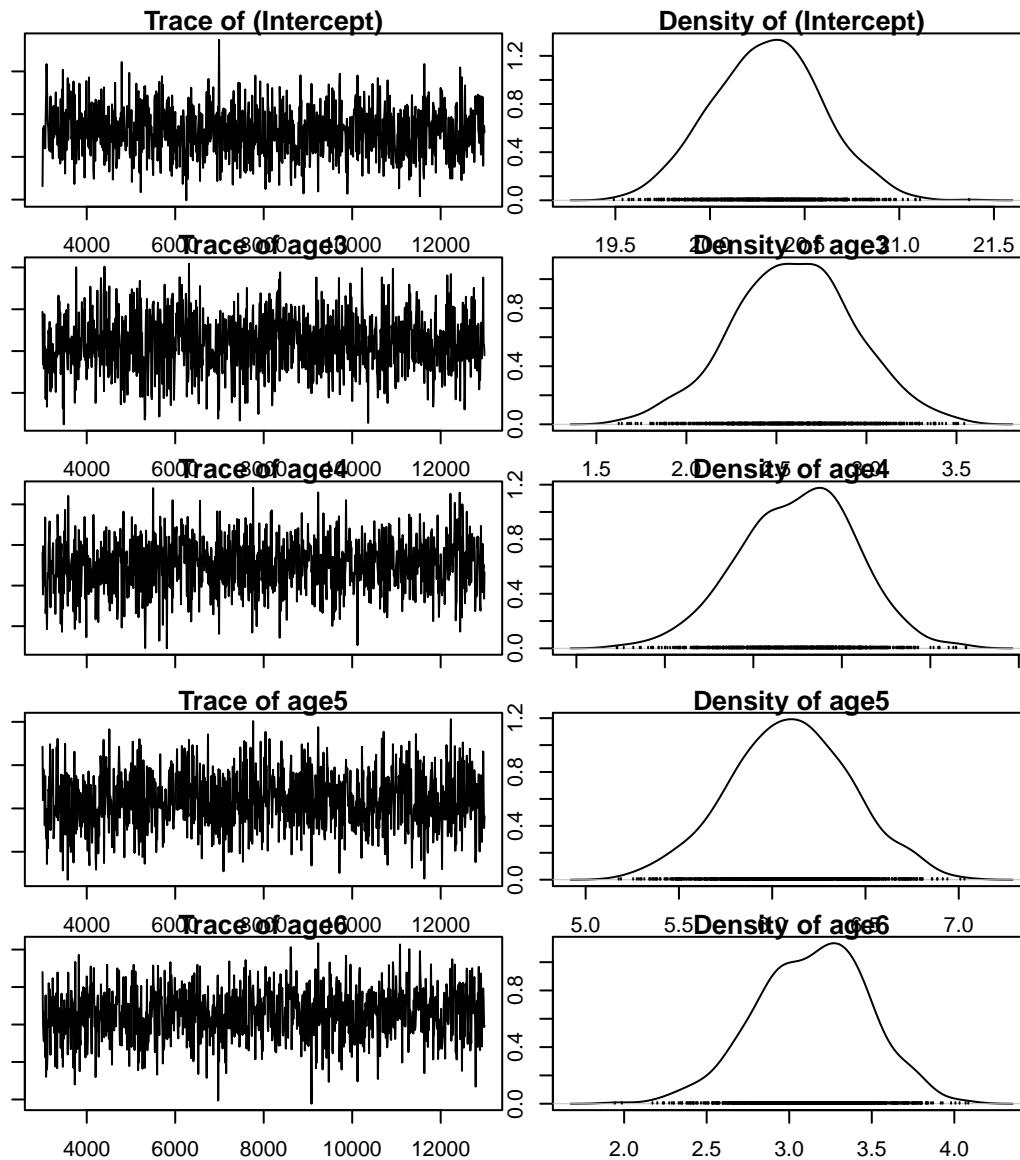
```
animal      units
10.67985 21.28520
```

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`.

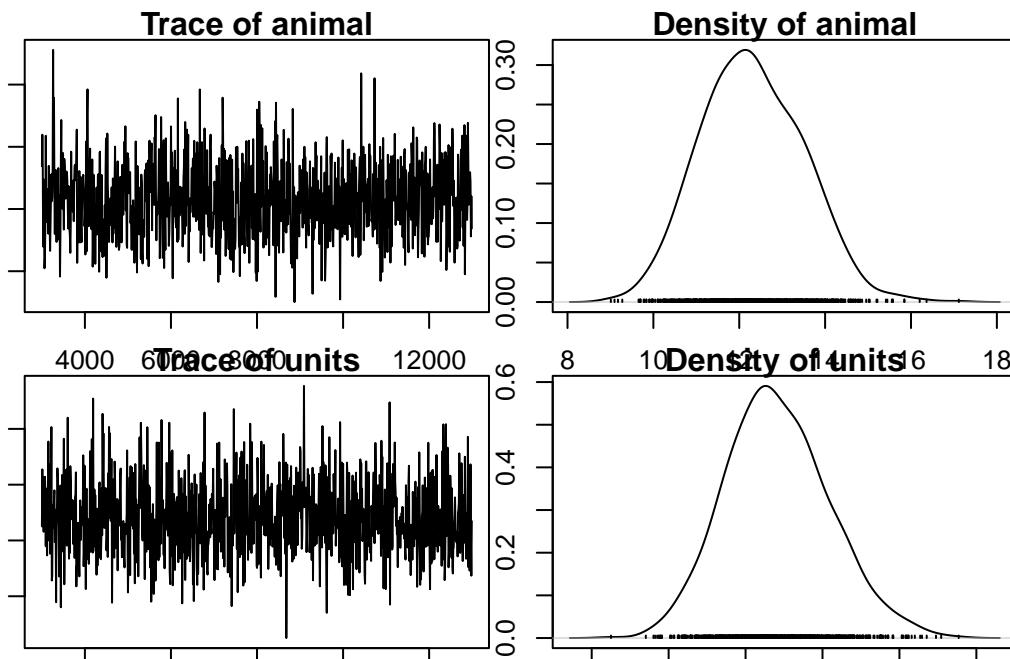
Here then the repeatability of the laydate can be determined as: 22.29 (*i.e.*, as $10.68/(10.68 + 21.285)$). Just a friendly reminder, we work with Monte Carlo chain with model iteration, so the point estimate can be different (but very similar) each time you run the model.

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
)
par(mar = c(1, 1, 1, 1))
plot(model3.2$Sol)
```



```
plot(model3.2$VCV)
```



```
posterior.mode(model3.2$VCV)
```

animal	units
12.18011	16.28056

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 22.29 (*i.e.*, as $10.68/(10.68 + 21.285)$). 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.

```
posterior.mode(model3.2$Sol)
```

(Intercept)	age3	age4	age5	age6
20.361160	2.743338	4.419162	6.038813	3.290132

```
HPDinterval(model3.2$Sol, 0.95)
```

```

      lower       upper
(Intercept) 19.775827 20.887996
age3         1.863914  3.209940
age4         3.657741  4.913932
age5         5.480571  6.753545
age6         2.509874  3.803416
attr(,"Probability")
[1] 0.95

```

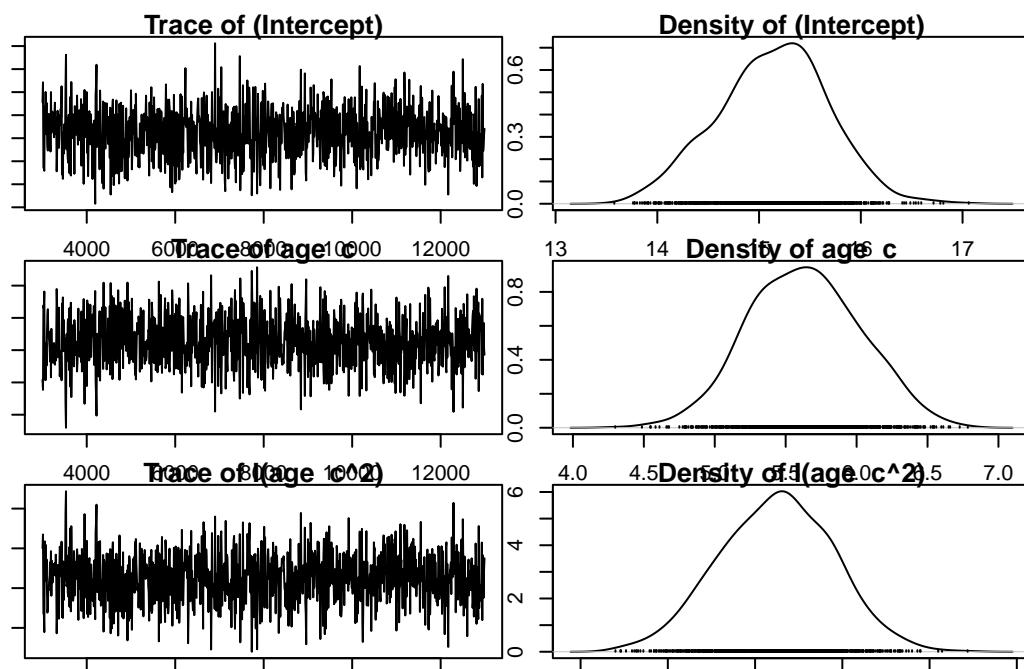
Here age is modeled as a 5-level factor (specified using the function `as.factor()` at the beginning of the analysis). We could equally have fitted it as a continuous variable, in which case, given potential for a late life decline, we would probably also include a quadratic term. In addition, using `age` as continuous variable can help in saving some degree of freedom in the analysis.

```

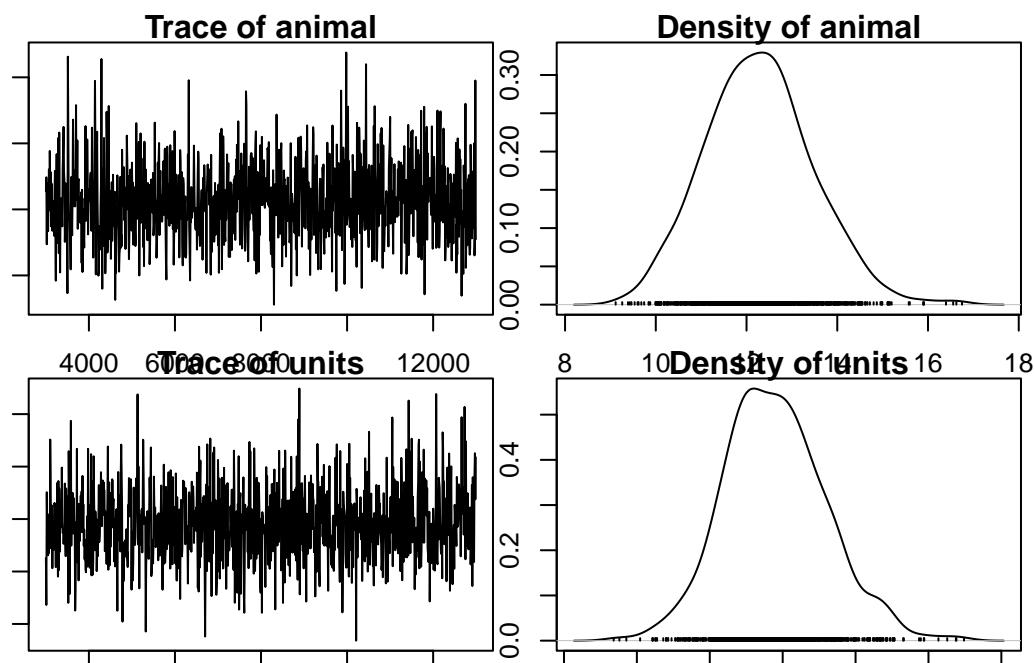
gryphonRM$age_c <- as.numeric(gryphonRM$age)

model3.2_2 <- MCMCglmm(laydate ~ age_c + I(age_c^2),
  random = ~animal, data = gryphonRM,
  prior = prior3.1, verbose = FALSE
)
par(mar = c(1, 1, 1, 1))
plot(model3.2_2$Sol)

```



```
plot(model3.2_2$VCV)
```



```
posterior.mode(model3.2_2$VCV)
```

animal	units
12.77266	16.51431

```
posterior.mode(model3.2$Sol)
```

```
(Intercept)      age_c   I(age_c^2)
15.3014700    5.5882993 -0.7634834
```

```
HPDinterval(model3.2$Sol, 0.95)
```

```
lower       upper
(Intercept) 14.0702157 16.1519997
age_c        4.9036170  6.4275478
I(age_c^2)  -0.9048494 -0.6561443
attr(,"Probability")
[1] 0.95
```

9.0.2. 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
13.79501 17.19446
```

```
posterior.mode(model3.2$VCV)
```

```
animal      units
12.18011 16.28056
```

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 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
5.000774  6.931818 16.712970
```

The estimate of V_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$VCV[, "units"]
model3.4.PE_VA <- model3.4$VCV[, "animal"] + model3.4$VCV[, "animal_pe"]
posterior.mode(model3.4.PE_VA / model3.4.VP)
```

```
var1
0.4304769
```

```
posterior.mode(model3.4$VCV[, "animal"] / model3.4.VP)
```

```
var1
0.1735927
```

9.0.3. 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
4.955518461 8.396521169 7.673492341 0.002060264 7.747678616

```

```
HPDinterval(model3.5$VCV, 0.95)
```

	lower	upper
animal	2.3685070901	8.3886556
animal_pe	5.5459568326	11.2385830
year	5.0750570665	12.8090116
byear	0.0003190255	0.2065312
units	7.1497435613	8.3953730

```

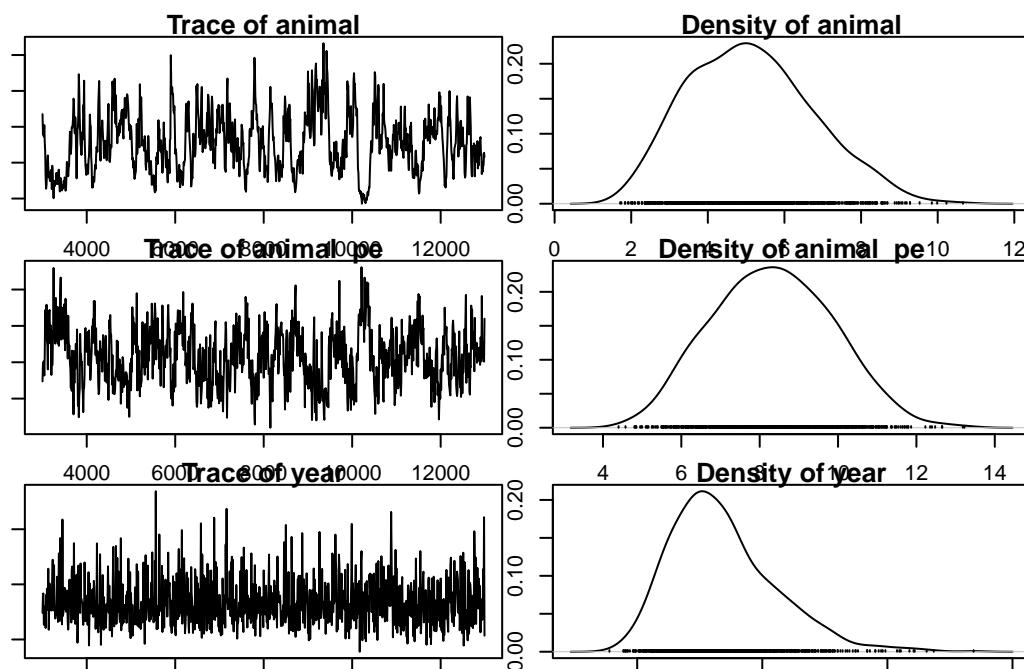
attr(,"Probability")
[1] 0.95

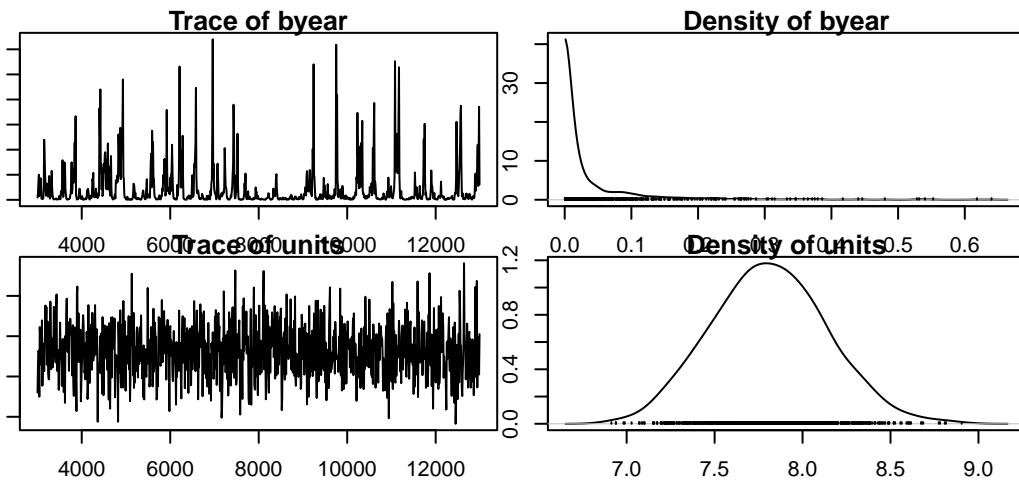
```

```

par(mar = c(1, 1, 1, 1))
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
4.725104	7.834043	8.109265	7.781416

```
model3.5$DIC
```

```
[1] 8290.793
```

```
model3.5_2$DIC
```

```
[1] 8290.662
```

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.

Chapter 10

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)
```

Chapter 11

Quick comparison of codes

11.1. Univariate model with repeated measures

11.1.1. **Asreml-R**

11.1.2. **gremlin**

11.1.3. **MCMCglmm**

11.1.4. **brms**

11.2. bivariate model

11.2.1. **Asreml-R**

11.2.2. **gremlin**

11.2.3. **MCMCglmm**

11.2.4. **brms**

References

R packages

This book was produced using all the following R packages

A large number of files (2811 in total) have been discovered.

It may take `renv` a long time to crawl these files for dependencies.

Consider using `.renvignore` to ignore irrelevant files.

See ``?renv::dependencies`` for more information.

Set ``options(renv.config.dependencies.limit = Inf)`` to disable this warning.

Package	Version	Citation
abind	1.4.5	Plate and Heiberger (2016)
asreml	4.2.0.302	The VSNI Team (2023)
base	4.4.1	R Core Team (2024)
brms	2.21.0	Bürkner (2017); Bürkner (2018); Bürkner (2021)
knitr	1.48	Xie (2014); Xie (2015); Xie (2024)
lme4	1.1.35.5	Bates et al. (2015)
MCMCglmm	2.36	Hadfield (2010)
nadiv	2.18.0	Wolak (2012)
rmarkdown	2.28	Xie et al. (2018); Xie et al. (2020); Allaire et al. (2024)
rptR	0.9.22	Stoffel et al. (2017)
tidyverse	2.0.0	Wickham et al. (2019)
visreg	2.7.0	Breheny and Burchett (2017)

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