Comment ajuster un modèle animal?

Un guide pour les écologiste

Julien Martin & Mathieu Videlier

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Preface

Ce livre est une collection de tutoriels tirés de l'excellent article de Wilson et al. (2010). Les tutoriels ont été mis à jour pour fonctionner avec les dernières versions des logiciels, complétés par des informations supplémentaires et d'autres logiciels ont été ajoutés. Eric Postma a aimablement fourni une version mise à jour du tutoriel original d'asreml-r de asreml-r v3 à asreml-r v4.

Il s'agit d'un document évolutif et les informations sont régulièrement mises à jour/ajoutées

Citer le livre

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Images

L’image de couverture a été générée par Julien Martin à l’aide du générateur d’images Nightcafe AI en utilisant l’appel “Family tree of legendary beast”.

Wui sommes-nous ?

Julien Martin est professeur à l'Université d'Ottawa et travaille sur l'écologie évolutive. Il a découvert R avec la version 1.8.1 et enseigne R depuis la version 2.4.0. Il a développé la première version du livre en février 2021 et continue maintenant à développer le livre et à maintenir le site pour toutes les langues (actuellement seulement l'anglais mais le français et l'espagnol seront bientôt disponibles).

- 🔖: uOttawa page, lab page
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Collant Hex

Chapitre 1

Introduction

Ce livre fournit une série de tutoriels (avec les fichiers de données) pour produire un modèle animal dans `R` à l'aide de différents paquets/modules (`ASReml-R`, `gremlin`, `MCMCglmm` et `brms/stan`).

Vous devrez suivre attentivement les instructions ci-dessous pour télécharger les fichiers de données et installer les modules R.

Avant de commencer le tutoriel, nous supposons que le lecteur a installé avec succès le programme R ainsi que les modules R de son choix sur son ordinateur et qu'il a sauvegardé les fichiers de données requis dans le répertoire approprié à partir duquel ils seront lus/utilisés.

Des instructions complètes sur la manière de procéder sont fournies avec les distributions de logiciels. Pour travailler avec les différents tutoriels, nous vous recommandons de créer un dossier dans lequel vous enregistrerez vos différents scripts `R` pour les tutoriels. De plus, le tutoriel est là pour aider les chercheurs dans leurs codes et leur compréhension des modèles et des résultats, mais il est nécessaire que vous lisiez et compreniez la littérature sur la génétique quantitative et le modèle animal.

1.1. Base de données

1.1.1. Fichiers de la base de données

Vous aurez besoin de télécharger 3 fichiers de données pour le tutoriel dans `R` :

- gryphon.csv : données sur le poids à la naissance et la morphologie du griffon
- gryphonRM.csv : données sur la mesure répétée de la date de ponte du griffon.
- gryphonped.csv : données sur le pedigree associé à la base de données griffon.

De plus, certains des modèles présentés dans les tutoriels peuvent prendre un certain temps à s'exécuter (parfois > 1 heure), c'est pourquoi nous fournissons également les sorties des modèles pour vous permettre de poursuivre le tutoriel sans attendre que le modèle s'exécute. (Mais vous êtes libre d'exécuter les modèles, et nous l'encourageons pour votre propre apprentissage). Les fichiers sont disponibles ici Je recommande de sauvegarder les fichiers data et Rdata dans un sous-dossier `data` dans le dossier que vous utiliserez comme répertoire de travail pour R et où vous sauvegarderez vos scripts R. Notez que le tutoriel utilise cette structure pour lire ou sauvegarder les données.

1.1.2. Notes sur la base de données et son pedigree

Il est toujours important de prendre le temps de réfléchir attentivement aux points forts et aux limites potentielles de votre pedigree (ou vos informations généalogiques) avant de vous lancer dans des analyses de génétique quantitative. Pedigree Viewer, écrit par Brian Kinghorn, est une application extrêmement utile pour visualiser les pedigrees, et peut être téléchargé à partir de : http://www-personal.une.edu.au/~bkinghor/pedigree.htm. `pedtricks`, un module R écrit par Martin et al. (2024) et disponible sur CRAN peut également être utilisé à cette fin et offre quelques fonctionnalités supplémentaires intéressantes pour visualiser les structures des pedigrees et générer les statistiques associées. Avant de commencer à parcourir les tutoriels, nous vous conseillons de prendre un moment pour regarder les fichiers de pedigree fournis avec eux en utilisant Pedigree Viewer ou pedtricks.

1.2. R

Vous devez vérifier que vous disposez de la version la plus récente de R et des modules R. Vous pouvez vérifier le numéro de la version actuelle sur le CRAN. Vous pouvez vérifier le numéro de la version actuelle sur le CRAN. Si vous avez besoin de mettre à jour (ou d'installer) des modules R, utilisez `install.packages()` et suivez les instructions qui vous sont données.

1.2.1. Modules R

1.2.1.1. asreml-r

ASReml-R est un logiciel commercial édité par VSN international (http://www.vsni.co.uk/software/asreml/). Ce logiciel n'est pas gratuit et nécessite une clé d'accès. Des informations supplémentaires et un guide peuvent être trouvés dans le manuel d'Asreml-R VSNI a pffert une licence gratuite pour 12 mois pour soutenir le développement de ce guide. De plus, VSNI propose un blog contenant des guides et des avis sur l'analyse des données (https://vsni.co.uk/blogs/) ainsi que des cours privés.

1.2.1.2. gremlin

’gremlin‘ est un petit monstre qui apparaît si vous nourrissez un mugwai après minuit. C’est aussi un logiciel génial et prometteur écrit par Matthew Wolak pour exécuter des modèles mixtes en utilisant une approche fréquentiste.

1.2.1.3. MCMCglmm

`MCMCglmm` est un module R pour l’analyse des modèles mixtes bayésiens écrit par Jarrod Hadfield. Il s’agit d’un logiciel gratuit distribué par le biais du CRAN (http://cran.r-project.org/). Des informations et des guides sur ce module peuvent être trouvés dans son manuel de l’utilisateur et ses vignettes (http://cran.r-project.org/web/packages/MCMCglmm/index.html). Référence : (Hadfield 2010). Cette partie fournit des informations qui s’appliquent aux analyses basées sur MCMCglmm en général, mais qui ne seront pas incluses dans d’autres tutoriels. Plus important encore, il fournit certaines méthodes les plus simples pour déterminer la performance d’une analyse utilisant MCMCglmm, c’est-à-dire la vérification de la validité de la distribution postérieur. Ce tutoriel ne remplace pas des notes de cours sur le MCMCglmm, disponibles sur le CRAN (Comprehensive R ArchiveNetwork, http://cran.r-project.org/, ou accessibles dans R à l’aide de la commande vignette (“CourseNotes”, “MCMCglmm”)). Ce tutoriel ne présente pas l’un des principaux avantages de l’utilisation de MCMCglmm pour l’analyse de données provenant de populations naturelles, à savoir la possibilité de modéliser correctement des réponses non normales. Ces capacités sont présentées dans la documentation distribuée avec MCMCglmm et disponible sur le CRAN. Un autre guide du modèle animal spécifique pour MCMCglmm peut être trouvé ici. Pr. Pierre de Villemereuil fournit plus d’informations sur le concept bayésien et se concentre davantage sur les variables non gaussiennes.

1.2.1.4. brms

`brms` fournit une interface pour exécuter des modèles généralisés bayésiens multivariés (non) linéaires à plusieurs niveaux en utilisant `Stan`, qui est un module C++ pour obtenir une inférence bayésienne complète (voir https://mc-stan.org/). La syntaxe des formules est une version étendue de la syntaxe appliquée du module ‘lme4’ pour fournir une interface familière et simple pour effectuer des analyses de régression. Il faut noter que si `brms` est capable d’exécuter un modèle animal, la paramétrisation utilisée n’est pas la plus efficace et peut prendre plus de temps que l’utilisation d’une paramétrisation différente directement dans `stan`.

partie 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)
```

```r
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 NA NA NA NA NA NA NA NA NA ...
 $ mother: int  NA NA NA NA NA NA NA NA NA NA ...
```

```r
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 NA NA NA NA NA NA NA NA NA ...
 $ mother: Factor w/ 429 levels "1","2","3","8",..: NA NA NA NA NA NA NA NA NA NA ...
```

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

Chapitre 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")
)
```

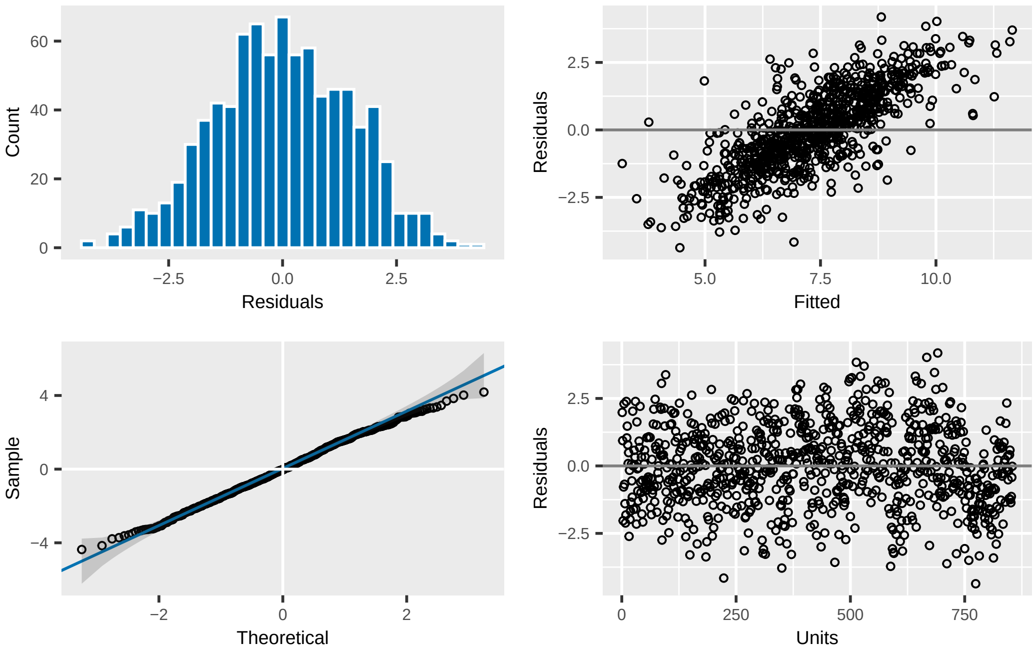
```
ASReml Version 4.2 08/10/2024 11:02:03
          LogLik        Sigma2     DF      wall
 1      -4128.454          1.0    853   11:02:03
 2      -3284.272          1.0    853   11:02:03
 3      -2354.992          1.0    853   11:02:03
 4      -1710.357          1.0    853   11:02:03
 5      -1363.555          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 relativeness or pedigree information.
`data=` specifies the name of the dataframe that contains our variables. Finally, we inform `asreml()` what to when it encounters `NA`s in either the dependent or predictor variables (in this case we choose to remove the records). If you use the argument "include" instead of "omit", model will keep the NA. With x="include", the model will exchange `NA` with 0. Be careful you need to standardize your trait so the mean will be equal to 0, if not estimates (including covariance in multivariate models) could be strongly biased due to the the missing values considered as 0. y="include" will exchange `NA` with a factor labeled `mv` which will be included in the sparse equation. For more details see Asreml-R manual.

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

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

```
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	0

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

2.0.2. 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:

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

```
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
```

```r
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

```r
(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 × (-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 (| | Estimate| |:——|———:| |h2.bwt | 0.25| and | | Estimate| |:——|———:| |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 (±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)
```

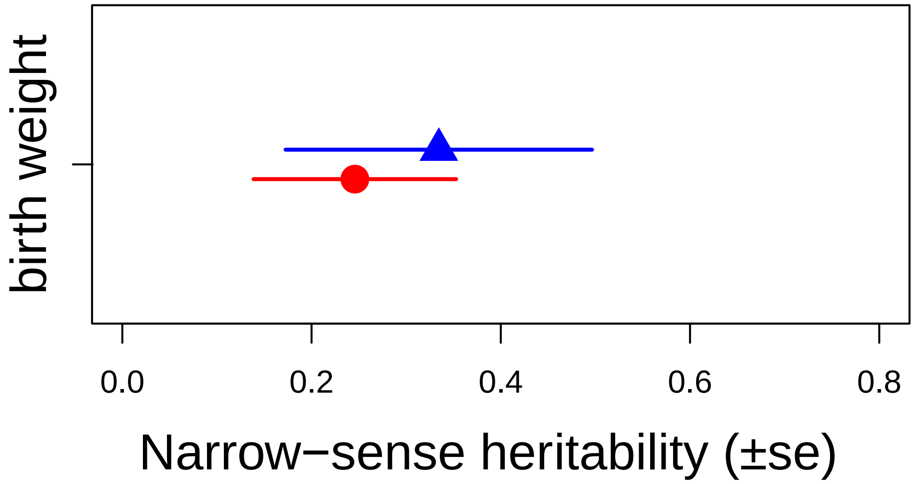


Figure 2.1.: Female and male heritability of birth weight

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
```

```r
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

```r
model.temp2 <- asreml(
  fixed = bwt ~ 1,
  random = ~ str(~ vm(animal, ainv) + vm(mother, ainv), ~ us(2):id(1309)) + byear,
  residual = ~ idv(units),
```

```
  data = gryphon,
  na.action = na.method(x = "omit", y = "omit"),
  start.values = T
)

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

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

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

Chapitre 3

MCMCglmm

3.0.1. Running the model

First load MCMCglmm:

```r
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:

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

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

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

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

```r
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)
```

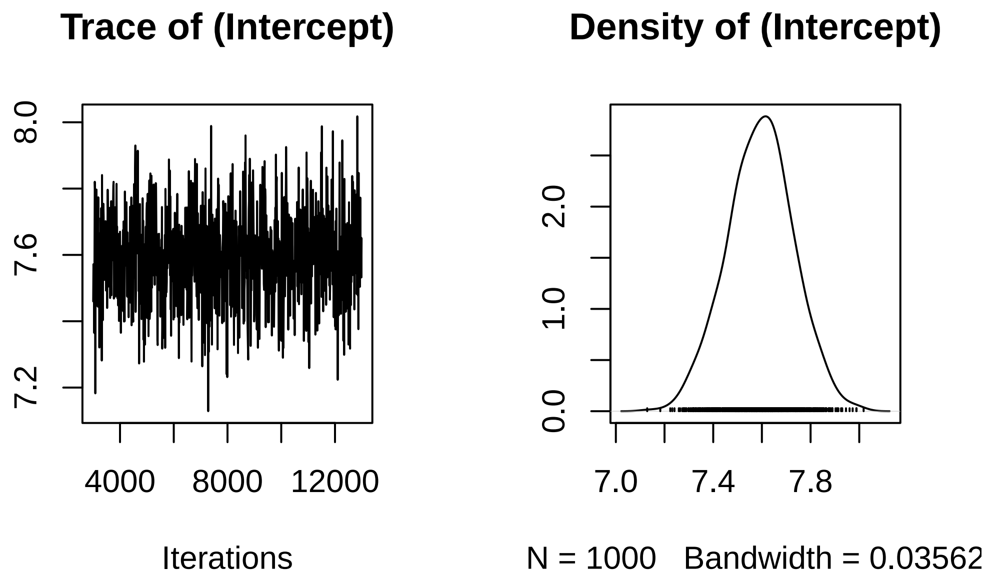


Figure 3.1.: The posterior distribution of the fixed effect (the intercept, or mean) in model 1.1

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)
```

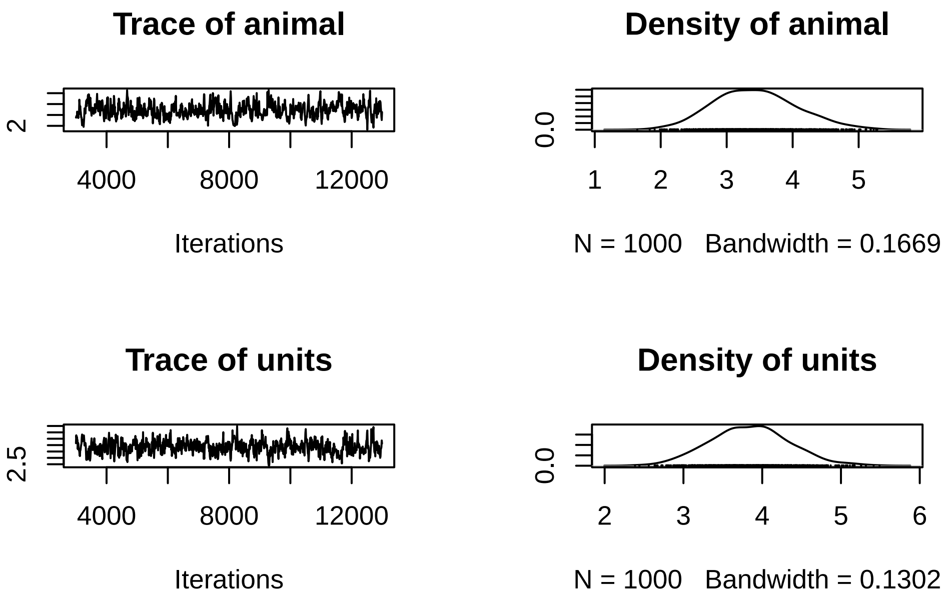


Figure 3.2.: The posterior distributions of the variance components of model 1.1, based on an analysis with the default values for nitt, burnin, and thin in MCMCglmm

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:

```r
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.

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

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

```
     var1 
0.4674414 
```

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

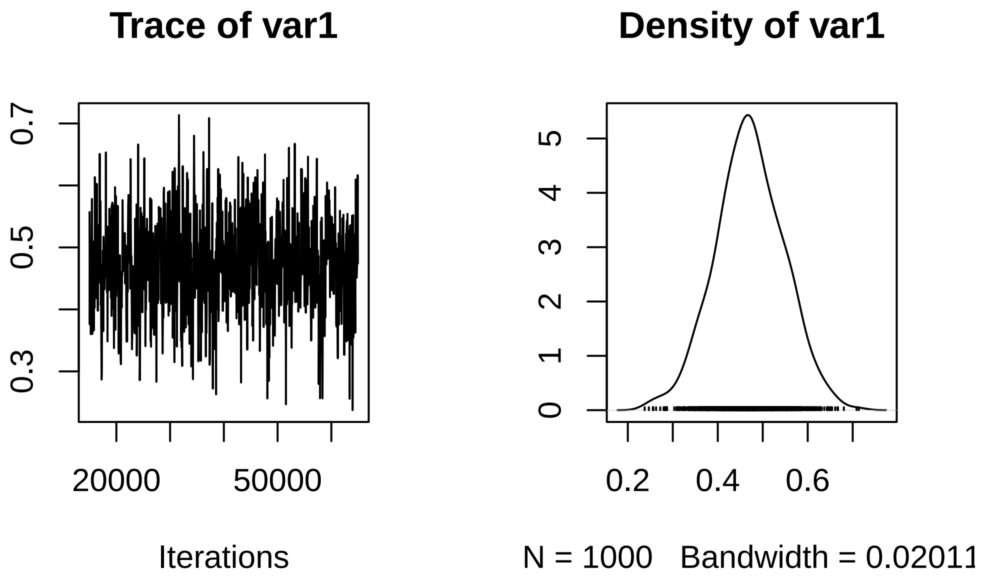


Figure 3.3.: The posterior distributions the heritability from model 1.1

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[,
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.

```r
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
  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
```

```r
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
```

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

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

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

```
     var1
0.2857213
```

```r
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"

```r
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)
```

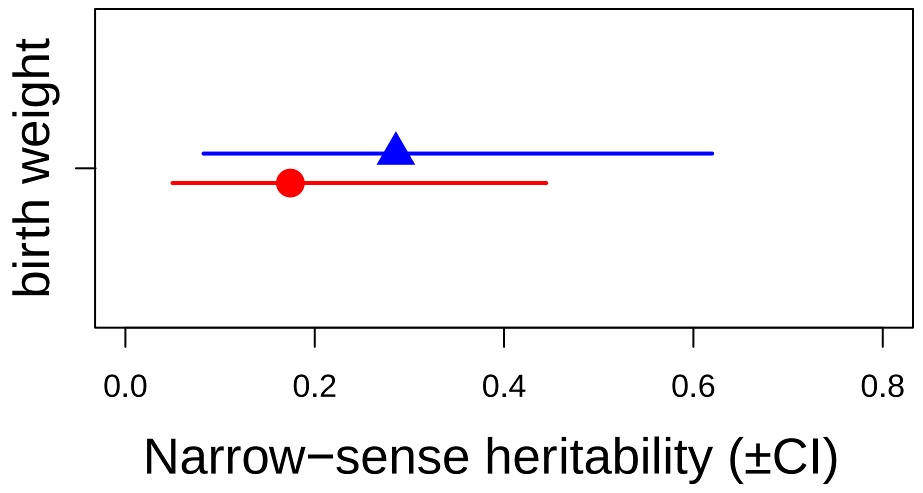


Figure 3.4.: Female and male heritability of birth weight

3.0.9. Modification of model parameter

Unfortunately (to our knowledge), it is not possible to alter the variance matricesand 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)
```

Chapitre 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 relativeness (relationship) matrix of the pedigree and not its inverse (as in other softwares). This can be estimated using the `nadiv` package created by Pr. Matthew Wolak (https://cran.r-project.org/web/packages/nadiv/index.html).

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

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

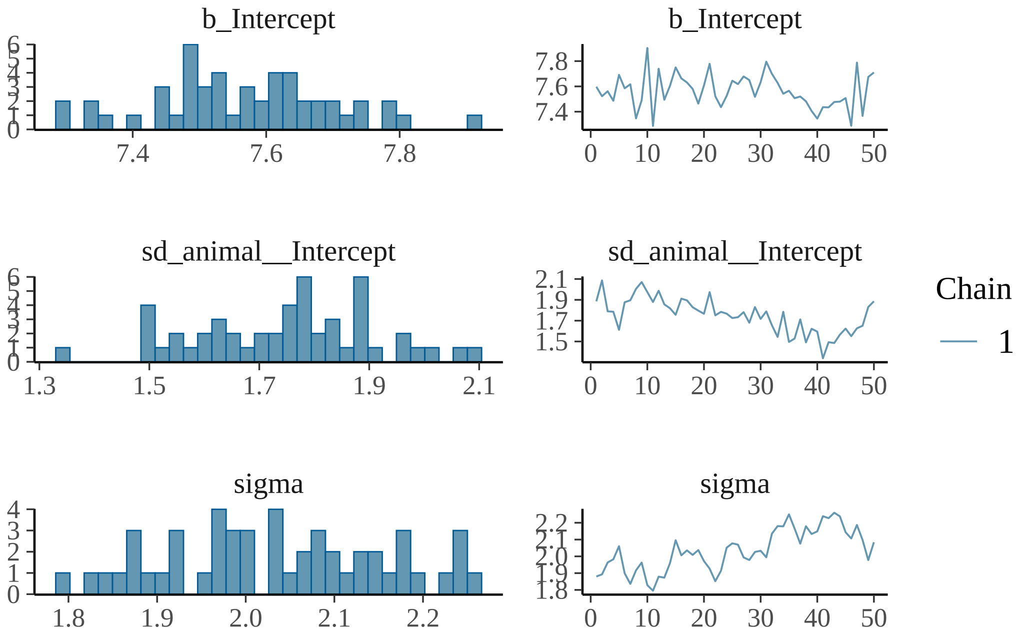
`bmrs` is a Bayesian Multilevel Models using Stan, doing so we can apply a prior to the model to better shape the distribution of the different variances estimated by the model. Given that `bmrs` fit the model using a Bayesian approach via the software `stan`, we need to specify priors for the model.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

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

save(brms_m1.1, file = "r-obj/brms_m1_1.rda")
```

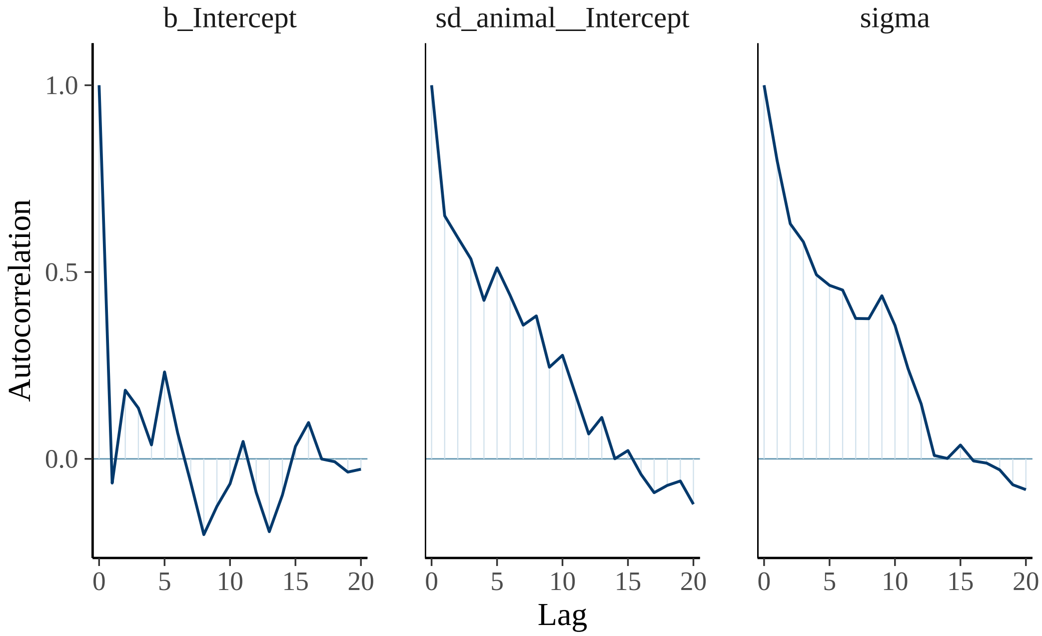
The result of the long model calculation is save in a spare file `brms_m1_1.rda"`. To help readers, we can directly reloading it. Two distinct plot can be produce to produce some diagnostics graphs `mcmc_plot`.Note, that `sigma` represents the residual standard deviation.

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

```
load("r-obj/brms_m1_1.rda")
plot(brms_m1.1)
```



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



```r
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).
```

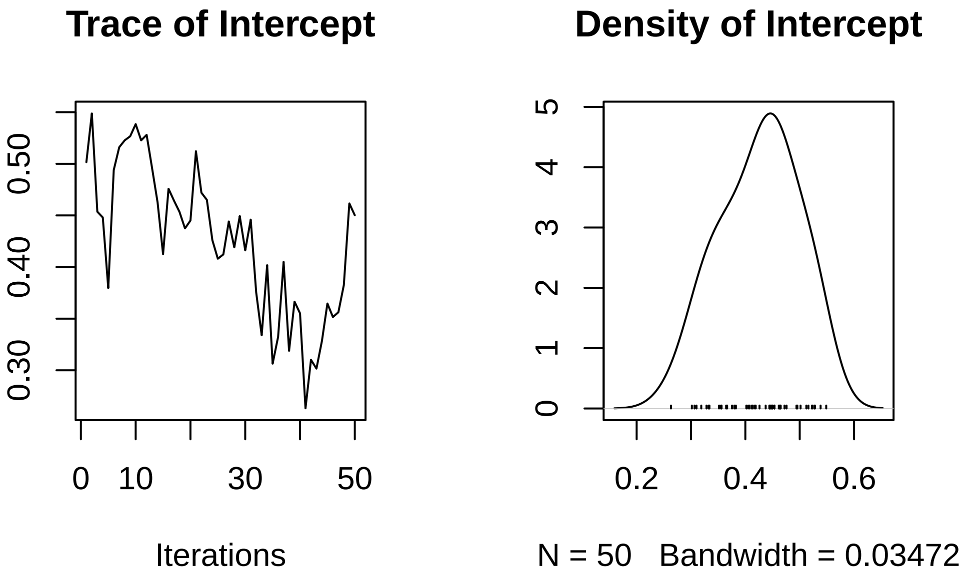
The `plot` of variance showed that the different variances have an normal distribution, the autocorrelation plot or 'acf' show that the autocorrelation is close to 0. The `summary` exposes the mean (Estimate) of each variance or fixed effect (here just the intercept) associated to their posterior distribution 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'

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

```

Iterations = 1:50
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
```

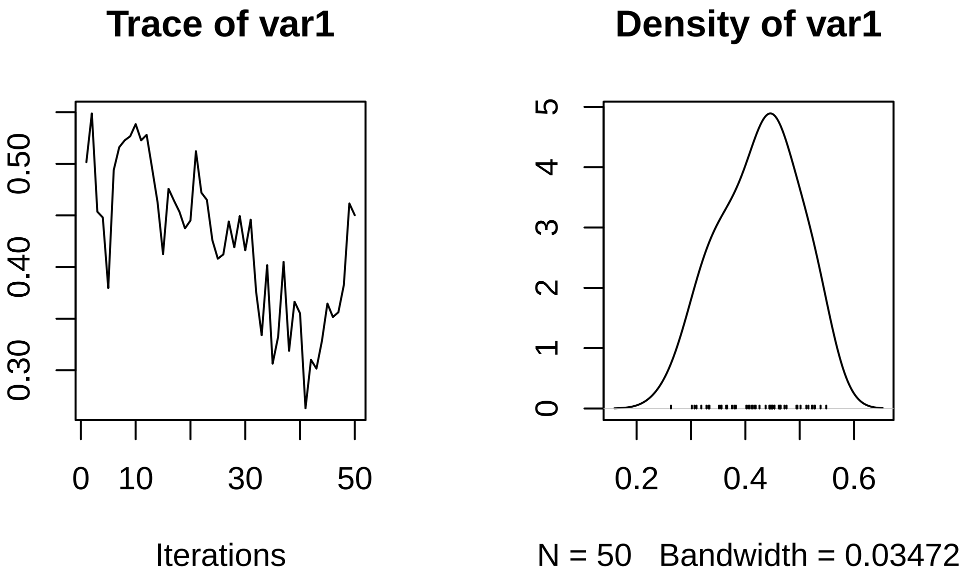
```r
plot(h.bwt.1)
```



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



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 = "r-obj/brms_m1_2.rda")
```

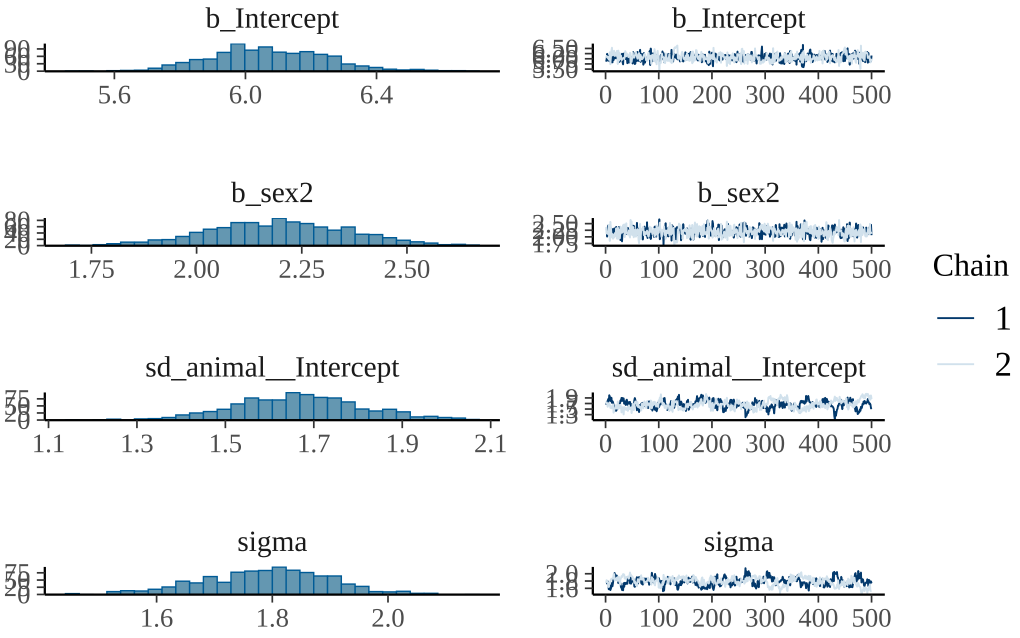
To save time, the results of the calculation is stored in the spare file `brms_m1_2.rda"`. We can assess the significance of `sex` as a fixed effect by examining its posterior distribution.

```
load("r-obj/brms_m1_2.rda")
summary(brms_m1.2)
```

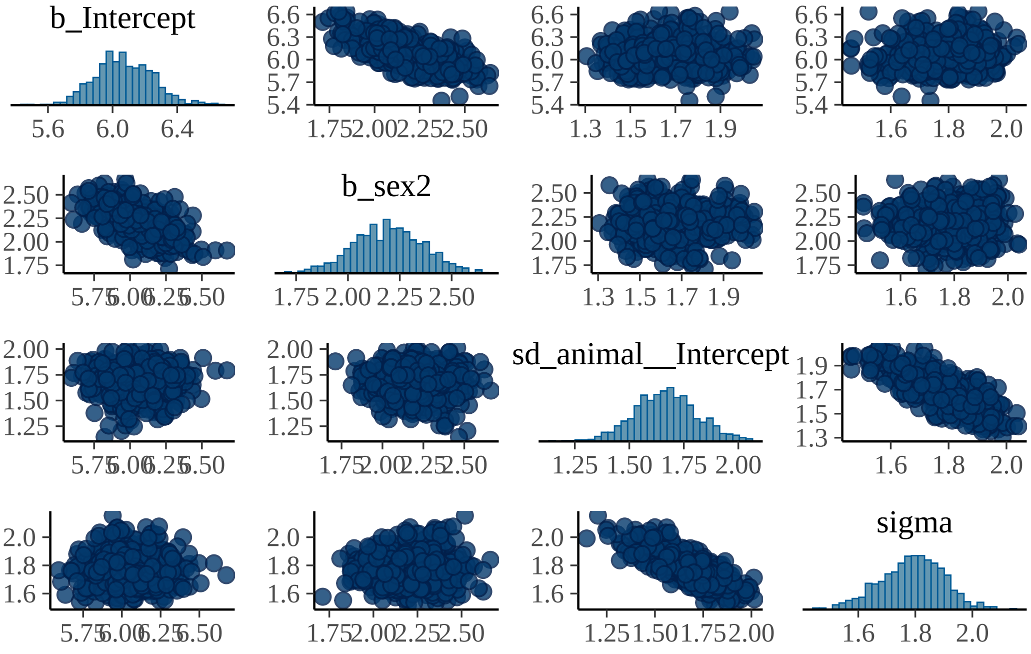
```
 Family: gaussian
  Links: mu = identity; sigma = identity
Formula: bwt ~ 1 + sex + (1 | gr(animal, cov = Amat))
   Data: gryphon (Number of observations: 854)
  Draws: 2 chains, each with iter = 1000; warmup = 500; thin = 1;
         total post-warmup draws = 1000

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       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).
```

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



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



```r
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

```r
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:

```r
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:

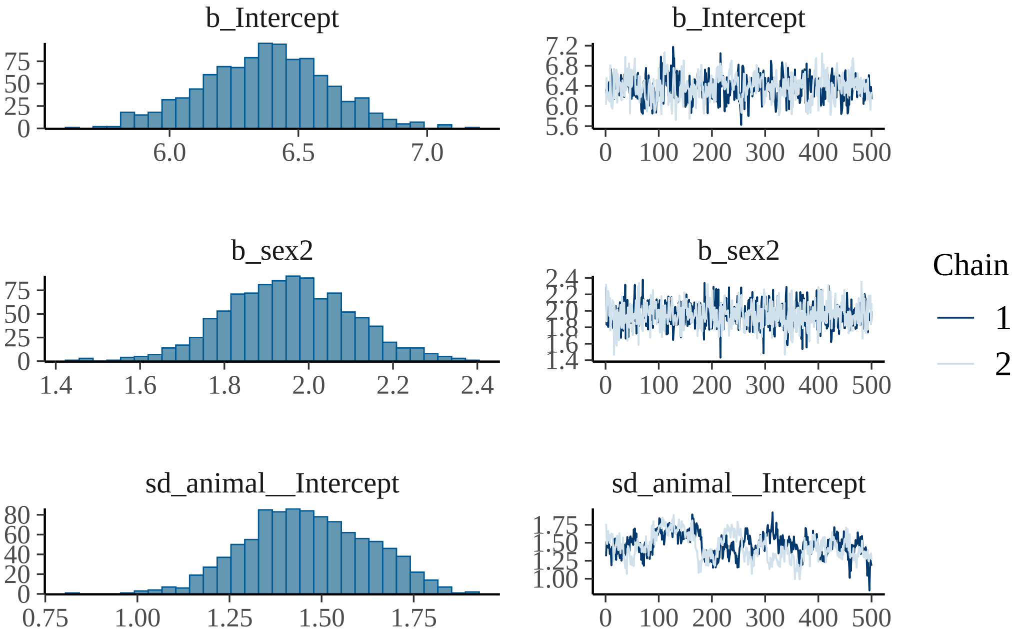
```
brms_m1.3 <- brm(
  bwt ~ 1 + sex + (1 | gr(animal, cov = Amat)) + (1 | byear) + (1 | mother),
  data = gryphon,
  data2 = list(Amat = Amat),
  family = gaussian(),
  chains = 2, cores = 2, iter = 1000
)
```

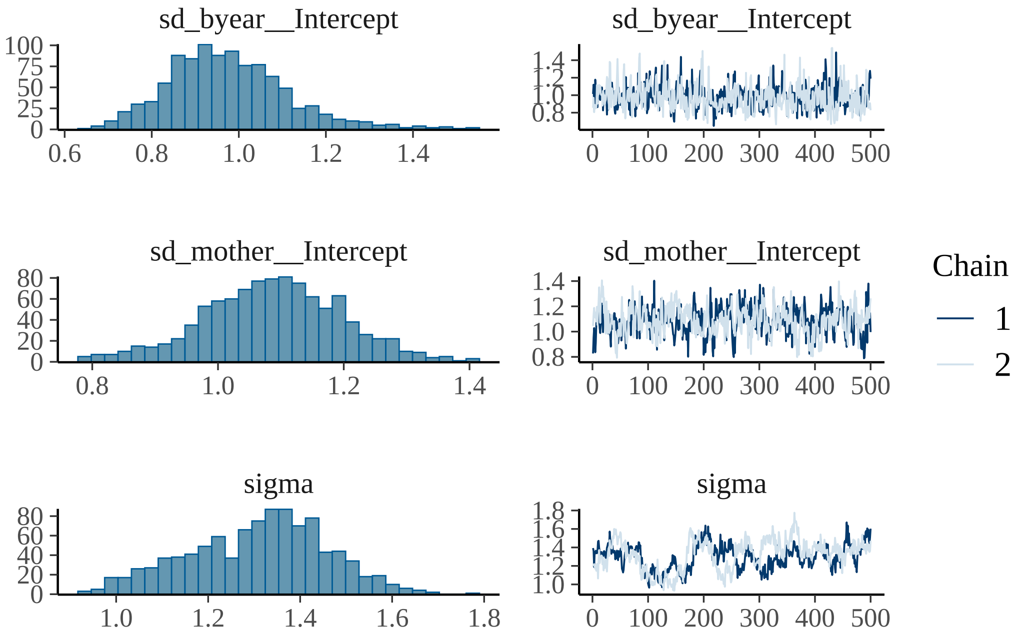
```r
save(brms_m1.3, file = "r-obj/brms_m1_3.rda")
```

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.

```r
load("r-obj/brms_m1_3.rda")

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

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





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

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

$animal
              Estimate Est.Error l-95% CI u-95% CI     Rhat Bulk_ESS Tail_ESS
sd(Intercept) 1.462757 0.1673822 1.153225 1.768881 1.079817 32.11486 156.8095

$byear
               Estimate Est.Error  l-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  l-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
```

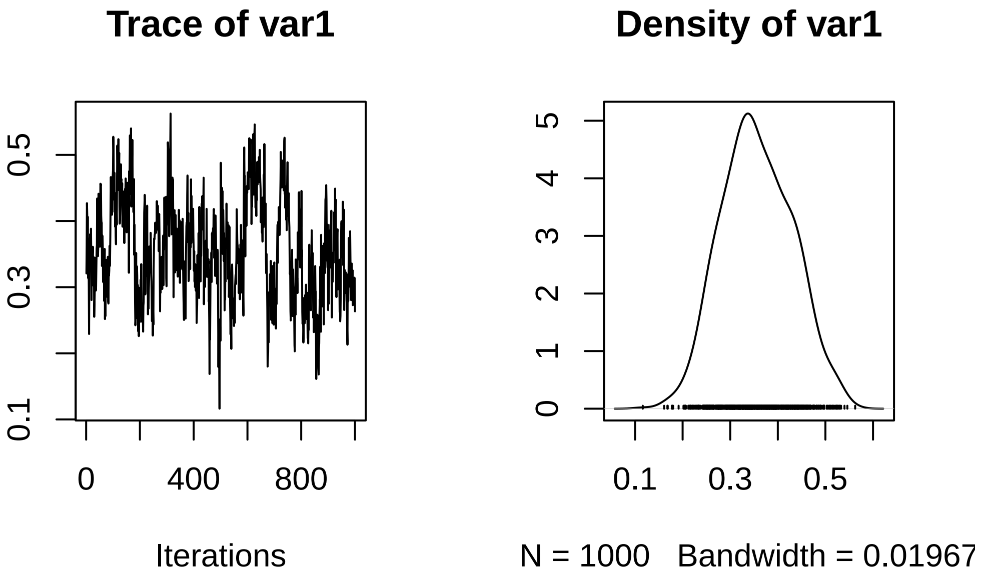
```r
summary(h.bwt.1)
```

```
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
```

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

```

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

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

          Mean             SD       Naive SE Time-series SE
      0.356562       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
```

```
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.

```r
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.
```

```r
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.
```

```r
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 approch can be done to partition the different random effect: using an extra argument `by=sex` or by adding `(0+sex|)` before the `|`. Notes, here we used `||` which not estimate a possible covariance between groups (female and male) for the random effect.

```
brms_m1.4 <- brm(
  #  bwt ~ 1 +  sex + (1 | gr(animal, cov = Amat, by = sex))+ (1 | gr(byear, by = sex)) + (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 = "r-obj/brms_m1_4.rda")
```

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

```
load("r-obj/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 l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
sd(sex1)     1.32      0.24     0.81     1.75 1.02       40      124
sd(sex2)     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(),
```

```r
  chains = 1, cores = 1, iter = 1000
)

save(brms_m1.5, file = "r-obj/brms_m1_5.rda")
```

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

```r
load("r-obj/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 l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
sd(sex1)     1.56      0.29     1.02     2.09 1.17        4       30
sd(sex2)     1.61      0.41     0.52     2.08 1.36        2       21

~byear (Number of levels: 34)
         Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
sd(sex1)     0.91      0.18     0.59     1.36 1.01      153      229
sd(sex2)     1.06      0.20     0.75     1.49 1.00      170      143

~mother (Number of levels: 394)
```

```
         Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
sd(sex1)     0.88      0.21     0.41     1.25 1.01       73      134
sd(sex2)     1.27      0.18     0.88     1.59 1.01       31       64

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).
```

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

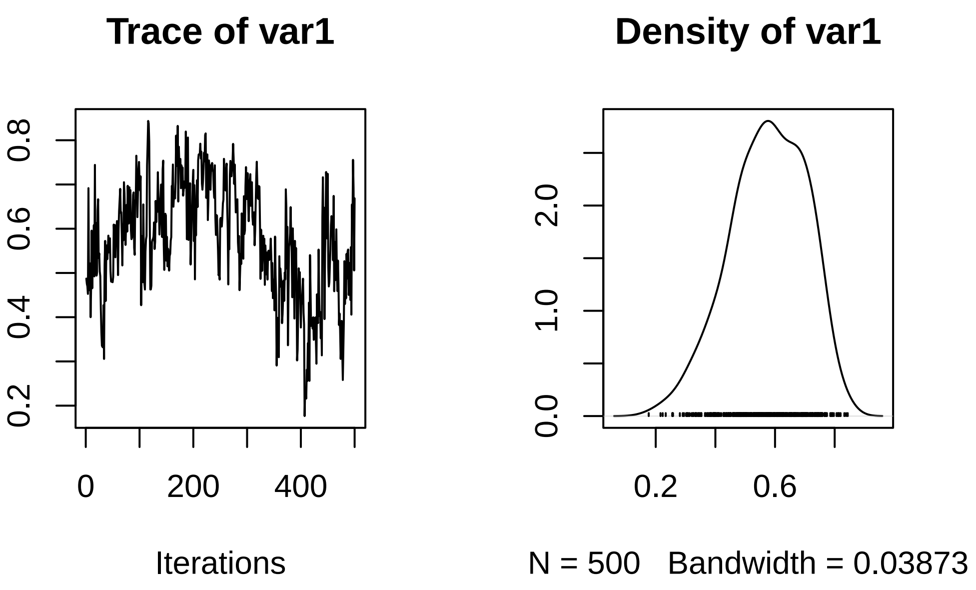
```

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 
```

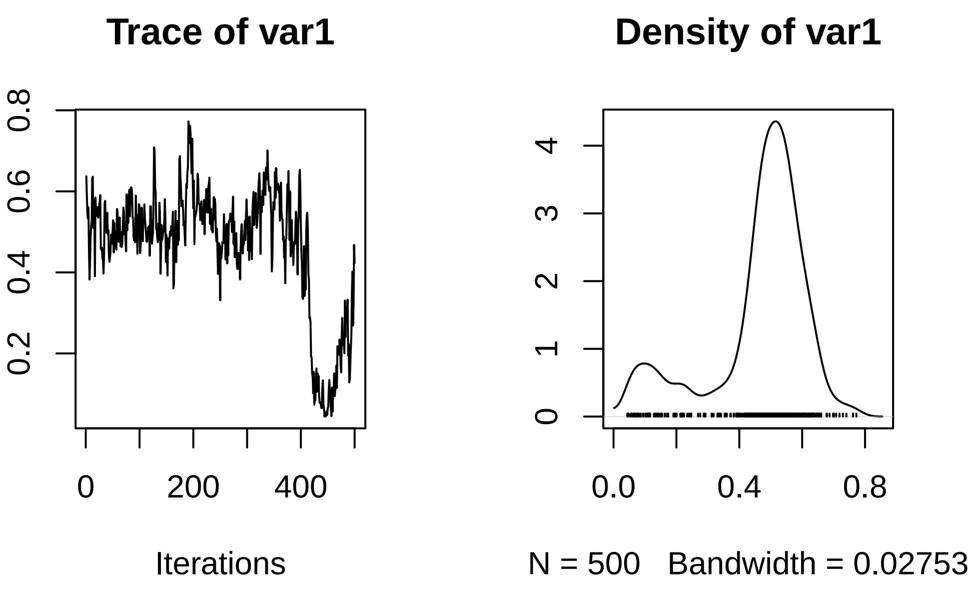
```r
summary(Var.table$h.bwt.m)
```

```
Iterations = 1:500
Thinning interval = 1 
Number of chains = 1 
Sample size per chain = 500 

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

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

2. Quantiles for each variable:

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

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



```
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], summar
  cbind(summary(Var.table$h.bwt.m)$statistics[1], summary(Var.table$h.bwt.m)$quantiles[1], summar
)


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)
```

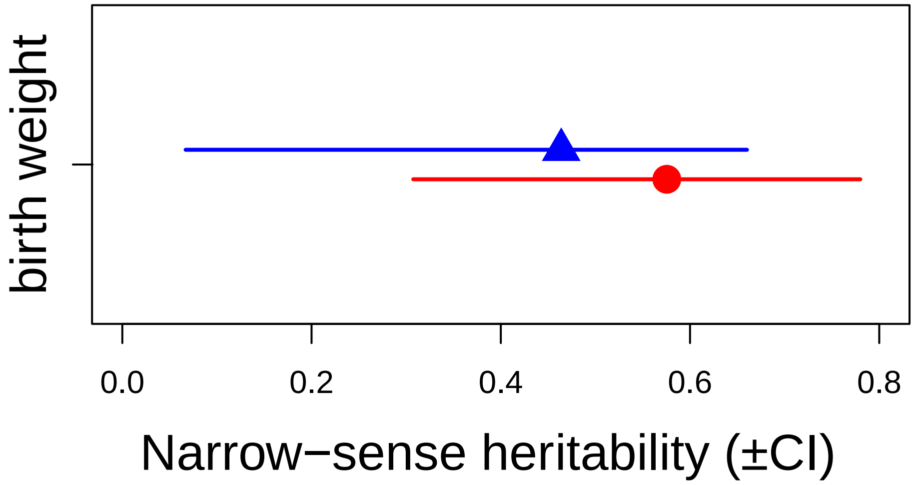


Figure 4.1.: Female and male heritability of birth weight

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.

partie 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)
```

Chapitre 5

Asreml-R

5.0.1. Running the model

First we need to load the `asreml` library:

```r
library(asreml)
```

```
Loading required package: Matrix
```

```
Attaching package: 'Matrix'
```

```
The following objects are masked from 'package:tidyr':

    expand, pack, unpack
```

```
Online License checked out Tue Oct  8 11:28:58 2024
```

```
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 repestively. We can also specify some starting values for the variance matrices. These can be very approximate *guestimates* or not at all, but having reasonable starting values can help convergence. It is also possible to let the model running without specifying starting values. Finally, we have increased the default maximum number of iterations (`maxiter`) which can help to achieve convergence for more complicated models. Another way to increase the number of iteration will be to use the `update` function. Notes that if the `LogLik` is not stabilized after several iterations, it is good indication of the model require more iteration.

```r
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
```

```r
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:

```r
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:traitr!R` component equals to 1, which again can be ignored. The final three terms relate to the residual matrix and correspond to $V_{R,bwt}$, COV_R, $V_{R,tarsus}$. Based on our quick and dirty check (is `z.ratio` > 1.96?) all components look to be statistically significant.

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

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

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

```
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)
```

```
ASReml Version 4.2 08/10/2024 11:29:00
          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:

```r
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`:

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

	Estimate	SE
r_byear	0.0850831	0.2134209

```r
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
```

```
ASReml Version 4.2 08/10/2024 11:29:00
          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
)
```

```
ASReml Version 4.2 08/10/2024 11:29:01
          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
```

```
ASReml Version 4.2 08/10/2024 11:29:02
          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:

```r
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):

```r
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
)
```

```
ASReml Version 4.2 08/10/2024 11:29:02
          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 χ^2_1= 11.6. The p-value that goes with this is obtained by:

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

```
[1] 0.0006601037
```

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

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

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

```
ASReml Version 4.2 08/10/2024 11:29:03
          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
)
```

```
ASReml Version 4.2 08/10/2024 11:29:04
          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)
```

```
ASReml Version 4.2 08/10/2024 11:29:05
          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
)
```

```
ASReml Version 4.2 08/10/2024 11:29:06
          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 normaly distributed, if not you need to check the assumption of your animal model.

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

```
gryphon$T1 <- gryphon$bwt
gryphon$T2 <- gryphon$tarsus
############
modele <- asreml(
  fixed = cbind(T1, T2) ~ trait + at(trait):sex,
  random = ~ corgh(trait, init = c(0.1, 1, 1)):vm(animal, ainv) +
    us(trait, init = c(1, 0.1, 1)):byear +
```

```
    us(trait, init = c(1, 0.1, 1)):mother,
  residual = ~ id(units):us(trait, init = c(1, 0.1, 1)),
  data = gryphon,
  na.action = na.method(x = "include", y = "include"),
  maxit = 20
)
```

```
ASReml Version 4.2 08/10/2024 11:29:07
          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
```

```r
nrow(BLUPS)
```

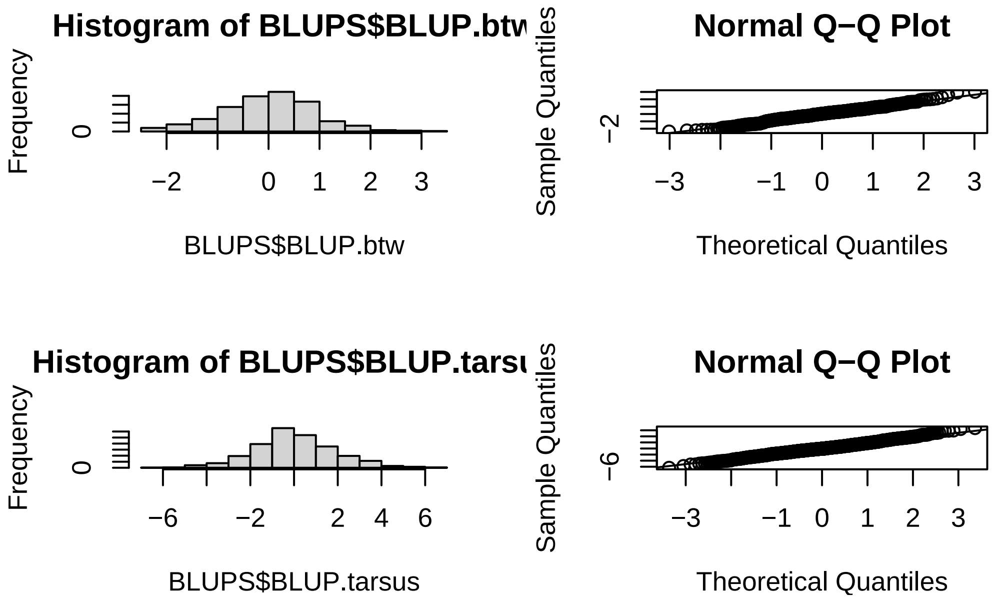
```
[1] 1310
```

```r
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
```

```r
# 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)
```

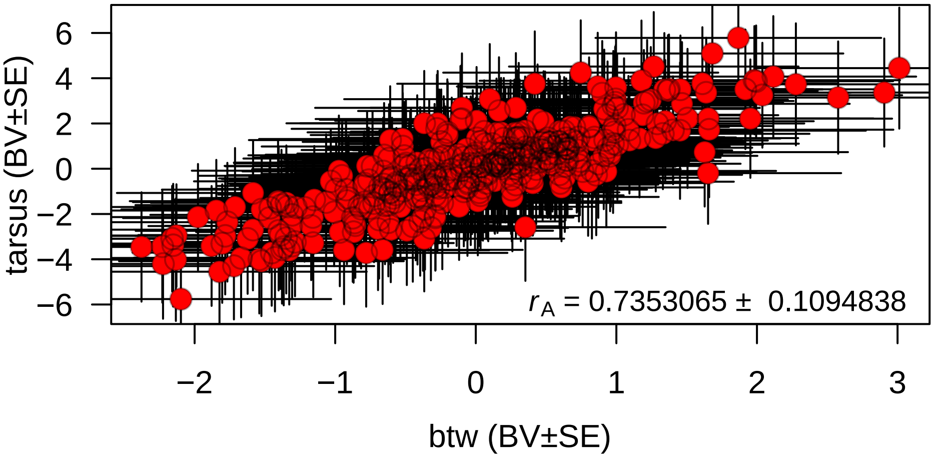
```
hist(BLUPS$BLUP.tarsus)
qqnorm(BLUPS$BLUP.tarsus)
qqline(BLUPS$BLUP.tarsus)
```



```
#
```

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 = B
arrows(x0 = BLUPS$BLUP.btw - BLUPS$SE.btw, y0 = BLUPS$BLUP.tarsus, x1 = BLUPS$BLUP.btw + BLUPS$SE
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 require to have important sample size within each group. For this example, we simplify the model !

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

```
ASReml Version 4.2 08/10/2024 11:29:09
           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.
```

```r
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
```

```r
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
```

```
ASReml Version 4.2 08/10/2024 11:29:12
          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).

```r
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

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

```
[1] 5.481033
```

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

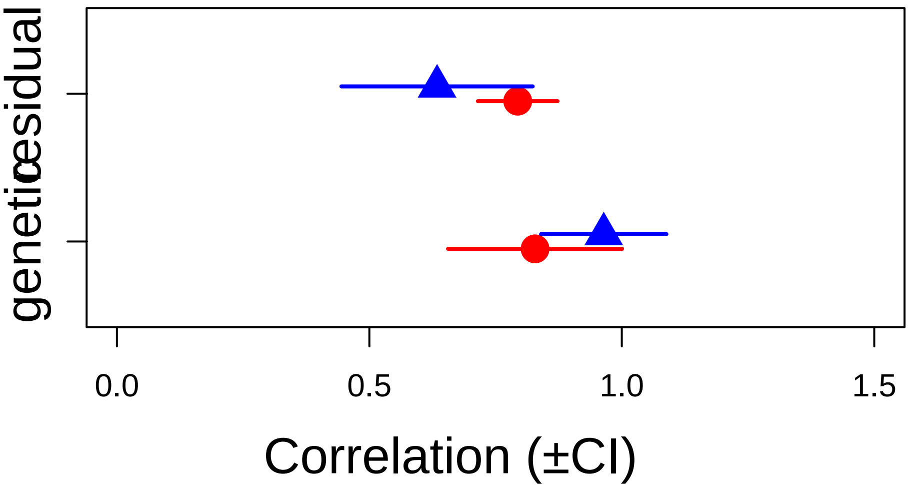
```
[1] 0.0192239
```

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 (±CI)", side = 1, las = 1, adj = 0.4, line = 3, cex = 1.6)
axis(2, at = 1, labels = c("genetic"), las = 3, cex.axis = 1.6)
axis(2, at = 2, labels = c("residual"), las = 3, cex.axis = 1.6)
```



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

```
gryphon$T1 <- gryphon$bwt
gryphon$T2 <- gryphon$tarsus
###
model_sex <- asreml(
  fixed = cbind(T1, T2) ~ trait + at(trait):sex,
  random = ~ at(sex):corgh(trait, init = c(0.1, 1, 1)):vm(animal, ainv) +
```

```
    us(trait, init = c(1, 0.1, 1)):byear +
    us(trait, init = c(1, 0.1, 1)):mother,
  residual = ~ dsum(~ id(units):us(trait) | sex),
  data = gryphon,
  na.action = na.method(x = "include", y = "include"),
  maxit = 20
)
```

```
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(grepl("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", dire
nrow(BLUPS)
```

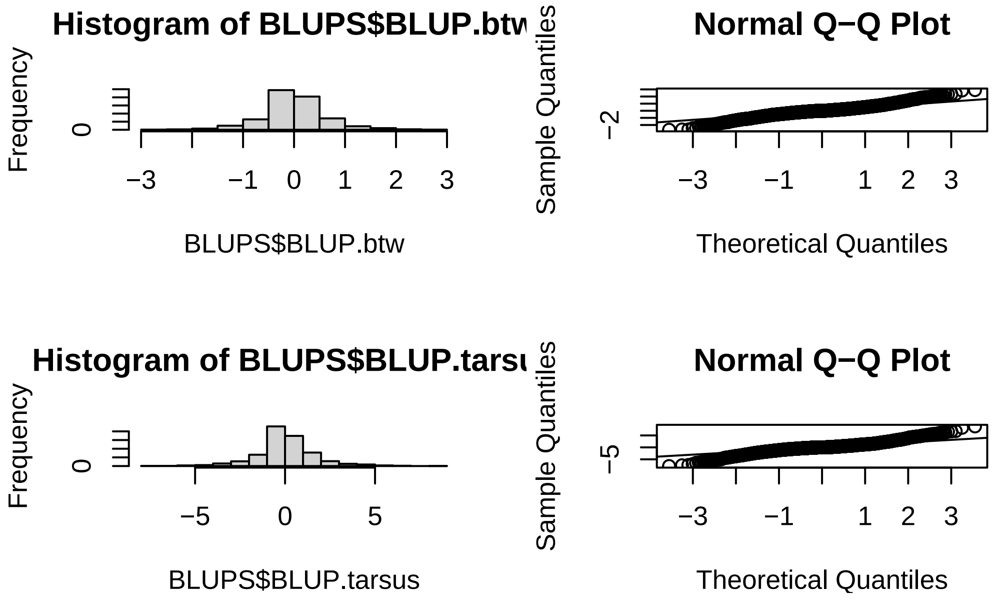
```
[1] 2618
```

```
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
```

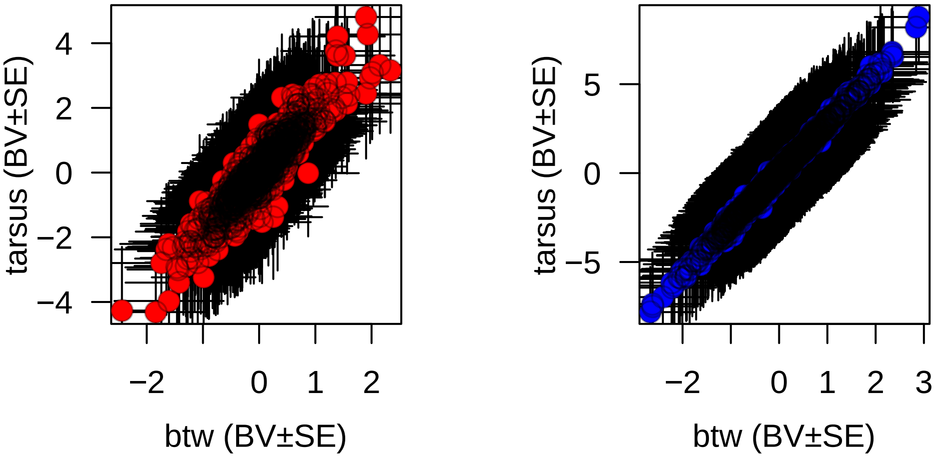
```
# write.csv(BLUPS,file="BLUPS_6x6_SEX.csv",row.names=F)
############
par(mfrow = c(2, 2))
hist(BLUPS$BLUP.btw)
qqnorm(BLUPS$BLUP.btw)
qqline(BLUPS$BLUP.btw)
hist(BLUPS$BLUP.tarsus)
qqnorm(BLUPS$BLUP.tarsus)
qqline(BLUPS$BLUP.tarsus)
```



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$BLUP.
arrows(x0 = FEM$BLUP.btw - FEM$SE.btw, y0 = FEM$BLUP.tarsus, x1 = FEM$BLUP.btw + FEM$SE.btw, y1 =
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$BLUP.
arrows(x0 = MAL$BLUP.btw - MAL$SE.btw, y0 = MAL$BLUP.tarsus, x1 = MAL$BLUP.btw + MAL$SE.btw, y1 =
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 ontogenic or sexual conflict, which can constraint or enhanced response to evolution. As an example, we estimate the cross-sex genetic correlation `r_{fm}`

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

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

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

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

```
model.BiV_Sex <- asreml(cbind(tarsus.1, tarsus.2) ~ trait,
  random = ~ us(trait):vm(animal, ainv) +
    diag(trait):byear + diag(trait):mother,
  residual = ~ units:us(trait),
  data = gryphon, na.action = na.method(y = "include", x = "include"), maxiter = 20,
  G.param = G, R.param = R
)
```

```
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 commun for a trait with low sexual dimorphism. If the selection is antagonistic between males and females, sexes can not evolve freely form the other sexes and a sexual conflict appears.

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

	Estimate	SE
r_fm	0.9112054	0.4229764

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

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

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

```
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(grepl("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
```

```r
#


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

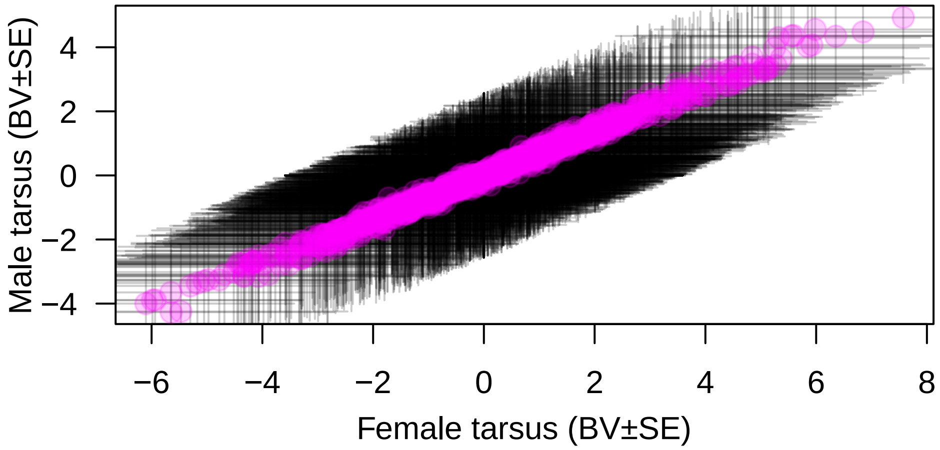
```
[1] 1309
```

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

```
      ID                BLUP.1             SE.1            BLUP.2
 Length: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
```

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


plot(X, Y, xlab = "", ylab = "", las = 1.2, bty = "o", col = "white")
arrows(x0 = X, y0 = Y - se.Y, x1 = X, y1 = Y + se.Y, col = rgb(0, 0, 0, 0.2), code = 3, angle = 9
```

```
arrows(x0 = X - se.X, y0 = Y, x1 = X + se.X, y1 = Y, col = rgb(0, 0, 0, 0.2), code = 3, angle = 9
points(X, Y, pch = 1, col = rgb(1, 0, 1, 0.2), cex = 1.5)
points(X, Y, pch = 16, col = rgb(1, 0, 1, 0.2), cex = 1.5)
# abline(v=0,lty=3);abline(h=0,lty=3)
mtext("Male tarsus (BV±SE)", side = 2, line = 2, las = 3)
mtext("Female tarsus (BV±SE)", side = 1, line = 2.2)
```



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

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

```
R$Constraint[8:9] <- "F"
#
# model.MultV_Sex<-asreml(cbind(tarsus.1,bwt.1,tarsus.2,bwt.2)~trait,
#          random=~us(trait):vm(animal,ainv)+
#         diag(trait):byear +   diag(trait):mother,
#         residual = ~units:us(trait),
#         data=gryphon,na.action=na.method(y="include",x="include"),maxiter=20,
#     G.param=G,R.param=R)
# model.MultV_Sex<-update.asreml(model.MultV_Sex)
#
# summary(model.MultV_Sex)$varcomp
```

Chapitre 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: 7148.288 
```

```
 G-structure:  ~us(trait):animal

                               post.mean l-95% CI u-95% CI eff.samp
traitbwt:traitbwt.animal           3.284  1.96750    4.782    87.44
traittarsus:traitbwt.animal        2.151 -0.06263    4.762    80.81
traitbwt:traittarsus.animal        2.151 -0.06263    4.762    80.81
traittarsus:traittarsus.animal    11.269  3.12870   17.882    52.06

 R-structure:  ~us(trait):units

                              post.mean l-95% CI u-95% CI eff.samp
traitbwt:traitbwt.units           3.938    2.761    5.225   142.34
traittarsus:traitbwt.units        3.567    1.294    5.694    87.65
traitbwt:traittarsus.units        3.567    1.294    5.694    87.65
traittarsus:traittarsus.units    18.688   12.623   26.200    49.61

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

            post.mean l-95% CI u-95% CI eff.samp  pMCMC
traitbwt        7.478    7.179    7.773   1000.0 <0.001 ***
traittarsus    20.445   19.861   21.008    955.9 <0.001 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

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

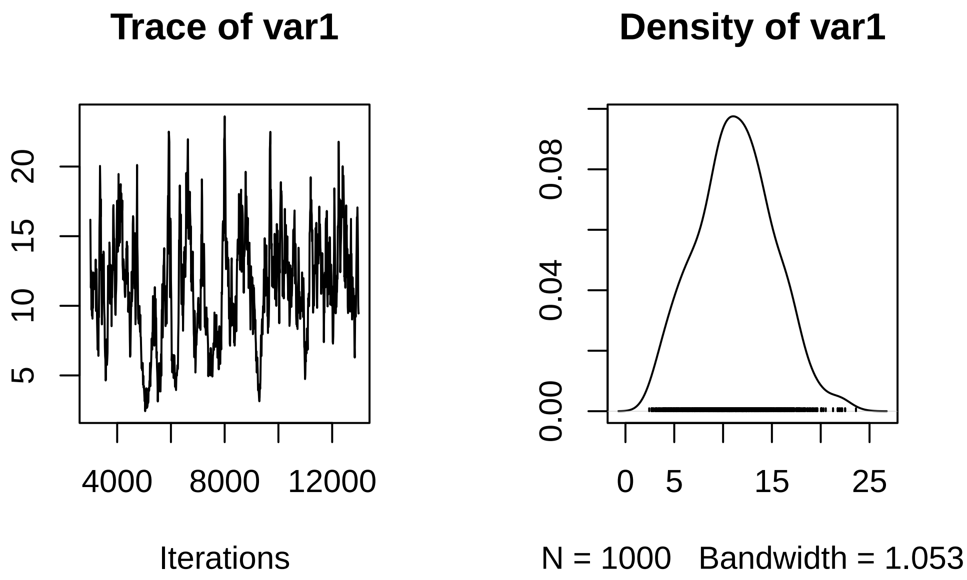


Figure 6.1.: The posterior distribution of the additive genetic effect for tarsus length in a MCMCglmm run with default values

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

```
   Lag 10
0.9009366
```

We have constructed the prior similarly to the those in the univariate models in tutorial 1, only we are specifying a 2x2 covariance matrix rather than a single variance. In order to provide proper priors, we have set the degree of belief parameter to greater than 1 (1.002). Those priors are not necessarily weak or uninformative in all circumstances. We will consider them adequate nonetheless for this tutorial. Please the vignette of the MCMCglmm packages (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 it is simply to large to include here. It can be viewed in the console as before. Here we have displayed only the autocorrelation for estimates of additive genetic effects for tarsus length with a lag of one samples (10 iterations given this MCMCglmm run with default values). This lag of 0.9009366 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 = "r-obj/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 = "r-obj/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$VCV[, "traittarsus:traittarsus.animal"] / (model2.1$VCV[, "tra
posterior.mode(heritability.tarsus2.1)
```

```
     var1
0.3719549
```

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

```r
  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 = "r-obj/MCMCglmm_model2_2_LongRun.rda")
```

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

```r
load(file = "r-obj/MCMCglmm_model2_2_LongRun.rda")
summary(model2.2)
```

```

 Iterations = 30001:129901
 Thinning interval  = 100
 Sample size  = 1000

 DIC: 5832.952

 G-structure:  ~us(trait):animal

                               post.mean l-95% CI u-95% CI eff.samp
traitbwt:traitbwt.animal           1.558   0.5616    2.488    230.8
traittarsus:traitbwt.animal        2.290   0.3241    4.264    274.8
traitbwt:traittarsus.animal        2.290   0.3241    4.264    274.8
traittarsus:traittarsus.animal     8.083   0.9063   13.599    228.1

               ~us(trait):byear

                              post.mean l-95% CI u-95% CI eff.samp
traitbwt:traitbwt.byear         0.96775   0.4124   1.5053     1000
traittarsus:traitbwt.byear      0.07332  -0.8100   0.9791     1000
traitbwt:traittarsus.byear      0.07332  -0.8100   0.9791     1000
```

```
traittarsus:traittarsus.byear   3.80720   1.6291   6.3986     1000

               ~us(trait):mother

                               post.mean  l-95% CI  u-95% CI  eff.samp
traitbwt:traitbwt.mother           1.335    0.8564    1.8090     871.2
traittarsus:traitbwt.mother       -1.508   -2.1667   -0.8288     648.6
traitbwt:traittarsus.mother       -1.508   -2.1667   -0.8288     648.6
traittarsus:traittarsus.mother     4.292    2.2380    6.6336     796.0

 R-structure:  ~us(trait):units

                              post.mean  l-95% CI  u-95% CI  eff.samp
traitbwt:traitbwt.units            2.13     1.304     2.939     469.2
traittarsus:traitbwt.units         4.81     3.111     6.568     414.7
traitbwt:traittarsus.units         4.81     3.111     6.568     414.7
traittarsus:traittarsus.units     14.51     9.419    19.892     261.3

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

                 post.mean  l-95% CI  u-95% CI  eff.samp  pMCMC
traitbwt            6.2734    5.8152    6.7272      1205 <0.001 ***
traittarsus        20.3985   19.4021   21.4106      1000 <0.001 ***
traitbwt:sex2       2.0354    1.7347    2.3529      1000 <0.001 ***
traittarsus:sex2    0.0705   -0.6949    0.7686      1000  0.868
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

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

```
[1] 0.1026744
```

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

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

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

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

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

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

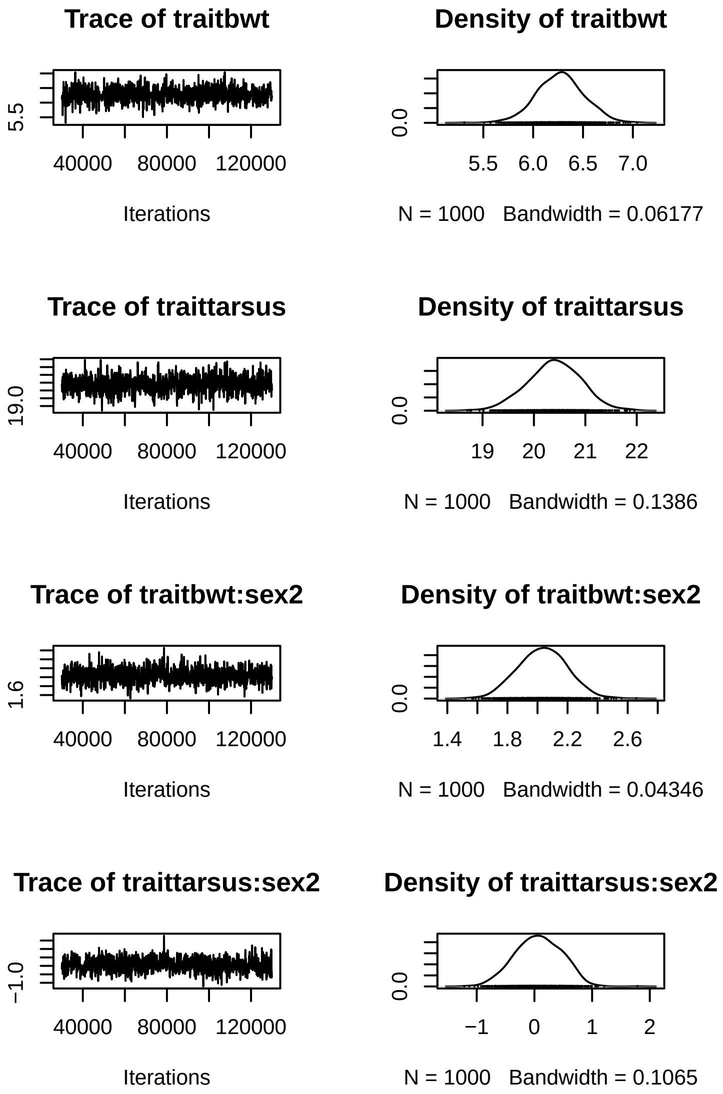


Figure 6.2.: Posterior trace and distribution for the fixed effects in model 2.2

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
```

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

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

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

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.

```r
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(trai
  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 = "r-obj/MCMCglmm_model2_4_LongRun.rda")
```

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

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

```

 Iterations = 30001:129901
 Thinning interval  = 100
 Sample size  = 1000

 DIC: 5576.328

 G-structure:  ~us(at.level(sex, "1"):trait):animal

                                                                          post.mean
at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.animal                1.122
at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.animal             1.127
at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.animal             1.127
at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.animal          3.379
                                                                          l-95% CI
at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.animal              0.1602
at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.animal          -0.6531
at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.animal          -0.6531
at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.animal        0.1844
                                                                          u-95% CI
at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.animal               2.359
at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.animal            3.496
at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.animal            3.496
```

```
at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.animal    8.918
                                                                      eff.samp
at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.animal          167.5
at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.animal       119.3
at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.animal       119.3
at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.animal    102.6

               ~us(at.level(sex, "2"):trait):animal


                                                                      post.mean
at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.animal            1.598
at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.animal         3.099
at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.animal         3.099
at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.animal     10.218
                                                                      l-95% CI
at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.animal          0.1895
at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.animal      -0.5506
at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.animal      -0.5506
at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.animal   0.2127
                                                                      u-95% CI
at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.animal           3.305
at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.animal        7.864
at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.animal        7.864
at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.animal   24.230
                                                                      eff.samp
at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.animal           57.28
at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.animal        42.01
at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.animal        42.01
at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.animal    37.21

               ~idh(trait):byear

                  post.mean l-95% CI u-95% CI eff.samp
```

```
traitbwt.byear       0.9309   0.4614    1.463     1000
traittarsus.byear    4.0310   1.9268    6.724     1000

               ~idh(trait):mother

                   post.mean l-95% CI u-95% CI eff.samp
traitbwt.mother        1.924    1.406    2.398    667.6
traittarsus.mother     7.093    4.626    9.681    698.5

 R-structure:  ~us(at.level(sex, "1"):trait):units

                                                                           post.mean
at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.units                  2.090
at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.units               4.533
at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.units               4.533
at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.units           14.113
                                                                           l-95% CI
at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.units                0.9958
at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.units             2.4185
at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.units             2.4185
at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.units          8.1848
                                                                           u-95% CI
at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.units                 3.128
at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.units              6.875
at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.units              6.875
at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.units          18.935
                                                                           eff.samp
at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.units                 207.2
at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.units              168.4
at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.units              168.4
at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.units           185.3

               ~us(at.level(sex, "2"):trait):units
```

```
                                                                    post.mean
at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.units           1.782
at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.units        3.697
at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.units        3.697
at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.units    12.437
                                                                    l-95% CI
at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.units         0.2776
at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.units     -0.3141
at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.units     -0.3141
at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.units   0.1776
                                                                    u-95% CI
at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.units          3.115
at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.units       7.218
at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.units       7.218
at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.units   21.903
                                                                    eff.samp
at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.units          52.55
at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.units       51.90
at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.units       51.90
at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.units    39.20

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

                 post.mean l-95% CI u-95% CI eff.samp  pMCMC
traitbwt           6.30098  5.89218  6.78834   1000.0 <0.001 ***
traittarsus       20.45577 19.53577 21.34719   1129.8 <0.001 ***
traitbwt:sex2      2.01306  1.63662  2.38011    887.4 <0.001 ***
traittarsus:sex2   0.05817 -0.86635  0.89119   1016.6  0.896
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

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

```
, , at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.animal

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

```
Lag 5000                                                    -0.02326421
         at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.animal
Lag 0                                                          -0.07404287
Lag 100                                                        -0.08742103
Lag 500                                                        -0.05376905
Lag 1000                                                       -0.03219125
Lag 5000                                                        0.02771727
         at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.animal
Lag 0                                                          -0.07404287
Lag 100                                                        -0.08742103
Lag 500                                                        -0.05376905
Lag 1000                                                       -0.03219125
Lag 5000                                                        0.02771727
         at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.animal
Lag 0                                                             -0.06663301
Lag 100                                                           -0.07398282
Lag 500                                                           -0.03873715
Lag 1000                                                          -0.03346102
Lag 5000                                                           0.06535632
         traitbwt.byear traittarsus.byear traitbwt.mother traittarsus.mother
Lag 0      -0.002044905        0.06061428     -0.13681757        0.063034744
Lag 100    -0.029101625        0.04741082     -0.09232454        0.062553003
Lag 500    -0.025891155        0.04101237     -0.01510511       -0.026837884
Lag 1000    0.029398462        0.02792539     -0.02514900        0.009578198
Lag 5000   -0.016122661        0.03081539      0.04189460       -0.039791141
         at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.units
Lag 0                                                     -0.842319278
Lag 100                                                   -0.569203867
Lag 500                                                   -0.167844469
Lag 1000                                                  -0.114647645
Lag 5000                                                  -0.002132053
         at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.units
Lag 0                                                        -0.708901550
```

```
Lag 100                                                       -0.517998161
Lag 500                                                       -0.167589741
Lag 1000                                                      -0.110500558
Lag 5000                                                       0.002914291
          at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.units
Lag 0                                                         -0.708901550
Lag 100                                                       -0.517998161
Lag 500                                                       -0.167589741
Lag 1000                                                      -0.110500558
Lag 5000                                                       0.002914291
          at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.units
Lag 0                                                            -0.438123204
Lag 100                                                          -0.337083166
Lag 500                                                          -0.129292647
Lag 1000                                                         -0.103678560
Lag 5000                                                         -0.001926232
          at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.units
Lag 0                                                       0.07807105
Lag 100                                                     0.10707885
Lag 500                                                     0.05568856
Lag 1000                                                    0.02521629
Lag 5000                                                    0.01402475
          at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.units
Lag 0                                                           0.06679340
Lag 100                                                         0.08704308
Lag 500                                                         0.05892190
Lag 1000                                                        0.02676188
Lag 5000                                                       -0.03056683
          at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.units
Lag 0                                                           0.06679340
Lag 100                                                         0.08704308
Lag 500                                                         0.05892190
Lag 1000                                                        0.02676188
```

```
Lag 5000                                                      -0.03056683
         at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.units
Lag 0                                                                 0.04797898
Lag 100                                                               0.05730717
Lag 500                                                               0.04727555
Lag 1000                                                              0.02677473
Lag 5000                                                             -0.06608227

, , at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.animal

         at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.animal
Lag 0                                                       0.847048735
Lag 100                                                     0.596411029
Lag 500                                                     0.228550625
Lag 1000                                                    0.137616124
Lag 5000                                                    0.009429906
         at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.animal
Lag 0                                                           1.00000000
Lag 100                                                         0.71730236
Lag 500                                                         0.27616079
Lag 1000                                                        0.13795063
Lag 5000                                                        0.01144749
         at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.animal
Lag 0                                                           1.00000000
Lag 100                                                         0.71730236
Lag 500                                                         0.27616079
Lag 1000                                                        0.13795063
Lag 5000                                                        0.01144749
         at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.animal
Lag 0                                                                0.7989970
Lag 100                                                              0.6014134
Lag 500                                                              0.2515262
Lag 1000                                                             0.1354306
```

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

```
Lag 100                                                     -0.52689086
Lag 500                                                     -0.22551523
Lag 1000                                                    -0.12616708
Lag 5000                                                    -0.04647821
         at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.units
Lag 0                                                          -0.82495927
Lag 100                                                        -0.60990914
Lag 500                                                        -0.24464022
Lag 1000                                                       -0.12721295
Lag 5000                                                       -0.03841367
         at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.units
Lag 0                                                          -0.82495927
Lag 100                                                        -0.60990914
Lag 500                                                        -0.24464022
Lag 1000                                                       -0.12721295
Lag 5000                                                       -0.03841367
         at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.units
Lag 0                                                             -0.64394327
Lag 100                                                           -0.48995337
Lag 500                                                           -0.19725633
Lag 1000                                                          -0.10852446
Lag 5000                                                          -0.02105523
         at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.units
Lag 0                                                       0.082481767
Lag 100                                                     0.105417000
Lag 500                                                     0.073280263
Lag 1000                                                    0.028355398
Lag 5000                                                   -0.006019758
         at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.units
Lag 0                                                           0.09308370
Lag 100                                                         0.10680733
Lag 500                                                         0.07810010
Lag 1000                                                        0.04359553
```

```
Lag 5000                                             -0.04726853
         at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.units
Lag 0                                                 0.09308370
Lag 100                                               0.10680733
Lag 500                                               0.07810010
Lag 1000                                              0.04359553
Lag 5000                                             -0.04726853
         at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.units
Lag 0                                                    0.08843633
Lag 100                                                  0.09343376
Lag 500                                                  0.06886426
Lag 1000                                                 0.05338682
Lag 5000                                                -0.09185034

, , at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.animal

         at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.animal
Lag 0                                              0.847048735
Lag 100                                            0.596411029
Lag 500                                            0.228550625
Lag 1000                                           0.137616124
Lag 5000                                           0.009429906
         at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.animal
Lag 0                                                  1.00000000
Lag 100                                                0.71730236
Lag 500                                                0.27616079
Lag 1000                                               0.13795063
Lag 5000                                               0.01144749
         at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.animal
Lag 0                                                  1.00000000
Lag 100                                                0.71730236
Lag 500                                                0.27616079
Lag 1000                                               0.13795063
```

```
Lag 5000                                                       0.01144749
         at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.animal
Lag 0                                                               0.7989970
Lag 100                                                             0.6014134
Lag 500                                                             0.2515262
Lag 1000                                                            0.1354306
Lag 5000                                                            0.0136445
         at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.animal
Lag 0                                                     -0.069644149
Lag 100                                                   -0.094348331
Lag 500                                                   -0.069174874
Lag 1000                                                  -0.030980734
Lag 5000                                                  -0.001770693
         at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.animal
Lag 0                                                         -0.09266557
Lag 100                                                       -0.10417316
Lag 500                                                       -0.06908668
Lag 1000                                                      -0.04934221
Lag 5000                                                       0.03968797
         at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.animal
Lag 0                                                         -0.09266557
Lag 100                                                       -0.10417316
Lag 500                                                       -0.06908668
Lag 1000                                                      -0.04934221
Lag 5000                                                       0.03968797
         at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.animal
Lag 0                                                            -0.10219567
Lag 100                                                          -0.10740690
Lag 500                                                          -0.05829130
Lag 1000                                                         -0.05667648
Lag 5000                                                          0.08311412
         traitbwt.byear traittarsus.byear traitbwt.mother traittarsus.mother
Lag 0       -0.03731153        0.05572330     -0.12626725         0.06865980
```

```
Lag 100     -0.04492620        0.05076637     -0.08142219          0.05404288
Lag 500     -0.03460527        0.03246607     -0.03107773         -0.02899561
Lag 1000     0.01459594        0.01717445     -0.05078674          0.01110690
Lag 5000    -0.01688700        0.03883380      0.02698184         -0.03307579
         at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.units
Lag 0                                                      -0.73143141
Lag 100                                                    -0.52689086
Lag 500                                                    -0.22551523
Lag 1000                                                   -0.12616708
Lag 5000                                                   -0.04647821
         at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.units
Lag 0                                                         -0.82495927
Lag 100                                                       -0.60990914
Lag 500                                                       -0.24464022
Lag 1000                                                      -0.12721295
Lag 5000                                                      -0.03841367
         at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.units
Lag 0                                                         -0.82495927
Lag 100                                                       -0.60990914
Lag 500                                                       -0.24464022
Lag 1000                                                      -0.12721295
Lag 5000                                                      -0.03841367
         at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.units
Lag 0                                                            -0.64394327
Lag 100                                                          -0.48995337
Lag 500                                                          -0.19725633
Lag 1000                                                         -0.10852446
Lag 5000                                                         -0.02105523
         at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.units
Lag 0                                                      0.082481767
Lag 100                                                    0.105417000
Lag 500                                                    0.073280263
Lag 1000                                                   0.028355398
```

```
Lag 5000                                                    -0.006019758
         at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.units
Lag 0                                                            0.09308370
Lag 100                                                          0.10680733
Lag 500                                                          0.07810010
Lag 1000                                                         0.04359553
Lag 5000                                                        -0.04726853
         at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.units
Lag 0                                                            0.09308370
Lag 100                                                          0.10680733
Lag 500                                                          0.07810010
Lag 1000                                                         0.04359553
Lag 5000                                                        -0.04726853
         at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.units
Lag 0                                                               0.08843633
Lag 100                                                             0.09343376
Lag 500                                                             0.06886426
Lag 1000                                                            0.05338682
Lag 5000                                                           -0.09185034

, , at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.animal

         at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.animal
Lag 0                                                           0.5304141
Lag 100                                                         0.3737195
Lag 500                                                         0.1441203
Lag 1000                                                        0.1503417
Lag 5000                                                        0.1187940
         at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.animal
Lag 0                                                              0.7989970
Lag 100                                                            0.5706521
Lag 500                                                            0.2430451
Lag 1000                                                           0.1680830
```

```
Lag 5000                                                    0.1259980
         at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.animal
Lag 0                                                       0.7989970
Lag 100                                                     0.5706521
Lag 500                                                     0.2430451
Lag 1000                                                    0.1680830
Lag 5000                                                    0.1259980
         at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.animal
Lag 0                                                         1.00000000
Lag 100                                                       0.73196692
Lag 500                                                       0.31335783
Lag 1000                                                      0.18501263
Lag 5000                                                      0.08438218
         at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.animal
Lag 0                                                  -0.01785209
Lag 100                                                -0.03508025
Lag 500                                                -0.04733762
Lag 1000                                               -0.01709422
Lag 5000                                               -0.01586047
         at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.animal
Lag 0                                                    -0.038020441
Lag 100                                                  -0.045171003
Lag 500                                                  -0.050004069
Lag 1000                                                 -0.054183547
Lag 5000                                                 -0.004955516
         at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.animal
Lag 0                                                    -0.038020441
Lag 100                                                  -0.045171003
Lag 500                                                  -0.050004069
Lag 1000                                                 -0.054183547
Lag 5000                                                 -0.004955516
         at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.animal
Lag 0                                                        -0.05447207
```

```
Lag 100                                                            -0.05998184
Lag 500                                                            -0.06158778
Lag 1000                                                           -0.08267333
Lag 5000                                                            0.02065741
         traitbwt.byear traittarsus.byear traitbwt.mother traittarsus.mother
Lag 0      -0.060159939        0.06450755   -0.0973321863       -0.009350685
Lag 100    -0.043720033        0.03483594   -0.0765923141       -0.006212912
Lag 500    -0.052466217        0.02987272   -0.0662772868       -0.030465249
Lag 1000   -0.001034192        0.03110963   -0.0728720391        0.009855596
Lag 5000   -0.034160786        0.05472996    0.0008533055        0.003426058
         at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.units
Lag 0                                                       -0.4637838
Lag 100                                                     -0.3337342
Lag 500                                                     -0.1618186
Lag 1000                                                    -0.1329387
Lag 5000                                                    -0.1239580
         at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.units
Lag 0                                                          -0.6583252
Lag 100                                                        -0.4881849
Lag 500                                                        -0.2287167
Lag 1000                                                       -0.1381960
Lag 5000                                                       -0.1179873
         at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.units
Lag 0                                                          -0.6583252
Lag 100                                                        -0.4881849
Lag 500                                                        -0.2287167
Lag 1000                                                       -0.1381960
Lag 5000                                                       -0.1179873
         at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.units
Lag 0                                                            -0.76001059
Lag 100                                                          -0.57358014
Lag 500                                                          -0.25179771
Lag 1000                                                         -0.12123408
```

```
Lag 5000                                                         -0.07986147
         at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.units
Lag 0                                                       0.02870904
Lag 100                                                     0.03399695
Lag 500                                                     0.05485675
Lag 1000                                                    0.01651664
Lag 5000                                                    0.01516504
         at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.units
Lag 0                                                         0.039633904
Lag 100                                                       0.041502118
Lag 500                                                       0.059018043
Lag 1000                                                      0.052958967
Lag 5000                                                     -0.002274568
         at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.units
Lag 0                                                         0.039633904
Lag 100                                                       0.041502118
Lag 500                                                       0.059018043
Lag 1000                                                      0.052958967
Lag 5000                                                     -0.002274568
         at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.units
Lag 0                                                                 0.04584246
Lag 100                                                               0.04763329
Lag 500                                                               0.06852725
Lag 1000                                                              0.08362165
Lag 5000                                                             -0.03430204

, , at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.animal

         at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.animal
Lag 0                                                       -0.07132000
Lag 100                                                     -0.06108550
Lag 500                                                     -0.06344456
Lag 1000                                                    -0.02628413
```

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

```
Lag 100                                                  0.8047694
Lag 500                                                  0.5857973
Lag 1000                                                 0.3552775
Lag 5000                                                -0.1485103
         at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.animal
Lag 0                                                       0.7704756
Lag 100                                                     0.7082472
Lag 500                                                     0.5569812
Lag 1000                                                    0.3517296
Lag 5000                                                   -0.1453072
         traitbwt.byear traittarsus.byear traitbwt.mother traittarsus.mother
Lag 0       -0.03784246        0.04916122    -0.025145260        -0.13999847
Lag 100     -0.01888261        0.04551933    -0.009748633        -0.14616483
Lag 500     -0.01864811        0.07395050     0.029035276        -0.12958636
Lag 1000    -0.02117775        0.06164183     0.068666314        -0.09577992
Lag 5000     0.01769136        0.04869291     0.037573009         0.01686724
         at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.units
Lag 0                                                 0.048426202
Lag 100                                               0.039795097
Lag 500                                               0.046311373
Lag 1000                                              0.005469282
Lag 5000                                             -0.104125437
         at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.units
Lag 0                                                    0.043207572
Lag 100                                                  0.043210916
Lag 500                                                  0.033044478
Lag 1000                                                -0.004411742
Lag 5000                                                -0.110707718
         at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.units
Lag 0                                                    0.043207572
Lag 100                                                  0.043210916
Lag 500                                                  0.033044478
Lag 1000                                                -0.004411742
```

```
Lag 5000                                                   -0.110707718
        at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.units
Lag 0                                                          0.01554818
Lag 100                                                        0.02352457
Lag 500                                                        0.01217491
Lag 1000                                                      -0.02394172
Lag 5000                                                      -0.13812594
        at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.units
Lag 0                                                       -0.9369474
Lag 100                                                     -0.8092241
Lag 500                                                     -0.5186132
Lag 1000                                                    -0.2947735
Lag 5000                                                     0.1226249
        at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.units
Lag 0                                                          -0.8725969
Lag 100                                                        -0.7954903
Lag 500                                                        -0.5688119
Lag 1000                                                       -0.3390939
Lag 5000                                                        0.1455303
        at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.units
Lag 0                                                          -0.8725969
Lag 100                                                        -0.7954903
Lag 500                                                        -0.5688119
Lag 1000                                                       -0.3390939
Lag 5000                                                        0.1455303
        at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.units
Lag 0                                                             -0.7525481
Lag 100                                                           -0.7086874
Lag 500                                                           -0.5421136
Lag 1000                                                          -0.3389906
Lag 5000                                                           0.1485387

, , at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.animal
```

```
         at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.animal
Lag 0                                                       -0.074042865
Lag 100                                                     -0.072737049
Lag 500                                                     -0.064855516
Lag 1000                                                    -0.004245299
Lag 5000                                                     0.126495395
         at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.animal
Lag 0                                                          -0.092665568
Lag 100                                                        -0.096939661
Lag 500                                                        -0.070837135
Lag 1000                                                        0.006501962
Lag 5000                                                        0.148898005
         at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.animal
Lag 0                                                          -0.092665568
Lag 100                                                        -0.096939661
Lag 500                                                        -0.070837135
Lag 1000                                                        0.006501962
Lag 5000                                                        0.148898005
         at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.animal
Lag 0                                                             -0.038020441
Lag 100                                                           -0.039681669
Lag 500                                                           -0.006820427
Lag 1000                                                           0.063529955
Lag 5000                                                           0.163665055
         at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.animal
Lag 0                                                          0.9099634
Lag 100                                                        0.7863387
Lag 500                                                        0.5413307
Lag 1000                                                       0.3118422
Lag 5000                                                      -0.1191809
         at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.animal
Lag 0                                                             1.0000000
```

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

```
Lag 5000                                              -0.13689966
        at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.units
Lag 0                                                  0.04900783
Lag 100                                                0.06050152
Lag 500                                                0.04114675
Lag 1000                                              -0.01839006
Lag 5000                                              -0.13689966
        at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.units
Lag 0                                                     0.02477085
Lag 100                                                   0.03939172
Lag 500                                                   0.02069295
Lag 1000                                                 -0.04020316
Lag 5000                                                 -0.16427556
        at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.units
Lag 0                                               -0.8748666
Lag 100                                             -0.7865075
Lag 500                                             -0.5347377
Lag 1000                                            -0.3099292
Lag 5000                                             0.1242901
        at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.units
Lag 0                                                  -0.9629330
Lag 100                                                -0.8851422
Lag 500                                                -0.6211970
Lag 1000                                               -0.3754777
Lag 5000                                                0.1511004
        at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.units
Lag 0                                                  -0.9629330
Lag 100                                                -0.8851422
Lag 500                                                -0.6211970
Lag 1000                                               -0.3754777
Lag 5000                                                0.1511004
        at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.units
Lag 0                                                     -0.9191068
```

```
Lag 100                                                    -0.8609263
Lag 500                                                    -0.6233180
Lag 1000                                                   -0.3879589
Lag 5000                                                    0.1606066

, , at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.animal


         at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.animal
Lag 0                                                 -0.074042865
Lag 100                                               -0.072737049
Lag 500                                               -0.064855516
Lag 1000                                              -0.004245299
Lag 5000                                               0.126495395
         at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.animal
Lag 0                                                    -0.092665568
Lag 100                                                  -0.096939661
Lag 500                                                  -0.070837135
Lag 1000                                                  0.006501962
Lag 5000                                                  0.148898005
         at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.animal
Lag 0                                                    -0.092665568
Lag 100                                                  -0.096939661
Lag 500                                                  -0.070837135
Lag 1000                                                  0.006501962
Lag 5000                                                  0.148898005
         at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.animal
Lag 0                                                       -0.038020441
Lag 100                                                     -0.039681669
Lag 500                                                     -0.006820427
Lag 1000                                                     0.063529955
Lag 5000                                                     0.163665055
         at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.animal
Lag 0                                                     0.9099634
```

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

```
Lag 5000                                                   -0.12752563
         at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.units
Lag 0                                                               0.04900783
Lag 100                                                             0.06050152
Lag 500                                                             0.04114675
Lag 1000                                                           -0.01839006
Lag 5000                                                           -0.13689966
         at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.units
Lag 0                                                               0.04900783
Lag 100                                                             0.06050152
Lag 500                                                             0.04114675
Lag 1000                                                           -0.01839006
Lag 5000                                                           -0.13689966
         at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.units
Lag 0                                                                  0.02477085
Lag 100                                                                0.03939172
Lag 500                                                                0.02069295
Lag 1000                                                              -0.04020316
Lag 5000                                                              -0.16427556
         at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.units
Lag 0                                                       -0.8748666
Lag 100                                                     -0.7865075
Lag 500                                                     -0.5347377
Lag 1000                                                    -0.3099292
Lag 5000                                                     0.1242901
         at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.units
Lag 0                                                          -0.9629330
Lag 100                                                        -0.8851422
Lag 500                                                        -0.6211970
Lag 1000                                                       -0.3754777
Lag 5000                                                        0.1511004
         at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.units
Lag 0                                                          -0.9629330
```

```
Lag 100                                                  -0.8851422
Lag 500                                                  -0.6211970
Lag 1000                                                 -0.3754777
Lag 5000                                                  0.1511004
         at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.units
Lag 0                                                       -0.9191068
Lag 100                                                     -0.8609263
Lag 500                                                     -0.6233180
Lag 1000                                                    -0.3879589
Lag 5000                                                     0.1606066

, , at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.animal

         at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.animal
Lag 0                                                -0.066633008
Lag 100                                              -0.069354252
Lag 500                                              -0.053416684
Lag 1000                                              0.001180564
Lag 5000                                              0.142470162
         at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.animal
Lag 0                                                   -0.102195672
Lag 100                                                 -0.107130141
Lag 500                                                 -0.073576929
Lag 1000                                                -0.004189061
Lag 5000                                                 0.167339055
         at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.animal
Lag 0                                                   -0.102195672
Lag 100                                                 -0.107130141
Lag 500                                                 -0.073576929
Lag 1000                                                -0.004189061
Lag 5000                                                 0.167339055
         at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.animal
Lag 0                                                       -0.05447207
```

```
Lag 100                                                           -0.05707224
Lag 500                                                           -0.01853426
Lag 1000                                                           0.04684883
Lag 5000                                                           0.17837197
         at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.animal
Lag 0                                                         0.7704756
Lag 100                                                       0.6843951
Lag 500                                                       0.5050605
Lag 1000                                                      0.2977972
Lag 5000                                                     -0.1058223
         at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.animal
Lag 0                                                            0.9445430
Lag 100                                                          0.8556548
Lag 500                                                          0.6303848
Lag 1000                                                         0.3904095
Lag 5000                                                        -0.1424423
         at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.animal
Lag 0                                                            0.9445430
Lag 100                                                          0.8556548
Lag 500                                                          0.6303848
Lag 1000                                                         0.3904095
Lag 5000                                                        -0.1424423
         at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.animal
Lag 0                                                               1.0000000
Lag 100                                                             0.9100529
Lag 500                                                             0.6616827
Lag 1000                                                            0.4121439
Lag 5000                                                           -0.1590568
         traitbwt.byear traittarsus.byear traitbwt.mother traittarsus.mother
Lag 0       -0.03974818        0.04854354      0.04924110        -0.22289117
Lag 100     -0.03767078        0.04176415      0.03930577        -0.20950998
Lag 500     -0.03440434        0.03555315      0.05305906        -0.18185253
Lag 1000    -0.02822560        0.04567963      0.06510782        -0.12092658
```

```
Lag 5000     0.05272181        0.04246380      0.02211597         0.02036647
         at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.units
Lag 0                                                       0.04061110
Lag 100                                                     0.04206692
Lag 500                                                     0.03373343
Lag 1000                                                   -0.01881550
Lag 5000                                                   -0.13859641
         at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.units
Lag 0                                                          0.05879880
Lag 100                                                        0.06872711
Lag 500                                                        0.04634425
Lag 1000                                                      -0.01579800
Lag 5000                                                      -0.14960797
         at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.units
Lag 0                                                          0.05879880
Lag 100                                                        0.06872711
Lag 500                                                        0.04634425
Lag 1000                                                      -0.01579800
Lag 5000                                                      -0.14960797
         at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.units
Lag 0                                                             0.04254878
Lag 100                                                           0.05461840
Lag 500                                                           0.03646094
Lag 1000                                                         -0.04023461
Lag 5000                                                         -0.17207003
         at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.units
Lag 0                                                       -0.7532567
Lag 100                                                     -0.6923793
Lag 500                                                     -0.5032427
Lag 1000                                                    -0.2991945
Lag 5000                                                     0.1154818
         at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.units
Lag 0                                                          -0.9140715
```

```
Lag 100                                                         -0.8493221
Lag 500                                                         -0.6164356
Lag 1000                                                        -0.3808768
Lag 5000                                                         0.1473936
         at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.units
Lag 0                                                           -0.9140715
Lag 100                                                         -0.8493221
Lag 500                                                         -0.6164356
Lag 1000                                                        -0.3808768
Lag 5000                                                         0.1473936
         at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.units
Lag 0                                                              -0.9650519
Lag 100                                                            -0.9008410
Lag 500                                                            -0.6496396
Lag 1000                                                           -0.4073019
Lag 5000                                                            0.1644354

, , traitbwt.byear

         at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.animal
Lag 0                                                      -0.002044905
Lag 100                                                     0.018082206
Lag 500                                                    -0.019694583
Lag 1000                                                   -0.033624772
Lag 5000                                                   -0.025949000
         at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.animal
Lag 0                                                              -0.03731153
Lag 100                                                            -0.01355344
Lag 500                                                            -0.01864081
Lag 1000                                                           -0.05745850
Lag 5000                                                           -0.01235998
         at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.animal
Lag 0                                                              -0.03731153
```

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

```
Lag 5000                                                          -0.007044631
         traitbwt.byear traittarsus.byear traitbwt.mother traittarsus.mother
Lag 0        1.00000000     -0.0251146296      0.03365469         0.03928862
Lag 100      0.03109454      0.0004436899     -0.05764761        -0.01264335
Lag 500      0.03937305      0.0006604187     -0.00457655         0.02746272
Lag 1000     0.01680424     -0.0194711518      0.03737600        -0.04627035
Lag 5000     0.03318792      0.0155533971     -0.02558374         0.05305580
         at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.units
Lag 0                                                        0.005983125
Lag 100                                                     -0.001889062
Lag 500                                                     -0.018793288
Lag 1000                                                     0.027363658
Lag 5000                                                     0.010334637
         at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.units
Lag 0                                                           0.052806759
Lag 100                                                         0.014657374
Lag 500                                                        -0.020921457
Lag 1000                                                        0.041519184
Lag 5000                                                       -0.000172048
         at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.units
Lag 0                                                           0.052806759
Lag 100                                                         0.014657374
Lag 500                                                        -0.020921457
Lag 1000                                                        0.041519184
Lag 5000                                                       -0.000172048
         at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.units
Lag 0                                                              0.072105699
Lag 100                                                            0.023891187
Lag 500                                                           -0.022626087
Lag 1000                                                           0.038071084
Lag 5000                                                           0.008022532
         at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.units
Lag 0                                                         0.02472261
```

```
Lag 100                                                    0.04922524
Lag 500                                                    0.05684465
Lag 1000                                                   0.02213746
Lag 5000                                                  -0.02587314
         at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.units
Lag 0                                                        0.035150019
Lag 100                                                      0.039823504
Lag 500                                                      0.058615425
Lag 1000                                                     0.039863168
Lag 5000                                                    -0.002768445
         at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.units
Lag 0                                                        0.035150019
Lag 100                                                      0.039823504
Lag 500                                                      0.058615425
Lag 1000                                                     0.039863168
Lag 5000                                                    -0.002768445
         at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.units
Lag 0                                                           0.032332494
Lag 100                                                         0.036826480
Lag 500                                                         0.056371336
Lag 1000                                                        0.037506421
Lag 5000                                                       -0.002071877

, , traittarsus.byear

         at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.animal
Lag 0                                                       0.06061428
Lag 100                                                     0.06276970
Lag 500                                                    -0.02842127
Lag 1000                                                    0.01799228
Lag 5000                                                    0.02740499
         at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.animal
Lag 0                                                          0.05572330
```

```
Lag 100                                            0.06655805
Lag 500                                           -0.02673025
Lag 1000                                           0.04345968
Lag 5000                                           0.05112113
         at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.animal
Lag 0                                              0.05572330
Lag 100                                            0.06655805
Lag 500                                           -0.02673025
Lag 1000                                           0.04345968
Lag 5000                                           0.05112113
         at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.animal
Lag 0                                                0.064507548
Lag 100                                              0.074840509
Lag 500                                             -0.003777881
Lag 1000                                             0.058609933
Lag 5000                                             0.063485567
         at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.animal
Lag 0                                          0.049161224
Lag 100                                        0.009105861
Lag 500                                        0.005065210
Lag 1000                                       0.016389664
Lag 5000                                      -0.029590445
         at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.animal
Lag 0                                             0.055056994
Lag 100                                           0.035711495
Lag 500                                           0.012368434
Lag 1000                                          0.004770290
Lag 5000                                         -0.009144398
         at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.animal
Lag 0                                             0.055056994
Lag 100                                           0.035711495
Lag 500                                           0.012368434
Lag 1000                                          0.004770290
```

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

```
Lag 100                                                         -0.049448255
Lag 500                                                          0.002404817
Lag 1000                                                        -0.086421792
Lag 5000                                                        -0.055605953
         at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.units
Lag 0                                                     -0.025767223
Lag 100                                                   -0.006184423
Lag 500                                                   -0.002201914
Lag 1000                                                  -0.011174601
Lag 5000                                                   0.029950491
         at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.units
Lag 0                                                        -0.049170830
Lag 100                                                      -0.040276502
Lag 500                                                       0.003528012
Lag 1000                                                     -0.010662330
Lag 5000                                                      0.002523808
         at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.units
Lag 0                                                        -0.049170830
Lag 100                                                      -0.040276502
Lag 500                                                       0.003528012
Lag 1000                                                     -0.010662330
Lag 5000                                                      0.002523808
         at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.units
Lag 0                                                           -0.053929470
Lag 100                                                         -0.043281273
Lag 500                                                          0.009317392
Lag 1000                                                        -0.010594624
Lag 5000                                                        -0.013754908

, , traitbwt.mother

         at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.animal
Lag 0                                                       -0.13681757
```

```
Lag 100                                                     -0.09694549
Lag 500                                                     -0.06857367
Lag 1000                                                    -0.04540954
Lag 5000                                                    -0.01652050
         at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.animal
Lag 0                                                          -0.12626725
Lag 100                                                        -0.12449687
Lag 500                                                        -0.05181080
Lag 1000                                                       -0.03932960
Lag 5000                                                       -0.01141931
         at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.animal
Lag 0                                                          -0.12626725
Lag 100                                                        -0.12449687
Lag 500                                                        -0.05181080
Lag 1000                                                       -0.03932960
Lag 5000                                                       -0.01141931
         at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.animal
Lag 0                                                             -0.09733219
Lag 100                                                           -0.10049386
Lag 500                                                           -0.04634235
Lag 1000                                                          -0.01749975
Lag 5000                                                          -0.03285757
         at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.animal
Lag 0                                                       -0.02514526
Lag 100                                                      0.01494004
Lag 500                                                     -0.05400749
Lag 1000                                                    -0.02644804
Lag 5000                                                    -0.02759428
         at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.animal
Lag 0                                                            0.0337229276
Lag 100                                                          0.0355284011
Lag 500                                                         -0.0008562576
Lag 1000                                                        -0.0192570169
```

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

```
Lag 100                                                         0.12608289
Lag 500                                                         0.03369955
Lag 1000                                                        0.04312267
Lag 5000                                                       -0.01418292
         at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.units
Lag 0                                                           0.1007331132
Lag 100                                                         0.0846271381
Lag 500                                                         0.0314559531
Lag 1000                                                        0.0313378649
Lag 5000                                                        0.0006030047
         at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.units
Lag 0                                                       -0.02385685
Lag 100                                                     -0.01929710
Lag 500                                                      0.05442789
Lag 1000                                                     0.02999688
Lag 5000                                                     0.02354946
         at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.units
Lag 0                                                           -0.037784916
Lag 100                                                         -0.040619404
Lag 500                                                          0.009246757
Lag 1000                                                         0.021585046
Lag 5000                                                         0.029657103
         at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.units
Lag 0                                                           -0.037784916
Lag 100                                                         -0.040619404
Lag 500                                                          0.009246757
Lag 1000                                                         0.021585046
Lag 5000                                                         0.029657103
         at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.units
Lag 0                                                                -0.04048151
Lag 100                                                              -0.04664306
Lag 500                                                              -0.02420607
Lag 1000                                                              0.03414246
```

```
Lag 5000                                                         0.04075949


, , traittarsus.mother


         at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.animal
Lag 0                                                        0.06303474
Lag 100                                                      0.09137304
Lag 500                                                      0.05137407
Lag 1000                                                     0.02569160
Lag 5000                                                    -0.08057411
         at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.animal
Lag 0                                                           0.06865980
Lag 100                                                         0.10336350
Lag 500                                                         0.01711371
Lag 1000                                                        0.03032742
Lag 5000                                                       -0.08530728
         at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.animal
Lag 0                                                           0.06865980
Lag 100                                                         0.10336350
Lag 500                                                         0.01711371
Lag 1000                                                        0.03032742
Lag 5000                                                       -0.08530728
         at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.animal
Lag 0                                                           -0.009350685
Lag 100                                                          0.024288467
Lag 500                                                         -0.016438414
Lag 1000                                                        -0.005767054
Lag 5000                                                        -0.063956859
         at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.animal
Lag 0                                                       -0.13999847
Lag 100                                                     -0.14330129
Lag 500                                                     -0.12944310
Lag 1000                                                    -0.08446537
```

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

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

```
Lag 5000                                                      -0.05664141
         at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.units
Lag 0                                                                0.17073426
Lag 100                                                              0.18983154
Lag 500                                                              0.15067362
Lag 1000                                                             0.07940280
Lag 5000                                                            -0.07670042

, , at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.units

         at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.animal
Lag 0                                                       -0.84231928
Lag 100                                                     -0.57945611
Lag 500                                                     -0.19062716
Lag 1000                                                    -0.08668794
Lag 5000                                                     0.01749515
         at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.animal
Lag 0                                                          -0.73143141
Lag 100                                                        -0.54471632
Lag 500                                                        -0.20876950
Lag 1000                                                       -0.08873424
Lag 5000                                                        0.01590906
         at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.animal
Lag 0                                                          -0.73143141
Lag 100                                                        -0.54471632
Lag 500                                                        -0.20876950
Lag 1000                                                       -0.08873424
Lag 5000                                                        0.01590906
         at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.animal
Lag 0                                                             -0.463783799
Lag 100                                                           -0.353636210
Lag 500                                                           -0.169902631
Lag 1000                                                          -0.092155921
```

```
Lag 5000                                              -0.009813848
         at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.animal
Lag 0                                            0.048426202
Lag 100                                          0.082944312
Lag 500                                          0.033604930
Lag 1000                                         0.005353498
Lag 5000                                         0.014843101
         at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.animal
Lag 0                                                0.04443896
Lag 100                                              0.05903744
Lag 500                                              0.02909782
Lag 1000                                             0.01112292
Lag 5000                                            -0.02822596
         at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.animal
Lag 0                                                0.04443896
Lag 100                                              0.05903744
Lag 500                                              0.02909782
Lag 1000                                             0.01112292
Lag 5000                                            -0.02822596
         at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.animal
Lag 0                                                   0.04061110
Lag 100                                                 0.04147746
Lag 500                                                 0.01338370
Lag 1000                                                0.01709317
Lag 5000                                               -0.05401662
         traitbwt.byear traittarsus.byear traitbwt.mother traittarsus.mother
Lag 0       0.005983125      -0.103356615    0.0938981727      -0.0428373611
Lag 100     0.042918382      -0.047853012    0.0762514968      -0.0699317580
Lag 500    -0.002564868      -0.017832691    0.0157985450       0.0235550018
Lag 1000    0.014867426      -0.027311021    0.0003829822      -0.0006460503
Lag 5000    0.009101393       0.004430949   -0.0233572527       0.0174497074
         at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.units
Lag 0                                           1.000000000
```

```
Lag 100                                                    0.503164974
Lag 500                                                    0.176766919
Lag 1000                                                   0.100125592
Lag 5000                                                   0.003858174
         at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.units
Lag 0                                                         0.862131977
Lag 100                                                       0.467009268
Lag 500                                                       0.173071923
Lag 1000                                                      0.091405415
Lag 5000                                                      0.001214249
         at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.units
Lag 0                                                         0.862131977
Lag 100                                                       0.467009268
Lag 500                                                       0.173071923
Lag 1000                                                      0.091405415
Lag 5000                                                      0.001214249
         at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.units
Lag 0                                                            0.556754885
Lag 100                                                          0.300025056
Lag 500                                                          0.130914950
Lag 1000                                                         0.084742808
Lag 5000                                                         0.008877657
         at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.units
Lag 0                                                     -0.066893803
Lag 100                                                   -0.088991169
Lag 500                                                   -0.041740101
Lag 1000                                                  -0.013627370
Lag 5000                                                  -0.004864431
         at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.units
Lag 0                                                        -0.041695516
Lag 100                                                      -0.058375215
Lag 500                                                      -0.038590340
Lag 1000                                                     -0.008465406
```

```
Lag 5000                                                      0.033653455
         at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.units
Lag 0                                                        -0.041695516
Lag 100                                                      -0.058375215
Lag 500                                                      -0.038590340
Lag 1000                                                     -0.008465406
Lag 5000                                                      0.033653455
         at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.units
Lag 0                                                           -0.020866307
Lag 100                                                         -0.024784750
Lag 500                                                         -0.024026474
Lag 1000                                                        -0.008875445
Lag 5000                                                         0.060413047

, , at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.units

         at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.animal
Lag 0                                                       -0.70890155
Lag 100                                                     -0.51875562
Lag 500                                                     -0.20600428
Lag 1000                                                    -0.10994315
Lag 5000                                                    -0.01039121
         at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.animal
Lag 0                                                          -0.82495927
Lag 100                                                        -0.61316330
Lag 500                                                        -0.24079957
Lag 1000                                                       -0.11403500
Lag 5000                                                       -0.01904085
         at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.animal
Lag 0                                                          -0.82495927
Lag 100                                                        -0.61316330
Lag 500                                                        -0.24079957
Lag 1000                                                       -0.11403500
```

```
Lag 5000                                                       -0.01904085
         at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.animal
Lag 0                                                             -0.65832516
Lag 100                                                           -0.49644020
Lag 500                                                           -0.22156354
Lag 1000                                                          -0.11606788
Lag 5000                                                          -0.03431864
         at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.animal
Lag 0                                                      0.0432075717
Lag 100                                                    0.0731729081
Lag 500                                                    0.0351321242
Lag 1000                                                   0.0008078044
Lag 5000                                                   0.0060255376
         at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.animal
Lag 0                                                           0.04900783
Lag 100                                                         0.06034422
Lag 500                                                         0.03147880
Lag 1000                                                        0.01663910
Lag 5000                                                       -0.02708842
         at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.animal
Lag 0                                                           0.04900783
Lag 100                                                         0.06034422
Lag 500                                                         0.03147880
Lag 1000                                                        0.01663910
Lag 5000                                                       -0.02708842
         at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.animal
Lag 0                                                              0.05879880
Lag 100                                                            0.06066830
Lag 500                                                            0.02143188
Lag 1000                                                           0.02664768
Lag 5000                                                          -0.05794619
         traitbwt.byear traittarsus.byear traitbwt.mother traittarsus.mother
Lag 0        0.05280676      -0.097464115      0.11659923       -0.080407800
```

```
Lag 100      0.06749027      -0.048884392      0.05889480       -0.042771302
Lag 500      0.01581190      -0.013402510      0.01353140        0.023637489
Lag 1000     0.02427770      -0.012851631      0.01997733        0.008272035
Lag 5000    -0.00118757       0.004909443     -0.02042686        0.001970307
         at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.units
Lag 0                                                    0.8621320
Lag 100                                                  0.4520274
Lag 500                                                  0.1932988
Lag 1000                                                 0.1091092
Lag 5000                                                 0.0303842
         at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.units
Lag 0                                                       1.00000000
Lag 100                                                     0.52253994
Lag 500                                                     0.19894517
Lag 1000                                                    0.10703411
Lag 5000                                                    0.03011013
         at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.units
Lag 0                                                       1.00000000
Lag 100                                                     0.52253994
Lag 500                                                     0.19894517
Lag 1000                                                    0.10703411
Lag 5000                                                    0.03011013
         at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.units
Lag 0                                                          0.83204286
Lag 100                                                        0.40931694
Lag 500                                                        0.16394862
Lag 1000                                                       0.09392225
Lag 5000                                                       0.02432038
         at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.units
Lag 0                                                 -0.066443086
Lag 100                                               -0.077647262
Lag 500                                               -0.036441782
Lag 1000                                              -0.007304102
```

```
Lag 5000                                                    -0.002379788
         at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.units
Lag 0                                                                -0.05557720
Lag 100                                                              -0.05970375
Lag 500                                                              -0.03617882
Lag 1000                                                             -0.01614682
Lag 5000                                                              0.03234714
         at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.units
Lag 0                                                                -0.05557720
Lag 100                                                              -0.05970375
Lag 500                                                              -0.03617882
Lag 1000                                                             -0.01614682
Lag 5000                                                              0.03234714
         at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.units
Lag 0                                                                   -0.04717349
Lag 100                                                                 -0.04356349
Lag 500                                                                 -0.02677549
Lag 1000                                                                -0.02460366
Lag 5000                                                                 0.06745537

, , at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.units

         at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.animal
Lag 0                                                           -0.70890155
Lag 100                                                         -0.51875562
Lag 500                                                         -0.20600428
Lag 1000                                                        -0.10994315
Lag 5000                                                        -0.01039121
         at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.animal
Lag 0                                                              -0.82495927
Lag 100                                                            -0.61316330
Lag 500                                                            -0.24079957
Lag 1000                                                           -0.11403500
```

```
Lag 5000                                                     -0.01904085
         at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.animal
Lag 0                                                        -0.82495927
Lag 100                                                      -0.61316330
Lag 500                                                      -0.24079957
Lag 1000                                                     -0.11403500
Lag 5000                                                     -0.01904085
         at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.animal
Lag 0                                                           -0.65832516
Lag 100                                                         -0.49644020
Lag 500                                                         -0.22156354
Lag 1000                                                        -0.11606788
Lag 5000                                                        -0.03431864
         at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.animal
Lag 0                                                    0.0432075717
Lag 100                                                  0.0731729081
Lag 500                                                  0.0351321242
Lag 1000                                                 0.0008078044
Lag 5000                                                 0.0060255376
         at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.animal
Lag 0                                                         0.04900783
Lag 100                                                       0.06034422
Lag 500                                                       0.03147880
Lag 1000                                                      0.01663910
Lag 5000                                                     -0.02708842
         at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.animal
Lag 0                                                         0.04900783
Lag 100                                                       0.06034422
Lag 500                                                       0.03147880
Lag 1000                                                      0.01663910
Lag 5000                                                     -0.02708842
         at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.animal
Lag 0                                                            0.05879880
```

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

```
Lag 5000                                                         0.02432038
         at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.units
Lag 0                                                     -0.066443086
Lag 100                                                   -0.077647262
Lag 500                                                   -0.036441782
Lag 1000                                                  -0.007304102
Lag 5000                                                  -0.002379788
         at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.units
Lag 0                                                         -0.05557720
Lag 100                                                       -0.05970375
Lag 500                                                       -0.03617882
Lag 1000                                                      -0.01614682
Lag 5000                                                       0.03234714
         at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.units
Lag 0                                                         -0.05557720
Lag 100                                                       -0.05970375
Lag 500                                                       -0.03617882
Lag 1000                                                      -0.01614682
Lag 5000                                                       0.03234714
         at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.units
Lag 0                                                            -0.04717349
Lag 100                                                          -0.04356349
Lag 500                                                          -0.02677549
Lag 1000                                                         -0.02460366
Lag 5000                                                          0.06745537

, , at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.units

         at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.animal
Lag 0                                                        -0.43812320
Lag 100                                                      -0.32924526
Lag 500                                                      -0.13020212
Lag 1000                                                     -0.13254862
```

```
Lag 5000                                                  -0.07309476
         at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.animal
Lag 0                                                        -0.64394327
Lag 100                                                      -0.46780888
Lag 500                                                      -0.20079012
Lag 1000                                                     -0.14480996
Lag 5000                                                     -0.09575862
         at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.animal
Lag 0                                                        -0.64394327
Lag 100                                                      -0.46780888
Lag 500                                                      -0.20079012
Lag 1000                                                     -0.14480996
Lag 5000                                                     -0.09575862
         at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.animal
Lag 0                                                           -0.76001059
Lag 100                                                         -0.54663983
Lag 500                                                         -0.24713058
Lag 1000                                                        -0.16089016
Lag 5000                                                        -0.08907569
         at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.animal
Lag 0                                                      0.01554818
Lag 100                                                    0.03347226
Lag 500                                                    0.03054674
Lag 1000                                                   0.01335762
Lag 5000                                                   0.01644186
         at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.animal
Lag 0                                                       0.0247708510
Lag 100                                                     0.0298811053
Lag 500                                                     0.0393319911
Lag 1000                                                    0.0410794684
Lag 5000                                                    0.0003106287
         at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.animal
Lag 0                                                       0.0247708510
```

```
Lag 100                                                       0.0298811053
Lag 500                                                       0.0393319911
Lag 1000                                                      0.0410794684
Lag 5000                                                      0.0003106287
         at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.animal
Lag 0                                                               0.04254878
Lag 100                                                             0.04748420
Lag 500                                                             0.04789053
Lag 1000                                                            0.06796255
Lag 5000                                                           -0.01851941
         traitbwt.byear traittarsus.byear traitbwt.mother traittarsus.mother
Lag 0       0.072105699     -0.1083934806    0.1007331132       -0.090750879
Lag 100     0.069867202     -0.0486077910    0.0545104394       -0.013859645
Lag 500     0.026575267     -0.0133212485    0.0286661585        0.008613454
Lag 1000    0.015663649     -0.0195256514    0.0413886079        0.020780006
Lag 5000   -0.002018726     -0.0001505633    0.0007733641       -0.036366883
         at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.units
Lag 0                                                    0.55675488
Lag 100                                                  0.28216537
Lag 500                                                  0.12989226
Lag 1000                                                 0.12353001
Lag 5000                                                 0.07787577
         at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.units
Lag 0                                                       0.83204286
Lag 100                                                     0.39760050
Lag 500                                                     0.17265831
Lag 1000                                                    0.12489795
Lag 5000                                                    0.08926567
         at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.units
Lag 0                                                       0.83204286
Lag 100                                                     0.39760050
Lag 500                                                     0.17265831
Lag 1000                                                    0.12489795
```

```
Lag 5000                                                     0.08926567
         at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.units
Lag 0                                                           1.00000000
Lag 100                                                         0.43985525
Lag 500                                                         0.18705457
Lag 1000                                                        0.11273003
Lag 5000                                                        0.07297707
         at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.units
Lag 0                                                   -0.03083664
Lag 100                                                 -0.03304267
Lag 500                                                 -0.03123886
Lag 1000                                                -0.02337670
Lag 5000                                                -0.02222725
         at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.units
Lag 0                                                     -0.0304234955
Lag 100                                                   -0.0241051816
Lag 500                                                   -0.0412351901
Lag 1000                                                  -0.0471997761
Lag 5000                                                   0.0005985541
         at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.units
Lag 0                                                     -0.0304234955
Lag 100                                                   -0.0241051816
Lag 500                                                   -0.0412351901
Lag 1000                                                  -0.0471997761
Lag 5000                                                   0.0005985541
         at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.units
Lag 0                                                          -0.03748483
Lag 100                                                        -0.02874080
Lag 500                                                        -0.04666191
Lag 1000                                                       -0.07162962
Lag 5000                                                        0.02693394

, , at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.units
```

```
         at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.animal
Lag 0                                                         0.07807105
Lag 100                                                       0.04809322
Lag 500                                                       0.07342298
Lag 1000                                                      0.02747559
Lag 5000                                                     -0.08865706
         at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.animal
Lag 0                                                           0.082481767
Lag 100                                                         0.069884466
Lag 500                                                         0.053669242
Lag 1000                                                       -0.003247808
Lag 5000                                                       -0.105675290
         at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.animal
Lag 0                                                           0.082481767
Lag 100                                                         0.069884466
Lag 500                                                         0.053669242
Lag 1000                                                       -0.003247808
Lag 5000                                                       -0.105675290
         at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.animal
Lag 0                                                              0.0287090438
Lag 100                                                            0.0207457037
Lag 500                                                            0.0006081912
Lag 1000                                                          -0.0572950737
Lag 5000                                                          -0.1156100914
         at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.animal
Lag 0                                                         -0.9369474
Lag 100                                                       -0.8074872
Lag 500                                                       -0.5046449
Lag 1000                                                      -0.2917207
Lag 5000                                                       0.1083680
         at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.animal
Lag 0                                                            -0.8748666
```

```
Lag 100                                                       -0.8019088
Lag 500                                                       -0.5689707
Lag 1000                                                      -0.3490005
Lag 5000                                                       0.1337402
         at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.animal
Lag 0                                                         -0.8748666
Lag 100                                                       -0.8019088
Lag 500                                                       -0.5689707
Lag 1000                                                      -0.3490005
Lag 5000                                                       0.1337402
         at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.animal
Lag 0                                                            -0.7532567
Lag 100                                                          -0.7106727
Lag 500                                                          -0.5497772
Lag 1000                                                         -0.3502307
Lag 5000                                                          0.1338020
         traitbwt.byear traittarsus.byear traitbwt.mother traittarsus.mother
Lag 0       0.024722609       -0.02576722     -0.02385685         0.14299876
Lag 100     0.017186912       -0.04974888     -0.00291607         0.12584167
Lag 500     0.027788923       -0.07216401     -0.03437633         0.12502432
Lag 1000    0.030599400       -0.05970350     -0.07019603         0.09866987
Lag 5000    0.003688852       -0.03623879     -0.01956357        -0.02929408
         at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.units
Lag 0                                                 -0.066893803
Lag 100                                               -0.023868973
Lag 500                                               -0.055699109
Lag 1000                                              -0.006728342
Lag 5000                                               0.089063097
         at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.units
Lag 0                                                       -0.06644309
Lag 100                                                     -0.03252225
Lag 500                                                     -0.03013542
Lag 1000                                                     0.00413424
```

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

```
Lag 100                                                                   0.7088815
Lag 500                                                                   0.5356249
Lag 1000                                                                  0.3410568
Lag 5000                                                                 -0.1407239

, , at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.units


         at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.animal
Lag 0                                                              0.066793402
Lag 100                                                            0.050378446
Lag 500                                                            0.077515159
Lag 1000                                                           0.008812794
Lag 5000                                                          -0.121465553
         at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.animal
Lag 0                                                                 0.093083697
Lag 100                                                               0.084384646
Lag 500                                                               0.074812950
Lag 1000                                                             -0.007598499
Lag 5000                                                             -0.145198558
         at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.animal
Lag 0                                                                 0.093083697
Lag 100                                                               0.084384646
Lag 500                                                               0.074812950
Lag 1000                                                             -0.007598499
Lag 5000                                                             -0.145198558
         at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.animal
Lag 0                                                                    0.039633904
Lag 100                                                                  0.030631751
Lag 500                                                                  0.008216661
Lag 1000                                                                -0.067574178
Lag 5000                                                                -0.158681853
         at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.animal
Lag 0                                                                -0.8725969
```

```
Lag 100                                                      -0.7772224
Lag 500                                                      -0.5293889
Lag 1000                                                     -0.3047292
Lag 5000                                                      0.1032909
         at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.animal
Lag 0                                                           -0.9629330
Lag 100                                                         -0.8857980
Lag 500                                                         -0.6314814
Lag 1000                                                        -0.3830396
Lag 5000                                                         0.1372333
         at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.animal
Lag 0                                                           -0.9629330
Lag 100                                                         -0.8857980
Lag 500                                                         -0.6314814
Lag 1000                                                        -0.3830396
Lag 5000                                                         0.1372333
         at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.animal
Lag 0                                                              -0.9140715
Lag 100                                                            -0.8566927
Lag 500                                                            -0.6364708
Lag 1000                                                           -0.3975119
Lag 5000                                                            0.1452190
         traitbwt.byear traittarsus.byear traitbwt.mother traittarsus.mother
Lag 0        0.03515002       -0.04917083     -0.03778492         0.16291072
Lag 100      0.03091121       -0.05304287     -0.03754739         0.16477625
Lag 500      0.02594763       -0.04411058     -0.04091176         0.15960207
Lag 1000     0.03943697       -0.05730659     -0.07505811         0.12634662
Lag 5000    -0.02494957       -0.03580137     -0.02083442        -0.01955372
         at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.units
Lag 0                                                      -0.04169552
Lag 100                                                    -0.02400995
Lag 500                                                    -0.05483846
Lag 1000                                                    0.01413904
```

```
Lag 5000                                                    0.12137475
         at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.units
Lag 0                                                         -0.05557720
Lag 100                                                       -0.04292481
Lag 500                                                       -0.04373833
Lag 1000                                                       0.01820822
Lag 5000                                                       0.13061028
         at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.units
Lag 0                                                         -0.05557720
Lag 100                                                       -0.04292481
Lag 500                                                       -0.04373833
Lag 1000                                                       0.01820822
Lag 5000                                                       0.13061028
         at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.units
Lag 0                                                            -0.03042350
Lag 100                                                          -0.02364770
Lag 500                                                          -0.02090983
Lag 1000                                                          0.03823823
Lag 5000                                                          0.15598999
         at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.units
Lag 0                                                        0.9162648
Lag 100                                                      0.7742948
Lag 500                                                      0.5235576
Lag 1000                                                     0.3032634
Lag 5000                                                    -0.1115658
         at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.units
Lag 0                                                           1.0000000
Lag 100                                                         0.8752177
Lag 500                                                         0.6156893
Lag 1000                                                        0.3715418
Lag 5000                                                       -0.1435973
         at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.units
Lag 0                                                           1.0000000
```

```
Lag 100                                            0.8752177
Lag 500                                            0.6156893
Lag 1000                                           0.3715418
Lag 5000                                          -0.1435973
         at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.units
Lag 0                                                 0.9475981
Lag 100                                               0.8522663
Lag 500                                               0.6217954
Lag 1000                                              0.3896947
Lag 5000                                             -0.1540929

, , at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.units

         at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.animal
Lag 0                                           0.066793402
Lag 100                                         0.050378446
Lag 500                                         0.077515159
Lag 1000                                        0.008812794
Lag 5000                                       -0.121465553
         at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.animal
Lag 0                                              0.093083697
Lag 100                                            0.084384646
Lag 500                                            0.074812950
Lag 1000                                          -0.007598499
Lag 5000                                          -0.145198558
         at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.animal
Lag 0                                              0.093083697
Lag 100                                            0.084384646
Lag 500                                            0.074812950
Lag 1000                                          -0.007598499
Lag 5000                                          -0.145198558
         at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.animal
Lag 0                                                 0.039633904
```

```
Lag 100                                                           0.030631751
Lag 500                                                           0.008216661
Lag 1000                                                         -0.067574178
Lag 5000                                                         -0.158681853
         at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.animal
Lag 0                                                        -0.8725969
Lag 100                                                      -0.7772224
Lag 500                                                      -0.5293889
Lag 1000                                                     -0.3047292
Lag 5000                                                      0.1032909
         at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.animal
Lag 0                                                           -0.9629330
Lag 100                                                         -0.8857980
Lag 500                                                         -0.6314814
Lag 1000                                                        -0.3830396
Lag 5000                                                         0.1372333
         at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.animal
Lag 0                                                           -0.9629330
Lag 100                                                         -0.8857980
Lag 500                                                         -0.6314814
Lag 1000                                                        -0.3830396
Lag 5000                                                         0.1372333
         at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.animal
Lag 0                                                              -0.9140715
Lag 100                                                            -0.8566927
Lag 500                                                            -0.6364708
Lag 1000                                                           -0.3975119
Lag 5000                                                            0.1452190
         traitbwt.byear traittarsus.byear traitbwt.mother traittarsus.mother
Lag 0        0.03515002       -0.04917083     -0.03778492         0.16291072
Lag 100      0.03091121       -0.05304287     -0.03754739         0.16477625
Lag 500      0.02594763       -0.04411058     -0.04091176         0.15960207
Lag 1000     0.03943697       -0.05730659     -0.07505811         0.12634662
```

```
Lag 5000    -0.02494957       -0.03580137     -0.02083442        -0.01955372
         at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.units
Lag 0                                                      -0.04169552
Lag 100                                                    -0.02400995
Lag 500                                                    -0.05483846
Lag 1000                                                    0.01413904
Lag 5000                                                    0.12137475
         at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.units
Lag 0                                                         -0.05557720
Lag 100                                                       -0.04292481
Lag 500                                                       -0.04373833
Lag 1000                                                       0.01820822
Lag 5000                                                       0.13061028
         at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.units
Lag 0                                                         -0.05557720
Lag 100                                                       -0.04292481
Lag 500                                                       -0.04373833
Lag 1000                                                       0.01820822
Lag 5000                                                       0.13061028
         at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.units
Lag 0                                                            -0.03042350
Lag 100                                                          -0.02364770
Lag 500                                                          -0.02090983
Lag 1000                                                          0.03823823
Lag 5000                                                          0.15598999
         at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.units
Lag 0                                                        0.9162648
Lag 100                                                      0.7742948
Lag 500                                                      0.5235576
Lag 1000                                                     0.3032634
Lag 5000                                                    -0.1115658
         at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.units
Lag 0                                                            1.0000000
```

```
Lag 100                                                   0.8752177
Lag 500                                                   0.6156893
Lag 1000                                                  0.3715418
Lag 5000                                                 -0.1435973
         at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.units
Lag 0                                                     1.0000000
Lag 100                                                   0.8752177
Lag 500                                                   0.6156893
Lag 1000                                                  0.3715418
Lag 5000                                                 -0.1435973
         at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.units
Lag 0                                                        0.9475981
Lag 100                                                      0.8522663
Lag 500                                                      0.6217954
Lag 1000                                                     0.3896947
Lag 5000                                                    -0.1540929

, , at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.units

         at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.animal
Lag 0                                                  0.047978981
Lag 100                                                0.045079451
Lag 500                                                0.067970538
Lag 1000                                              -0.006909171
Lag 5000                                              -0.132371879
         at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.animal
Lag 0                                                      0.08843633
Lag 100                                                    0.08879180
Lag 500                                                    0.08319912
Lag 1000                                                  -0.00586568
Lag 5000                                                  -0.15675135
         at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.animal
Lag 0                                                      0.08843633
```

```
Lag 100                                                         0.08879180
Lag 500                                                         0.08319912
Lag 1000                                                       -0.00586568
Lag 5000                                                       -0.15675135
         at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.animal
Lag 0                                                                 0.04584246
Lag 100                                                               0.04189200
Lag 500                                                               0.02195919
Lag 1000                                                             -0.05747491
Lag 5000                                                             -0.16717974
         at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.animal
Lag 0                                                       -0.75254810
Lag 100                                                     -0.68626575
Lag 500                                                     -0.50089775
Lag 1000                                                    -0.29031256
Lag 5000                                                     0.09258748
         at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.animal
Lag 0                                                           -0.9191068
Lag 100                                                         -0.8549977
Lag 500                                                         -0.6281177
Lag 1000                                                        -0.3837276
Lag 5000                                                         0.1299735
         at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.animal
Lag 0                                                           -0.9191068
Lag 100                                                         -0.8549977
Lag 500                                                         -0.6281177
Lag 1000                                                        -0.3837276
Lag 5000                                                         0.1299735
         at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.animal
Lag 0                                                               -0.9650519
Lag 100                                                             -0.9020388
Lag 500                                                             -0.6603730
Lag 1000                                                            -0.4085407
```

```
Lag 5000                                                        0.1451290
         traitbwt.byear traittarsus.byear traitbwt.mother traittarsus.mother
Lag 0        0.03233249       -0.05392947     -0.04048151         0.17073426
Lag 100      0.03971497       -0.04863212     -0.04603016         0.19100707
Lag 500      0.02833531       -0.02831174     -0.04356222         0.17180604
Lag 1000     0.03018475       -0.05344380     -0.07230573         0.12082866
Lag 5000    -0.04000580       -0.02623878     -0.01322038        -0.01980137
         at.level(sex, "1"):traitbwt:at.level(sex, "1"):traitbwt.units
Lag 0                                                         -0.02086631
Lag 100                                                       -0.02091564
Lag 500                                                       -0.04738890
Lag 1000                                                       0.02308918
Lag 5000                                                       0.12589958
         at.level(sex, "1"):traittarsus:at.level(sex, "1"):traitbwt.units
Lag 0                                                            -0.04717349
Lag 100                                                          -0.04819145
Lag 500                                                          -0.05369332
Lag 1000                                                          0.02184183
Lag 5000                                                          0.13760532
         at.level(sex, "1"):traitbwt:at.level(sex, "1"):traittarsus.units
Lag 0                                                            -0.04717349
Lag 100                                                          -0.04819145
Lag 500                                                          -0.05369332
Lag 1000                                                          0.02184183
Lag 5000                                                          0.13760532
         at.level(sex, "1"):traittarsus:at.level(sex, "1"):traittarsus.units
Lag 0                                                               -0.03748483
Lag 100                                                             -0.03257654
Lag 500                                                             -0.03463265
Lag 1000                                                             0.04295442
Lag 5000                                                             0.15951258
         at.level(sex, "2"):traitbwt:at.level(sex, "2"):traitbwt.units
Lag 0                                                           0.7818908
```

```
Lag 100                                                      0.6906357
Lag 500                                                      0.4994770
Lag 1000                                                     0.2932880
Lag 5000                                                    -0.1017144
         at.level(sex, "2"):traittarsus:at.level(sex, "2"):traitbwt.units
Lag 0                                                           0.9475981
Lag 100                                                         0.8462154
Lag 500                                                         0.6150082
Lag 1000                                                        0.3748486
Lag 5000                                                       -0.1355925
         at.level(sex, "2"):traitbwt:at.level(sex, "2"):traittarsus.units
Lag 0                                                           0.9475981
Lag 100                                                         0.8462154
Lag 500                                                         0.6150082
Lag 1000                                                        0.3748486
Lag 5000                                                       -0.1355925
         at.level(sex, "2"):traittarsus:at.level(sex, "2"):traittarsus.units
Lag 0                                                              1.0000000
Lag 100                                                            0.8919817
Lag 500                                                            0.6480975
Lag 1000                                                           0.4037684
Lag 5000                                                          -0.1516651
```

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

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

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

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

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

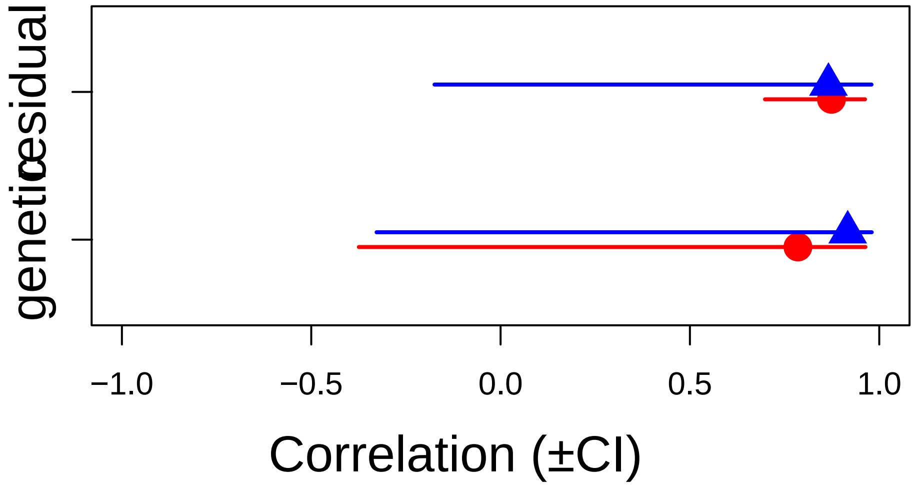
```
HPDinterval(residual.correlation2.4.M, 0.95)
```

```
          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, , 0.9
  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 (±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 ontogenic or sexual conflict, which can constraint or enhanced response to evolution. As an example, we estimate the cross-sex genetic correlation `r_{fm}`

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

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

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

```r
  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 = "r-obj/MCMCglmm_model_BivSex_LongRun.rda")
```

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

```r
load(file = "r-obj/MCMCglmm_model_BivSex_LongRun.rda")
summary(model.BivSex)
```

```

 Iterations = 30001:129901
 Thinning interval  = 100
 Sample size  = 1000

 DIC: 1670.599

 G-structure:  ~us(trait):animal

                                   post.mean l-95% CI u-95% CI eff.samp
traittarsus.1:traittarsus.1.animal     6.632    2.136    12.69    85.74
traittarsus.2:traittarsus.1.animal     8.043    2.389    13.54   117.04
traittarsus.1:traittarsus.2.animal     8.043    2.389    13.54   117.04
traittarsus.2:traittarsus.2.animal    16.145    3.128    28.93    21.81

               ~idh(trait):byear

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

```
               ~idh(trait):mother

                     post.mean l-95% CI u-95% CI eff.samp
traittarsus.1.mother     1.777  0.07858    4.714   299.68
traittarsus.2.mother     2.980  0.12204    7.328    70.26

 R-structure:  ~us(trait):units

                                  post.mean l-95% CI u-95% CI eff.samp
traittarsus.1:traittarsus.1.units    15.455    8.998    21.84  104.923
traittarsus.2:traittarsus.1.units    -1.497  -15.500    15.53    8.767
traittarsus.1:traittarsus.2.units    -1.497  -15.500    15.53    8.767
traittarsus.2:traittarsus.2.units     9.356    0.239    19.10   21.548

 Location effects: cbind(tarsus.1, tarsus.2) ~ trait - 1

              post.mean l-95% CI u-95% CI eff.samp  pMCMC
traittarsus.1     20.48    19.62    21.48    703.9 <0.001 ***
traittarsus.2     20.46    19.42    21.40    846.8 <0.001 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

```r
autocorr(model.BivSex$VCV)
```

```
, , traittarsus.1:traittarsus.1.animal

         traittarsus.1:traittarsus.1.animal traittarsus.2:traittarsus.1.animal
Lag 0                            1.00000000                         0.48422763
Lag 100                          0.73797990                         0.27701934
Lag 500                          0.43151596                         0.08460564
Lag 1000                         0.27709357                         0.03138071
Lag 5000                         0.09623473                         0.02508175
         traittarsus.1:traittarsus.2.animal traittarsus.2:traittarsus.2.animal
Lag 0                            0.48422763                        -0.20835012
```

```
Lag 100                         0.27701934                        -0.26518087
Lag 500                         0.08460564                        -0.27929151
Lag 1000                        0.03138071                        -0.23408954
Lag 5000                        0.02508175                        -0.02431482
         traittarsus.1.byear traittarsus.2.byear traittarsus.1.mother
Lag 0             0.05650214        -0.059474225         -0.038396947
Lag 100           0.03805347        -0.063250151         -0.012779432
Lag 500           0.03353186        -0.031583736          0.059794328
Lag 1000          0.02971111         0.032191172         -0.004310584
Lag 5000          0.04021796        -0.001198619         -0.065221991
         traittarsus.2.mother traittarsus.1:traittarsus.1.units
Lag 0               0.1285643                        -0.7394524
Lag 100             0.1416089                        -0.5874113
Lag 500             0.1227812                        -0.3892610
Lag 1000            0.1054744                        -0.2272794
Lag 5000            0.1046093                        -0.0490914
         traittarsus.2:traittarsus.1.units traittarsus.1:traittarsus.2.units
Lag 0                         -0.030661923                      -0.030661923
Lag 100                       -0.009066847                      -0.009066847
Lag 500                       -0.014021640                      -0.014021640
Lag 1000                      -0.038727365                      -0.038727365
Lag 5000                      -0.053406989                      -0.053406989
         traittarsus.2:traittarsus.2.units
Lag 0                           0.24444681
Lag 100                         0.28630940
Lag 500                         0.28676382
Lag 1000                        0.25016902
Lag 5000                       -0.01889626

, , traittarsus.2:traittarsus.1.animal


         traittarsus.1:traittarsus.1.animal traittarsus.2:traittarsus.1.animal
Lag 0                            0.48422763                         1.00000000
```

```
Lag 100                    0.25316393                          0.68722653
Lag 500                   -0.01525426                          0.30994286
Lag 1000                  -0.13117432                          0.12750201
Lag 5000                  -0.03481149                          0.01967858
         traittarsus.1:traittarsus.2.animal traittarsus.2:traittarsus.2.animal
Lag 0                      1.00000000                           0.4372811
Lag 100                    0.68722653                           0.3171927
Lag 500                    0.30994286                           0.2173200
Lag 1000                   0.12750201                           0.2034517
Lag 5000                   0.01967858                           0.1155543
         traittarsus.1.byear traittarsus.2.byear traittarsus.1.mother
Lag 0           -0.028123268         -0.10117282          0.068035501
Lag 100         -0.036441213         -0.06326083          0.058376180
Lag 500         -0.017206400         -0.06159010         -0.002869166
Lag 1000        -0.004346341          0.06173108         -0.017320527
Lag 5000        -0.044798021          0.07734401         -0.083350187
         traittarsus.2.mother traittarsus.1:traittarsus.1.units
Lag 0            -0.261520775                       -0.32691256
Lag 100          -0.219989670                       -0.19037150
Lag 500          -0.171008994                        0.03568009
Lag 1000         -0.073253782                        0.15052971
Lag 5000         -0.002628408                        0.06147675
         traittarsus.2:traittarsus.1.units traittarsus.1:traittarsus.2.units
Lag 0                          -0.15561461                       -0.15561461
Lag 100                        -0.11940169                       -0.11940169
Lag 500                        -0.10722180                       -0.10722180
Lag 1000                       -0.11888700                       -0.11888700
Lag 5000                       -0.07749379                       -0.07749379
         traittarsus.2:traittarsus.2.units
Lag 0                           -0.3304177
Lag 100                         -0.2624116
Lag 500                         -0.1893048
Lag 1000                        -0.2045441
```

```
Lag 5000                        -0.1580773

, , traittarsus.1:traittarsus.2.animal

         traittarsus.1:traittarsus.1.animal traittarsus.2:traittarsus.1.animal
Lag 0                            0.48422763                         1.00000000
Lag 100                          0.25316393                         0.68722653
Lag 500                         -0.01525426                         0.30994286
Lag 1000                        -0.13117432                         0.12750201
Lag 5000                        -0.03481149                         0.01967858
         traittarsus.1:traittarsus.2.animal traittarsus.2:traittarsus.2.animal
Lag 0                            1.00000000                          0.4372811
Lag 100                          0.68722653                          0.3171927
Lag 500                          0.30994286                          0.2173200
Lag 1000                         0.12750201                          0.2034517
Lag 5000                         0.01967858                          0.1155543
         traittarsus.1.byear traittarsus.2.byear traittarsus.1.mother
Lag 0           -0.028123268         -0.10117282          0.068035501
Lag 100         -0.036441213         -0.06326083          0.058376180
Lag 500         -0.017206400         -0.06159010         -0.002869166
Lag 1000        -0.004346341          0.06173108         -0.017320527
Lag 5000        -0.044798021          0.07734401         -0.083350187
         traittarsus.2.mother traittarsus.1:traittarsus.1.units
Lag 0            -0.261520775                       -0.32691256
Lag 100          -0.219989670                       -0.19037150
Lag 500          -0.171008994                        0.03568009
Lag 1000         -0.073253782                        0.15052971
Lag 5000         -0.002628408                        0.06147675
         traittarsus.2:traittarsus.1.units traittarsus.1:traittarsus.2.units
Lag 0                          -0.15561461                       -0.15561461
Lag 100                        -0.11940169                       -0.11940169
Lag 500                        -0.10722180                       -0.10722180
Lag 1000                       -0.11888700                       -0.11888700
```

```
Lag 5000                       -0.07749379                       -0.07749379
         traittarsus.2:traittarsus.2.units
Lag 0                           -0.3304177
Lag 100                         -0.2624116
Lag 500                         -0.1893048
Lag 1000                        -0.2045441
Lag 5000                        -0.1580773

, , traittarsus.2:traittarsus.2.animal


         traittarsus.1:traittarsus.1.animal traittarsus.2:traittarsus.1.animal
Lag 0                            -0.2083501                         0.43728107
Lag 100                          -0.2828015                         0.29272735
Lag 500                          -0.3313152                         0.14658444
Lag 1000                         -0.3483078                         0.06012732
Lag 5000                         -0.1542996                        -0.06471744
         traittarsus.1:traittarsus.2.animal traittarsus.2:traittarsus.2.animal
Lag 0                            0.43728107                         1.00000000
Lag 100                          0.29272735                         0.87775419
Lag 500                          0.14658444                         0.72227084
Lag 1000                         0.06012732                         0.61062886
Lag 5000                        -0.06471744                         0.08074184
         traittarsus.1.byear traittarsus.2.byear traittarsus.1.mother
Lag 0           -0.020084226        -0.013645105          0.007263224
Lag 100         -0.015303798         0.015235251          0.013922907
Lag 500         -0.009604004        -0.004276257         -0.022794079
Lag 1000        -0.036443873         0.045216146          0.038406389
Lag 5000        -0.046131641         0.012581835         -0.012187074
         traittarsus.2.mother traittarsus.1:traittarsus.1.units
Lag 0             -0.50677816                        0.23024103
Lag 100           -0.46549011                        0.26517948
Lag 500           -0.35999881                        0.31894466
Lag 1000          -0.26148886                        0.30787546
```

```
Lag 5000          -0.09601646                        0.09998448
         traittarsus.2:traittarsus.1.units traittarsus.1:traittarsus.2.units
Lag 0                           0.03215520                        0.03215520
Lag 100                         0.04234930                        0.04234930
Lag 500                         0.01485912                        0.01485912
Lag 1000                       -0.02777646                       -0.02777646
Lag 5000                       -0.10000281                       -0.10000281
         traittarsus.2:traittarsus.2.units
Lag 0                          -0.90778147
Lag 100                        -0.84400702
Lag 500                        -0.70957533
Lag 1000                       -0.62450980
Lag 5000                       -0.06262314


, , traittarsus.1.byear


         traittarsus.1:traittarsus.1.animal traittarsus.2:traittarsus.1.animal
Lag 0                            0.05650214                        -0.02812327
Lag 100                          0.06068975                        -0.02687949
Lag 500                          0.02342116                        -0.03285780
Lag 1000                         0.03532201                        -0.03419221
Lag 5000                         0.02786557                        -0.01481811
         traittarsus.1:traittarsus.2.animal traittarsus.2:traittarsus.2.animal
Lag 0                           -0.02812327                        -0.02008423
Lag 100                         -0.02687949                        -0.02175035
Lag 500                         -0.03285780                        -0.01196604
Lag 1000                        -0.03419221                        -0.03085934
Lag 5000                        -0.01481811                         0.01496886
         traittarsus.1.byear traittarsus.2.byear traittarsus.1.mother
Lag 0             1.00000000        -0.008840935         -0.034026465
Lag 100           0.23201455        -0.040849216          0.006952432
Lag 500           0.10173419         0.018677216          0.021915445
Lag 1000          0.05656314         0.045347703         -0.069023041
```

```
Lag 5000         -0.02674433         0.003879773         -0.031727649
         traittarsus.2.mother traittarsus.1:traittarsus.1.units
Lag 0             0.041524616                      -0.131561587
Lag 100           0.022654125                      -0.091920671
Lag 500          -0.003137523                      -0.023174815
Lag 1000          0.093233105                       0.017723781
Lag 5000         -0.001576843                       0.003971118
         traittarsus.2:traittarsus.1.units traittarsus.1:traittarsus.2.units
Lag 0                           0.06264243                        0.06264243
Lag 100                         0.06240060                        0.06240060
Lag 500                         0.03789653                        0.03789653
Lag 1000                        0.03352306                        0.03352306
Lag 5000                        0.05768588                        0.05768588
         traittarsus.2:traittarsus.2.units
Lag 0                          0.013826338
Lag 100                        0.015690413
Lag 500                        0.020546446
Lag 1000                      -0.006052117
Lag 5000                      -0.020241900

, , traittarsus.2.byear


         traittarsus.1:traittarsus.1.animal traittarsus.2:traittarsus.1.animal
Lag 0                           -0.059474225                        -0.10117282
Lag 100                         -0.029542673                        -0.06571088
Lag 500                          0.019127206                         0.02553144
Lag 1000                        -0.006675716                         0.03933732
Lag 5000                        -0.020363086                        -0.01801919
         traittarsus.1:traittarsus.2.animal traittarsus.2:traittarsus.2.animal
Lag 0                            -0.10117282                       -0.013645105
Lag 100                          -0.06571088                       -0.001743299
Lag 500                           0.02553144                        0.024080673
Lag 1000                          0.03933732                        0.020998801
```

```
Lag 5000                        -0.01801919                       -0.036422613
        traittarsus.1.byear traittarsus.2.byear traittarsus.1.mother
Lag 0           -0.008840935          1.00000000          0.019871390
Lag 100          0.003895756          0.15813110          0.000200299
Lag 500         -0.028206511          0.02861588          0.028238837
Lag 1000        -0.022327614          0.02577769          0.069995240
Lag 5000         0.054519302         -0.01863939          0.021348106
        traittarsus.2.mother traittarsus.1:traittarsus.1.units
Lag 0             0.02790731                        0.04582166
Lag 100          -0.02533496                        0.01584625
Lag 500          -0.04228406                       -0.01965332
Lag 1000         -0.03776489                       -0.05592538
Lag 5000          0.04026220                        0.02293994
        traittarsus.2:traittarsus.1.units traittarsus.1:traittarsus.2.units
Lag 0                         -0.01692229                       -0.01692229
Lag 100                       -0.03014201                       -0.03014201
Lag 500                       -0.05685394                       -0.05685394
Lag 1000                      -0.05775898                       -0.05775898
Lag 5000                      -0.04474406                       -0.04474406
        traittarsus.2:traittarsus.2.units
Lag 0                         -0.05647151
Lag 100                       -0.01120227
Lag 500                       -0.02826105
Lag 1000                      -0.01902149
Lag 5000                       0.04653422

, , traittarsus.1.mother

        traittarsus.1:traittarsus.1.animal traittarsus.2:traittarsus.1.animal
Lag 0                          -0.03839695                        0.068035501
Lag 100                        -0.01125448                        0.090872487
Lag 500                        -0.01822303                        0.074904451
Lag 1000                       -0.06684368                       -0.009049799
```

```
Lag 5000                         0.01882807                        -0.038704215
         traittarsus.1:traittarsus.2.animal traittarsus.2:traittarsus.2.animal
Lag 0                           0.068035501                         0.007263224
Lag 100                         0.090872487                         0.009427782
Lag 500                         0.074904451                        -0.008966636
Lag 1000                       -0.009049799                        -0.062208885
Lag 5000                       -0.038704215                        -0.090802212
         traittarsus.1.byear traittarsus.2.byear traittarsus.1.mother
Lag 0            -0.034026465         0.019871390           1.00000000
Lag 100          -0.044009625        -0.022642909           0.53848292
Lag 500           0.033149894        -0.058758981           0.05060514
Lag 1000         -0.034811076        -0.041691079          -0.01263351
Lag 5000          0.003520887        -0.007417182          -0.01561154
         traittarsus.2.mother traittarsus.1:traittarsus.1.units
Lag 0            -0.053312892                      -0.274551627
Lag 100          -0.021399368                      -0.183188795
Lag 500           0.001127949                      -0.004741630
Lag 1000          0.017008055                       0.049168722
Lag 5000         -0.013865361                      -0.003898312
         traittarsus.2:traittarsus.1.units traittarsus.1:traittarsus.2.units
Lag 0                          0.021389916                       0.021389916
Lag 100                        0.010504830                       0.010504830
Lag 500                        0.005067944                       0.005067944
Lag 1000                       0.024425517                       0.024425517
Lag 5000                      -0.004626176                      -0.004626176
         traittarsus.2:traittarsus.2.units
Lag 0                           0.02429791
Lag 100                         0.01285473
Lag 500                         0.02017728
Lag 1000                        0.06093906
Lag 5000                        0.10720949

, , traittarsus.2.mother
```

```
         traittarsus.1:traittarsus.1.animal traittarsus.2:traittarsus.1.animal
Lag 0                            0.12856434                         -0.2615208
Lag 100                          0.14693139                         -0.2325836
Lag 500                          0.21342005                         -0.1621874
Lag 1000                         0.23353394                         -0.1119149
Lag 5000                         0.02771044                          0.0396288
         traittarsus.1:traittarsus.2.animal traittarsus.2:traittarsus.2.animal
Lag 0                            -0.2615208                        -0.50677816
Lag 100                          -0.2325836                        -0.48725853
Lag 500                          -0.1621874                        -0.40888208
Lag 1000                         -0.1119149                        -0.34699264
Lag 5000                          0.0396288                         0.02549716
         traittarsus.1.byear traittarsus.2.byear traittarsus.1.mother
Lag 0             0.04152462         0.027907314          -0.05331289
Lag 100           0.02194445         0.054336046          -0.04284508
Lag 500          -0.03327513        -0.020857444          -0.02968159
Lag 1000          0.02573536        -0.040238713          -0.03336616
Lag 5000          0.01374507         0.005808512           0.07687084
         traittarsus.2.mother traittarsus.1:traittarsus.1.units
Lag 0              1.00000000                       -0.13910701
Lag 100            0.70222369                       -0.13691118
Lag 500            0.35625516                       -0.18735521
Lag 1000           0.19638031                       -0.21082439
Lag 5000          -0.04114072                       -0.04387536
         traittarsus.2:traittarsus.1.units traittarsus.1:traittarsus.2.units
Lag 0                           0.04614450                        0.04614450
Lag 100                         0.04486226                        0.04486226
Lag 500                         0.04022585                        0.04022585
Lag 1000                        0.05277963                        0.05277963
Lag 5000                        0.04252673                        0.04252673
         traittarsus.2:traittarsus.2.units
Lag 0                          0.268960307
```

```
Lag 100                       0.289158808
Lag 500                       0.345252707
Lag 1000                      0.323960441
Lag 5000                     -0.002082367

, , traittarsus.1:traittarsus.1.units

         traittarsus.1:traittarsus.1.animal traittarsus.2:traittarsus.1.animal
Lag 0                            -0.7394524                        -0.32691256
Lag 100                          -0.5906993                        -0.20009588
Lag 500                          -0.3828210                        -0.08127245
Lag 1000                         -0.2031251                         0.02298348
Lag 5000                         -0.0979703                        -0.01920779
         traittarsus.1:traittarsus.2.animal traittarsus.2:traittarsus.2.animal
Lag 0                           -0.32691256                         0.23024103
Lag 100                         -0.20009588                         0.28084172
Lag 500                         -0.08127245                         0.28272296
Lag 1000                         0.02298348                         0.28283381
Lag 5000                        -0.01920779                         0.05177093
         traittarsus.1.byear traittarsus.2.byear traittarsus.1.mother
Lag 0            -0.13156159          0.04582166          -0.27455163
Lag 100          -0.05719958          0.04337991          -0.16825519
Lag 500          -0.06997182          0.07140946          -0.07087194
Lag 1000         -0.02088140          0.01426241           0.03955072
Lag 5000         -0.01887279          0.04431921           0.06767122
         traittarsus.2.mother traittarsus.1:traittarsus.1.units
Lag 0              -0.1391070                        1.00000000
Lag 100            -0.1379410                        0.56579808
Lag 500            -0.1301093                        0.35250381
Lag 1000           -0.1253506                        0.15585076
Lag 5000           -0.0735286                        0.05909602
         traittarsus.2:traittarsus.1.units traittarsus.1:traittarsus.2.units
Lag 0                           0.04896537                        0.04896537
```

```
Lag 100                         0.02746645                        0.02746645
Lag 500                         0.03218528                        0.03218528
Lag 1000                        0.05596211                        0.05596211
Lag 5000                        0.05413531                        0.05413531
         traittarsus.2:traittarsus.2.units
Lag 0                           -0.2610614
Lag 100                         -0.3079509
Lag 500                         -0.2969894
Lag 1000                        -0.2847495
Lag 5000                        -0.0427216


, , traittarsus.2:traittarsus.1.units


         traittarsus.1:traittarsus.1.animal traittarsus.2:traittarsus.1.animal
Lag 0                          -0.030661923                        -0.15561461
Lag 100                         0.003884354                        -0.11920858
Lag 500                         0.042099074                        -0.08915914
Lag 1000                        0.042025296                        -0.07981143
Lag 5000                       -0.018911064                        -0.09774452
         traittarsus.1:traittarsus.2.animal traittarsus.2:traittarsus.2.animal
Lag 0                           -0.15561461                         0.03215520
Lag 100                         -0.11920858                         0.04834806
Lag 500                         -0.08915914                         0.05802195
Lag 1000                        -0.07981143                         0.02656239
Lag 5000                        -0.09774452                        -0.04245498
         traittarsus.1.byear traittarsus.2.byear traittarsus.1.mother
Lag 0             0.06264243        -0.016922288           0.02138992
Lag 100           0.06751797        -0.004991909           0.02085557
Lag 500           0.06731777        -0.030284706           0.05500122
Lag 1000          0.06629827        -0.044495833           0.10333723
Lag 5000          0.08927471        -0.038637660           0.06016204
         traittarsus.2.mother traittarsus.1:traittarsus.1.units
Lag 0              0.04614450                       0.048965370
```

```
Lag 100             0.04880037                          0.017340477
Lag 500             0.04329157                         -0.013844496
Lag 1000            0.06724925                         -0.039591736
Lag 5000            0.04795409                         -0.003568665
         traittarsus.2:traittarsus.1.units traittarsus.1:traittarsus.2.units
Lag 0                            1.0000000                         1.0000000
Lag 100                          0.9675526                         0.9675526
Lag 500                          0.9029928                         0.9029928
Lag 1000                         0.8401123                         0.8401123
Lag 5000                         0.4663345                         0.4663345
         traittarsus.2:traittarsus.2.units
Lag 0                          -0.04275237
Lag 100                        -0.06227874
Lag 500                        -0.06672641
Lag 1000                       -0.04382724
Lag 5000                        0.03699475

, , traittarsus.1:traittarsus.2.units

         traittarsus.1:traittarsus.1.animal traittarsus.2:traittarsus.1.animal
Lag 0                          -0.030661923                        -0.15561461
Lag 100                         0.003884354                        -0.11920858
Lag 500                         0.042099074                        -0.08915914
Lag 1000                        0.042025296                        -0.07981143
Lag 5000                       -0.018911064                        -0.09774452
         traittarsus.1:traittarsus.2.animal traittarsus.2:traittarsus.2.animal
Lag 0                           -0.15561461                         0.03215520
Lag 100                         -0.11920858                         0.04834806
Lag 500                         -0.08915914                         0.05802195
Lag 1000                        -0.07981143                         0.02656239
Lag 5000                        -0.09774452                        -0.04245498
         traittarsus.1.byear traittarsus.2.byear traittarsus.1.mother
Lag 0             0.06264243        -0.016922288           0.02138992
```

```
Lag 100           0.06751797        -0.004991909              0.02085557
Lag 500           0.06731777        -0.030284706              0.05500122
Lag 1000          0.06629827        -0.044495833              0.10333723
Lag 5000          0.08927471        -0.038637660              0.06016204
         traittarsus.2.mother traittarsus.1:traittarsus.1.units
Lag 0              0.04614450                       0.048965370
Lag 100            0.04880037                       0.017340477
Lag 500            0.04329157                      -0.013844496
Lag 1000           0.06724925                      -0.039591736
Lag 5000           0.04795409                      -0.003568665
         traittarsus.2:traittarsus.1.units traittarsus.1:traittarsus.2.units
Lag 0                            1.0000000                         1.0000000
Lag 100                          0.9675526                         0.9675526
Lag 500                          0.9029928                         0.9029928
Lag 1000                         0.8401123                         0.8401123
Lag 5000                         0.4663345                         0.4663345
         traittarsus.2:traittarsus.2.units
Lag 0                          -0.04275237
Lag 100                        -0.06227874
Lag 500                        -0.06672641
Lag 1000                       -0.04382724
Lag 5000                        0.03699475

, , traittarsus.2:traittarsus.2.units


         traittarsus.1:traittarsus.1.animal traittarsus.2:traittarsus.1.animal
Lag 0                             0.2444468                        -0.33041768
Lag 100                           0.2953169                        -0.24524259
Lag 500                           0.3257997                        -0.12021844
Lag 1000                          0.3204576                        -0.05040170
Lag 5000                          0.1966910                         0.07386444
         traittarsus.1:traittarsus.2.animal traittarsus.2:traittarsus.2.animal
Lag 0                           -0.33041768                         -0.9077815
```

```
Lag 100                       -0.24524259                         -0.8410651
Lag 500                       -0.12021844                         -0.6969304
Lag 1000                      -0.05040170                         -0.5893775
Lag 5000                       0.07386444                         -0.1004775
         traittarsus.1.byear traittarsus.2.byear traittarsus.1.mother
Lag 0             0.01382634        -0.056471508          0.024297909
Lag 100           0.01730830        -0.030701856          0.017739447
Lag 500           0.03968933         0.004065694          0.010636299
Lag 1000          0.03341332        -0.048898719         -0.028816725
Lag 5000          0.05219060        -0.013503372         -0.005167407
         traittarsus.2.mother traittarsus.1:traittarsus.1.units
Lag 0               0.2689603                        -0.2610614
Lag 100             0.3013532                        -0.3031510
Lag 500             0.3094825                        -0.3179085
Lag 1000            0.2400190                        -0.2838200
Lag 5000            0.1233946                        -0.1252443
         traittarsus.2:traittarsus.1.units traittarsus.1:traittarsus.2.units
Lag 0                          -0.04275237                       -0.04275237
Lag 100                        -0.05037125                       -0.05037125
Lag 500                        -0.01879502                       -0.01879502
Lag 1000                        0.02100080                        0.02100080
Lag 5000                        0.10654662                        0.10654662
         traittarsus.2:traittarsus.2.units
Lag 0                           1.00000000
Lag 100                         0.87986649
Lag 500                         0.70214749
Lag 1000                        0.61035106
Lag 5000                        0.07522425
```

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

```
rfm <- model.BivSex$VCV[, "traittarsus.1:traittarsus.2.animal"] / sqrt(model.BivSex$VCV[, "traitt
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
```

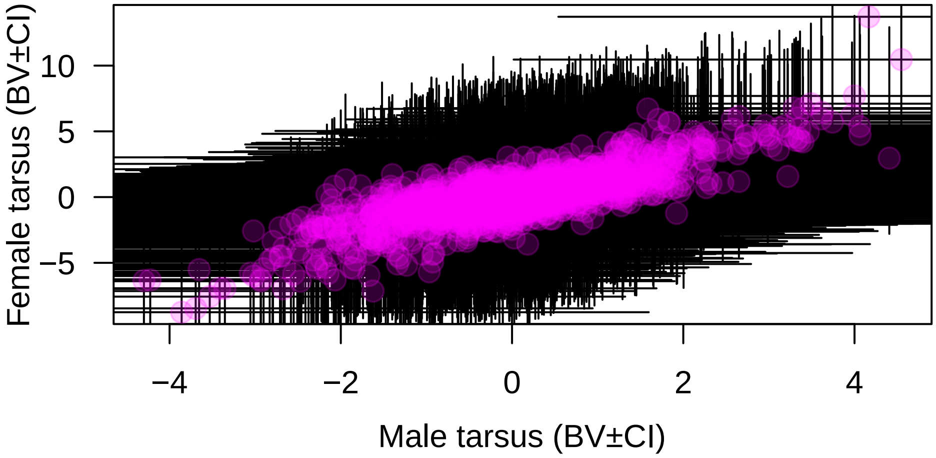
```
DvsS$Trait <- NULL
BLUPS <- reshape(DvsS, v.names = c("BLUP", "CI.lower", "CI.upper"), idvar = "ID", timevar = "TRAI
nrow(BLUPS)
```

```
[1] 1309
```

```
rownames(BLUPS) <- c()
colnames(BLUPS) <- c("ID", "BLUP.btw", "CI.L.btw", "CI.U.btw", "BLUP.tarsus", "CI.L.tarsus", "CI.
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 = "r-obj/MCMCglmm_model_MultivSex_LongRun.rda")
```

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

```
load(file = "r-obj/MCMCglmm_model_MultivSex_LongRun.rda")
summary(model.MultivSex)
```

```

 Iterations = 30001:129901
 Thinning interval  = 100
 Sample size  = 1000

 DIC: 2590.513

 G-structure:  ~us(trait):animal

                                   post.mean   l-95% CI u-95% CI eff.samp
traittarsus.1:traittarsus.1.animal    5.2542  0.6145315   11.414    28.46
traitbwt.1:traittarsus.1.animal       1.2682 -0.7026690    3.298    63.97
traittarsus.2:traittarsus.1.animal    5.9945  0.3482679   13.405    21.59
traitbwt.2:traittarsus.1.animal       1.4467 -0.3853824    4.110    35.84
traittarsus.1:traitbwt.1.animal       1.2682 -0.7026690    3.298    63.97
traitbwt.1:traitbwt.1.animal          1.7891  0.5620761    3.005    97.87
traittarsus.2:traitbwt.1.animal       0.7719 -1.8038433    4.190    22.64
traitbwt.2:traitbwt.1.animal          0.9939  0.0009052    2.069    50.24
traittarsus.1:traittarsus.2.animal    5.9945  0.3482679   13.405    21.59
traitbwt.1:traittarsus.2.animal       0.7719 -1.8038433    4.190    22.64
traittarsus.2:traittarsus.2.animal   12.7341  1.4093961   23.690    28.81
traitbwt.2:traittarsus.2.animal       2.7675 -0.5938976    6.927    20.64
traittarsus.1:traitbwt.2.animal       1.4467 -0.3853824    4.110    35.84
traitbwt.1:traitbwt.2.animal          0.9939  0.0009052    2.069    50.24
traittarsus.2:traitbwt.2.animal       2.7675 -0.5938976    6.927    20.64
traitbwt.2:traitbwt.2.animal          1.5560  0.2002403    3.046    27.21
```

```
               ~idh(trait):byear

                    post.mean l-95% CI u-95% CI eff.samp
traittarsus.1.byear    3.3123   0.9318    6.450    391.3
traitbwt.1.byear       0.6822   0.2403    1.253    522.1
traittarsus.2.byear    4.2198   1.3966    7.713    245.2
traitbwt.2.byear       1.1743   0.5405    1.992    669.6

               ~idh(trait):mother

                     post.mean l-95% CI u-95% CI eff.samp
traittarsus.1.mother     4.858   0.5149    8.841    122.5
traitbwt.1.mother        1.307   0.5752    2.041    369.0
traittarsus.2.mother     5.389   0.7457    9.557    140.4
traitbwt.2.mother        2.003   1.2844    2.770    409.1

 R-structure:  ~us(trait):units

                                  post.mean l-95% CI u-95% CI eff.samp
traittarsus.1:traittarsus.1.units   14.0783   8.6213   20.698   76.808
traitbwt.1:traittarsus.1.units       4.0764   2.2358    6.357   47.762
traittarsus.2:traittarsus.1.units   -3.6471 -16.9514   14.938    4.746
traitbwt.2:traittarsus.1.units      -1.3655  -6.7308    4.970    7.185
traittarsus.1:traitbwt.1.units       4.0764   2.2358    6.357   47.762
traitbwt.1:traitbwt.1.units          1.7295   0.7344    2.785   57.968
traittarsus.2:traitbwt.1.units      -1.1455  -5.8008    4.672    6.837
traitbwt.2:traitbwt.1.units         -0.4245  -2.3300    1.630    7.646
traittarsus.1:traittarsus.2.units   -3.6471 -16.9514   14.938    4.746
traitbwt.1:traittarsus.2.units      -1.1455  -5.8008    4.672    6.837
traittarsus.2:traittarsus.2.units   10.8365   0.5947   19.576   26.795
traitbwt.2:traittarsus.2.units       3.7358  -0.1168    6.848   25.426
traittarsus.1:traitbwt.2.units      -1.3655  -6.7308    4.970    7.185
```

```
traitbwt.1:traitbwt.2.units         -0.4245  -2.3300    1.630    7.646
traittarsus.2:traitbwt.2.units       3.7358  -0.1168    6.848   25.426
traitbwt.2:traitbwt.2.units          1.7825   0.2691    2.916   28.817

 Location effects: cbind(tarsus.1, bwt.1, tarsus.2, bwt.2) ~ trait - 1

              post.mean l-95% CI u-95% CI eff.samp  pMCMC
traittarsus.1    20.424   19.488   21.324    484.6 <0.001 ***
traitbwt.1        6.143    5.686    6.550    596.7 <0.001 ***
traittarsus.2    20.487   19.421   21.461    587.3 <0.001 ***
traitbwt.2        8.247    7.744    8.741    876.7 <0.001 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

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

```
, , traittarsus.1:traittarsus.1.animal

         traittarsus.1:traittarsus.1.animal traitbwt.1:traittarsus.1.animal
Lag 0                             1.0000000                       0.6872795
Lag 100                           0.8646238                       0.6023267
Lag 500                           0.6217623                       0.4701016
Lag 1000                          0.4759845                       0.3306117
Lag 5000                          0.1189988                       0.1665003
         traittarsus.2:traittarsus.1.animal traitbwt.2:traittarsus.1.animal
Lag 0                             0.6821642                       0.5157628
Lag 100                           0.5837197                       0.4557449
Lag 500                           0.4393984                       0.3819538
Lag 1000                          0.3626317                       0.3277211
Lag 5000                          0.1659171                       0.2490413
         traittarsus.1:traitbwt.1.animal traitbwt.1:traitbwt.1.animal
Lag 0                          0.6872795                    0.2316436
Lag 100                        0.6023267                    0.1917562
Lag 500                        0.4701016                    0.1506507
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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
```

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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
```

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Lag 1000                     -0.3341455                  -0.1864674
Lag 5000                     -0.1703888                  -0.1779074
         traittarsus.2:traitbwt.1.units traitbwt.2:traitbwt.1.units
Lag 0                         0.1148525                   0.1045202
Lag 100                       0.1322561                   0.1205853
Lag 500                       0.1661494                   0.1609281
Lag 1000                      0.2078063                   0.2097516
Lag 5000                      0.2120391                   0.2411848
         traittarsus.1:traittarsus.2.units traitbwt.1:traittarsus.2.units
Lag 0                            0.1834123                      0.1148525
Lag 100                          0.1989318                      0.1322561
Lag 500                          0.2183849                      0.1661494
Lag 1000                         0.2393546                      0.2078063
Lag 5000                         0.1874294                      0.2120391
         traittarsus.2:traittarsus.2.units traitbwt.2:traittarsus.2.units
Lag 0                          -0.09279221                    -0.09066377
Lag 100                        -0.06552157                    -0.08137057
Lag 500                        -0.03120806                    -0.06842888
Lag 1000                       -0.04688856                    -0.07652447
Lag 5000                       -0.22692538                    -0.31476665
         traittarsus.1:traitbwt.2.units traitbwt.1:traitbwt.2.units
Lag 0                         0.1843936                   0.1045202
Lag 100                       0.1972224                   0.1205853
Lag 500                       0.2244201                   0.1609281
Lag 1000                      0.2533883                   0.2097516
Lag 5000                      0.2352808                   0.2411848
         traittarsus.2:traitbwt.2.units traitbwt.2:traitbwt.2.units
Lag 0                       -0.09066377                 -0.04305989
Lag 100                     -0.08137057                 -0.04967401
Lag 500                     -0.06842888                 -0.06533316
Lag 1000                    -0.07652447                 -0.05918369
Lag 5000                    -0.31476665                 -0.34290345
```

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, , 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
```

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Lag 0                           0.096601163                      0.14997594
Lag 100                         0.063514030                      0.11517198
Lag 500                         0.007343656                      0.08445112
Lag 1000                        0.062005867                      0.13299248
Lag 5000                        0.138711493                      0.22091811
         traittarsus.1:traitbwt.2.animal traitbwt.1:traitbwt.2.animal
Lag 0                          0.5234222                    0.4293517
Lag 100                        0.4545868                    0.3303034
Lag 500                        0.3427345                    0.2612182
Lag 1000                       0.3004179                    0.2248089
Lag 5000                       0.1589172                    0.2268437
         traittarsus.2:traitbwt.2.animal traitbwt.2:traitbwt.2.animal
Lag 0                         0.14997594                   0.14180302
Lag 100                       0.11517198                   0.11177118
Lag 500                       0.08445112                   0.09651159
Lag 1000                      0.13299248                   0.13501835
Lag 5000                      0.22091811                   0.25836873
         traittarsus.1.byear traitbwt.1.byear traittarsus.2.byear
Lag 0             0.06781216      -0.04857154        -0.001115860
Lag 100           0.05744185      -0.04365919        -0.003028122
Lag 500           0.04182580      -0.01683610        -0.013871766
Lag 1000          0.08409670       0.04075709        -0.088936973
Lag 5000          0.07211397       0.04755605         0.061879136
         traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother
Lag 0        -0.026101857          0.015326642      -0.015001711
Lag 100      -0.026229006          0.004791955      -0.002553299
Lag 500      -0.004795139          0.018197593      -0.001734987
Lag 1000     -0.025567829         -0.014419690      -0.054320480
Lag 5000     -0.011401634         -0.003782365      -0.012255190
         traittarsus.2.mother traitbwt.2.mother
Lag 0              0.05171415       -0.01155255
Lag 100            0.04549989       -0.01648838
Lag 500            0.09888411       -0.02579001
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Lag 1000          0.07526847       -0.03519968
Lag 5000          0.07495551       -0.03929467
         traittarsus.1:traittarsus.1.units traitbwt.1:traittarsus.1.units
Lag 0                           -0.5374156                     -0.7822168
Lag 100                         -0.4631107                     -0.6561709
Lag 500                         -0.3115622                     -0.4297448
Lag 1000                        -0.2502951                     -0.3378405
Lag 5000                        -0.1757000                     -0.1812141
         traittarsus.2:traittarsus.1.units traitbwt.2:traittarsus.1.units
Lag 0                            0.1247101                      0.1399193
Lag 100                          0.1426212                      0.1604774
Lag 500                          0.1604094                      0.2063094
Lag 1000                         0.1703454                      0.2249688
Lag 5000                         0.1859265                      0.1911673
         traittarsus.1:traitbwt.1.units traitbwt.1:traitbwt.1.units
Lag 0                        -0.7822168                  -0.6444049
Lag 100                      -0.6561709                  -0.5391921
Lag 500                      -0.4297448                  -0.3429426
Lag 1000                     -0.3378405                  -0.2744658
Lag 5000                     -0.1812141                  -0.1591715
         traittarsus.2:traitbwt.1.units traitbwt.2:traitbwt.1.units
Lag 0                         0.1003793                   0.1067549
Lag 100                       0.1314503                   0.1404067
Lag 500                       0.1658186                   0.1981668
Lag 1000                      0.1899850                   0.2354607
Lag 5000                      0.2090708                   0.1964048
         traittarsus.1:traittarsus.2.units traitbwt.1:traittarsus.2.units
Lag 0                            0.1247101                      0.1003793
Lag 100                          0.1426212                      0.1314503
Lag 500                          0.1604094                      0.1658186
Lag 1000                         0.1703454                      0.1899850
Lag 5000                         0.1859265                      0.2090708
         traittarsus.2:traittarsus.2.units traitbwt.2:traittarsus.2.units
```

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Lag 0                          -0.09677793                    -0.12847847
Lag 100                        -0.06212434                    -0.10051402
Lag 500                        -0.01671120                    -0.07130994
Lag 1000                       -0.07460059                    -0.11790351
Lag 5000                       -0.16171357                    -0.21125583
         traittarsus.1:traitbwt.2.units traitbwt.1:traitbwt.2.units
Lag 0                         0.1399193                   0.1067549
Lag 100                       0.1604774                   0.1404067
Lag 500                       0.2063094                   0.1981668
Lag 1000                      0.2249688                   0.2354607
Lag 5000                      0.1911673                   0.1964048
         traittarsus.2:traitbwt.2.units traitbwt.2:traitbwt.2.units
Lag 0                       -0.12847847                 -0.10947233
Lag 100                     -0.10051402                 -0.09309607
Lag 500                     -0.07130994                 -0.08545450
Lag 1000                    -0.11790351                 -0.11149356
Lag 5000                    -0.21125583                 -0.23203853

, , traittarsus.2:traittarsus.1.animal

         traittarsus.1:traittarsus.1.animal traitbwt.1:traittarsus.1.animal
Lag 0                           0.682164176                      0.38634307
Lag 100                         0.591700877                      0.34935277
Lag 500                         0.451559860                      0.32828629
Lag 1000                        0.378373002                      0.27249926
Lag 5000                        0.004289439                      0.08293975
         traittarsus.2:traittarsus.1.animal traitbwt.2:traittarsus.1.animal
Lag 0                            1.00000000                      0.78206164
Lag 100                          0.87865696                      0.70110541
Lag 500                          0.69161215                      0.56910648
Lag 1000                         0.56265051                      0.44347532
Lag 5000                        -0.04003226                      0.01712343
         traittarsus.1:traitbwt.1.animal traitbwt.1:traitbwt.1.animal
```

```
Lag 0                        0.38634307                   0.09679049
Lag 100                      0.34935277                   0.10017661
Lag 500                      0.32828629                   0.12775760
Lag 1000                     0.27249926                   0.11433423
Lag 5000                     0.08293975                   0.09000388
         traittarsus.2:traitbwt.1.animal traitbwt.2:traitbwt.1.animal
Lag 0                        0.71265304                   0.46511587
Lag 100                      0.64354820                   0.41849123
Lag 500                      0.54967619                   0.35510793
Lag 1000                     0.45077032                   0.27846473
Lag 5000                     0.02763651                   0.08826768
         traittarsus.1:traittarsus.2.animal traitbwt.1:traittarsus.2.animal
Lag 0                                1.00000000                      0.71265304
Lag 100                              0.87865696                      0.64354820
Lag 500                              0.69161215                      0.54967619
Lag 1000                             0.56265051                      0.45077032
Lag 5000                            -0.04003226                      0.02763651
         traittarsus.2:traittarsus.2.animal traitbwt.2:traittarsus.2.animal
Lag 0                                 0.5942621                       0.5613010
Lag 100                               0.5307170                       0.5141865
Lag 500                               0.4678297                       0.4619296
Lag 1000                              0.4001045                       0.3816713
Lag 5000                              0.1478270                       0.1489578
         traittarsus.1:traitbwt.2.animal traitbwt.1:traitbwt.2.animal
Lag 0                        0.78206164                   0.46511587
Lag 100                      0.70110541                   0.41849123
Lag 500                      0.56910648                   0.35510793
Lag 1000                     0.44347532                   0.27846473
Lag 5000                     0.01712343                   0.08826768
         traittarsus.2:traitbwt.2.animal traitbwt.2:traitbwt.2.animal
Lag 0                         0.5613010                    0.4107260
Lag 100                       0.5141865                    0.3793894
Lag 500                       0.4619296                    0.3449678
```

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Lag 1000                       0.3816713                    0.2731469
Lag 5000                       0.1489578                    0.1431489
         traittarsus.1.byear traitbwt.1.byear traittarsus.2.byear
Lag 0             0.01620495       0.04295234         0.052223393
Lag 100           0.02029711       0.05648775         0.034069858
Lag 500           0.04765917       0.03285861         0.007554307
Lag 1000          0.03767470       0.07587887         0.003191847
Lag 5000         -0.02249363       0.05599353         0.040862718
         traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother
Lag 0         -0.04161269         -0.102952660        0.04055573
Lag 100       -0.05474586         -0.077407539        0.03752540
Lag 500       -0.01536913         -0.009985327        0.02041393
Lag 1000      -0.02242552         -0.016880479        0.02095844
Lag 5000       0.05382429          0.093039192       -0.03853343
         traittarsus.2.mother traitbwt.2.mother
Lag 0             -0.15988076        0.11172969
Lag 100           -0.14920373        0.08235912
Lag 500           -0.10669450        0.07860308
Lag 1000          -0.09563279        0.04882603
Lag 5000          -0.03477033        0.03882608
         traittarsus.1:traittarsus.1.units traitbwt.1:traittarsus.1.units
Lag 0                          -0.48510213                    -0.35513667
Lag 100                        -0.43884380                    -0.32128424
Lag 500                        -0.37005382                    -0.29419691
Lag 1000                       -0.29875897                    -0.25541065
Lag 5000                       -0.06651357                    -0.08518695
         traittarsus.2:traittarsus.1.units traitbwt.2:traittarsus.1.units
Lag 0                            0.1906441                      0.2159001
Lag 100                          0.2109187                      0.2292953
Lag 500                          0.2433902                      0.2525070
Lag 1000                         0.2670207                      0.2801991
Lag 5000                         0.2055428                      0.2202544
         traittarsus.1:traitbwt.1.units traitbwt.1:traitbwt.1.units
```

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Lag 0                  -0.35513667                 -0.16353731
Lag 100                -0.32128424                 -0.14737332
Lag 500                -0.29419691                 -0.14406290
Lag 1000               -0.25541065                 -0.15449858
Lag 5000               -0.08518695                 -0.09726346
         traittarsus.2:traitbwt.1.units traitbwt.2:traitbwt.1.units
Lag 0                    0.1588923                   0.1751169
Lag 100                  0.1763493                   0.1863279
Lag 500                  0.2035612                   0.2019259
Lag 1000                 0.2408050                   0.2434815
Lag 5000                 0.2188271                   0.2190020
         traittarsus.1:traittarsus.2.units traitbwt.1:traittarsus.2.units
Lag 0                       0.1906441                      0.1588923
Lag 100                     0.2109187                      0.1763493
Lag 500                     0.2433902                      0.2035612
Lag 1000                    0.2670207                      0.2408050
Lag 5000                    0.2055428                      0.2188271
         traittarsus.2:traittarsus.2.units traitbwt.2:traittarsus.2.units
Lag 0                      -0.5600992                     -0.5208193
Lag 100                    -0.5263626                     -0.5010452
Lag 500                    -0.4620756                     -0.4434018
Lag 1000                   -0.4037773                     -0.3729971
Lag 5000                   -0.1493219                     -0.1529356
         traittarsus.1:traitbwt.2.units traitbwt.1:traitbwt.2.units
Lag 0                    0.2159001                   0.1751169
Lag 100                  0.2292953                   0.1863279
Lag 500                  0.2525070                   0.2019259
Lag 1000                 0.2801991                   0.2434815
Lag 5000                 0.2202544                   0.2190020
         traittarsus.2:traitbwt.2.units traitbwt.2:traitbwt.2.units
Lag 0                   -0.5208193                  -0.3939711
Lag 100                 -0.5010452                  -0.3851102
Lag 500                 -0.4434018                  -0.3487254
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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
         traittarsus.2:traittarsus.2.animal traitbwt.2:traittarsus.2.animal
Lag 0                        0.5635407                     0.6729793
Lag 100                      0.5125673                     0.6052812
Lag 500                      0.4465910                     0.5277439
Lag 1000                     0.4070664                     0.4538221
Lag 5000                     0.1850370                     0.1792542
         traittarsus.1:traitbwt.2.animal traitbwt.1:traitbwt.2.animal
Lag 0                        1.00000000                    0.6478170
Lag 100                      0.87453824                    0.5573055
Lag 500                      0.65219311                    0.4418750
Lag 1000                     0.48957859                    0.3442054
Lag 5000                     0.01842864                    0.1125165
         traittarsus.2:traitbwt.2.animal traitbwt.2:traitbwt.2.animal
Lag 0                         0.6729793                    0.6191252
Lag 100                       0.6052812                    0.5529718
Lag 500                       0.5277439                    0.4729419
Lag 1000                      0.4538221                    0.3884032
Lag 5000                      0.1792542                    0.1542326
         traittarsus.1.byear traitbwt.1.byear traittarsus.2.byear
Lag 0             0.063463728       0.02730871         0.051964042
Lag 100           0.066558472       0.03961464         0.040967359
Lag 500           0.076728186       0.05374642        -0.012930939
Lag 1000          0.100842393       0.09752083        -0.062954038
Lag 5000         -0.006751012       0.04984406         0.002434151
         traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother
Lag 0         -0.09337461           0.02006907       -0.06942502
Lag 100       -0.09001277           0.02763705       -0.07262374
Lag 500       -0.04869538           0.02000750       -0.09505843
Lag 1000      -0.05831890           0.02560894       -0.08617648
Lag 5000       0.04246982           0.06392166       -0.03722137
         traittarsus.2.mother traitbwt.2.mother
```

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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
         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
```

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Lag 0                         0.14997594                   0.14180302
Lag 100                       0.11517198                   0.11177118
Lag 500                       0.08445112                   0.09651159
Lag 1000                      0.13299248                   0.13501835
Lag 5000                      0.22091811                   0.25836873
         traittarsus.1.byear traitbwt.1.byear traittarsus.2.byear
Lag 0             0.06781216      -0.04857154        -0.001115860
Lag 100           0.05744185      -0.04365919        -0.003028122
Lag 500           0.04182580      -0.01683610        -0.013871766
Lag 1000          0.08409670       0.04075709        -0.088936973
Lag 5000          0.07211397       0.04755605         0.061879136
         traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother
Lag 0        -0.026101857          0.015326642      -0.015001711
Lag 100      -0.026229006          0.004791955      -0.002553299
Lag 500      -0.004795139          0.018197593      -0.001734987
Lag 1000     -0.025567829         -0.014419690      -0.054320480
Lag 5000     -0.011401634         -0.003782365      -0.012255190
         traittarsus.2.mother traitbwt.2.mother
Lag 0              0.05171415       -0.01155255
Lag 100            0.04549989       -0.01648838
Lag 500            0.09888411       -0.02579001
Lag 1000           0.07526847       -0.03519968
Lag 5000           0.07495551       -0.03929467
         traittarsus.1:traittarsus.1.units traitbwt.1:traittarsus.1.units
Lag 0                           -0.5374156                     -0.7822168
Lag 100                         -0.4631107                     -0.6561709
Lag 500                         -0.3115622                     -0.4297448
Lag 1000                        -0.2502951                     -0.3378405
Lag 5000                        -0.1757000                     -0.1812141
         traittarsus.2:traittarsus.1.units traitbwt.2:traittarsus.1.units
Lag 0                            0.1247101                      0.1399193
Lag 100                          0.1426212                      0.1604774
Lag 500                          0.1604094                      0.2063094
```

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Lag 1000                         0.1703454                      0.2249688
Lag 5000                         0.1859265                      0.1911673
         traittarsus.1:traitbwt.1.units traitbwt.1:traitbwt.1.units
Lag 0                        -0.7822168                  -0.6444049
Lag 100                      -0.6561709                  -0.5391921
Lag 500                      -0.4297448                  -0.3429426
Lag 1000                     -0.3378405                  -0.2744658
Lag 5000                     -0.1812141                  -0.1591715
         traittarsus.2:traitbwt.1.units traitbwt.2:traitbwt.1.units
Lag 0                         0.1003793                   0.1067549
Lag 100                       0.1314503                   0.1404067
Lag 500                       0.1658186                   0.1981668
Lag 1000                      0.1899850                   0.2354607
Lag 5000                      0.2090708                   0.1964048
         traittarsus.1:traittarsus.2.units traitbwt.1:traittarsus.2.units
Lag 0                            0.1247101                      0.1003793
Lag 100                          0.1426212                      0.1314503
Lag 500                          0.1604094                      0.1658186
Lag 1000                         0.1703454                      0.1899850
Lag 5000                         0.1859265                      0.2090708
         traittarsus.2:traittarsus.2.units traitbwt.2:traittarsus.2.units
Lag 0                          -0.09677793                    -0.12847847
Lag 100                        -0.06212434                    -0.10051402
Lag 500                        -0.01671120                    -0.07130994
Lag 1000                       -0.07460059                    -0.11790351
Lag 5000                       -0.16171357                    -0.21125583
         traittarsus.1:traitbwt.2.units traitbwt.1:traitbwt.2.units
Lag 0                         0.1399193                   0.1067549
Lag 100                       0.1604774                   0.1404067
Lag 500                       0.2063094                   0.1981668
Lag 1000                      0.2249688                   0.2354607
Lag 5000                      0.1911673                   0.1964048
         traittarsus.2:traitbwt.2.units traitbwt.2:traitbwt.2.units
```

```
Lag 0                       -0.12847847                 -0.10947233
Lag 100                     -0.10051402                 -0.09309607
Lag 500                     -0.07130994                 -0.08545450
Lag 1000                    -0.11790351                 -0.11149356
Lag 5000                    -0.21125583                 -0.23203853

, , traitbwt.1:traitbwt.1.animal

         traittarsus.1:traittarsus.1.animal traitbwt.1:traittarsus.1.animal
Lag 0                            0.23164362                      0.70010050
Lag 100                          0.18054608                      0.54456316
Lag 500                          0.08781934                      0.30301892
Lag 1000                         0.03769032                      0.17531595
Lag 5000                         0.09013727                      0.08812775
         traittarsus.2:traittarsus.1.animal traitbwt.2:traittarsus.1.animal
Lag 0                            0.09679049                     0.329994492
Lag 100                          0.07358032                     0.280145064
Lag 500                          0.03161374                     0.197610680
Lag 1000                         0.07044623                     0.170452855
Lag 5000                         0.09611101                     0.004847697
         traittarsus.1:traitbwt.1.animal traitbwt.1:traitbwt.1.animal
Lag 0                         0.70010050                    1.0000000
Lag 100                       0.54456316                    0.6856952
Lag 500                       0.30301892                    0.3598203
Lag 1000                      0.17531595                    0.2634115
Lag 5000                      0.08812775                    0.0581774
         traittarsus.2:traitbwt.1.animal traitbwt.2:traitbwt.1.animal
Lag 0                          0.2789729                   0.50673141
Lag 100                        0.2383906                   0.37724913
Lag 500                        0.1850306                   0.26913927
Lag 1000                       0.1760392                   0.21403804
Lag 5000                       0.1959228                   0.08822723
         traittarsus.1:traittarsus.2.animal traitbwt.1:traittarsus.2.animal
```

```
Lag 0                              0.09679049                       0.2789729
Lag 100                            0.07358032                       0.2383906
Lag 500                            0.03161374                       0.1850306
Lag 1000                           0.07044623                       0.1760392
Lag 5000                           0.09611101                       0.1959228
         traittarsus.2:traittarsus.2.animal traitbwt.2:traittarsus.2.animal
Lag 0                              0.10548333                      0.17131088
Lag 100                            0.08666667                      0.15141502
Lag 500                            0.03855034                      0.12592562
Lag 1000                           0.09753802                      0.15461525
Lag 5000                           0.05868589                      0.07881607
         traittarsus.1:traitbwt.2.animal traitbwt.1:traitbwt.2.animal
Lag 0                        0.329994492                   0.50673141
Lag 100                      0.280145064                   0.37724913
Lag 500                      0.197610680                   0.26913927
Lag 1000                     0.170452855                   0.21403804
Lag 5000                     0.004847697                   0.08822723
         traittarsus.2:traitbwt.2.animal traitbwt.2:traitbwt.2.animal
Lag 0                         0.17131088                   0.21046169
Lag 100                       0.15141502                   0.17525516
Lag 500                       0.12592562                   0.17738787
Lag 1000                      0.15461525                   0.17597147
Lag 5000                      0.07881607                   0.08328384
         traittarsus.1.byear traitbwt.1.byear traittarsus.2.byear
Lag 0            0.065188114     -0.054239888       -0.0315843380
Lag 100          0.038096586     -0.064724456       -0.0570202816
Lag 500         -0.002027739      0.020824115        0.0009269064
Lag 1000         0.057546907      0.008429484       -0.0456402525
Lag 5000         0.105389029      0.003598701        0.0158576632
         traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother
Lag 0         -0.02489988          0.063535708      -0.301057181
Lag 100       -0.02027214          0.044670327      -0.205303237
Lag 500       -0.01893478          0.000885945      -0.083381850
```

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Lag 1000      -0.01593842          -0.053672083       -0.098869582
Lag 5000      -0.06322669           0.022199101        0.007755258
         traittarsus.2.mother traitbwt.2.mother
Lag 0              0.02830176       -0.06829043
Lag 100            0.01508424       -0.03965583
Lag 500            0.07970255       -0.07134929
Lag 1000           0.03715760       -0.03341572
Lag 5000           0.05894613       -0.03420041
         traittarsus.1:traittarsus.1.units traitbwt.1:traittarsus.1.units
Lag 0                         -0.224526532                      -0.57857216
Lag 100                       -0.156949752                      -0.45706691
Lag 500                       -0.038181523                      -0.25766540
Lag 1000                      -0.006974297                      -0.17163469
Lag 5000                      -0.082791880                      -0.06775113
         traittarsus.2:traittarsus.1.units traitbwt.2:traittarsus.1.units
Lag 0                           0.08095300                       0.11864383
Lag 100                         0.08975567                       0.13271891
Lag 500                         0.10744809                       0.16596526
Lag 1000                        0.10586708                       0.15987797
Lag 5000                        0.11020681                       0.08507017
         traittarsus.1:traitbwt.1.units traitbwt.1:traitbwt.1.units
Lag 0                       -0.57857216                 -0.72140390
Lag 100                     -0.45706691                 -0.56413893
Lag 500                     -0.25766540                 -0.34043397
Lag 1000                    -0.17163469                 -0.22135712
Lag 5000                    -0.06775113                 -0.03117589
         traittarsus.2:traitbwt.1.units traitbwt.2:traitbwt.1.units
Lag 0                         0.1206260                  0.15466547
Lag 100                       0.1358748                  0.17988396
Lag 500                       0.1545988                  0.21095632
Lag 1000                      0.1778949                  0.23064318
Lag 5000                      0.1189483                  0.08708938
         traittarsus.1:traittarsus.2.units traitbwt.1:traittarsus.2.units
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Lag 0                           0.08095300                      0.1206260
Lag 100                         0.08975567                      0.1358748
Lag 500                         0.10744809                      0.1545988
Lag 1000                        0.10586708                      0.1778949
Lag 5000                        0.11020681                      0.1189483
         traittarsus.2:traittarsus.2.units traitbwt.2:traittarsus.2.units
Lag 0                          -0.11346055                     -0.1672807
Lag 100                        -0.08013985                     -0.1375357
Lag 500                        -0.05850422                     -0.1306059
Lag 1000                       -0.11497643                     -0.1592872
Lag 5000                       -0.07297426                     -0.0658664
         traittarsus.1:traitbwt.2.units traitbwt.1:traitbwt.2.units
Lag 0                        0.11864383                  0.15466547
Lag 100                      0.13271891                  0.17988396
Lag 500                      0.16596526                  0.21095632
Lag 1000                     0.15987797                  0.23064318
Lag 5000                     0.08507017                  0.08708938
         traittarsus.2:traitbwt.2.units traitbwt.2:traitbwt.2.units
Lag 0                        -0.1672807                  -0.1878114
Lag 100                      -0.1375357                  -0.1655553
Lag 500                      -0.1306059                  -0.1703498
Lag 1000                     -0.1592872                  -0.1664878
Lag 5000                     -0.0658664                  -0.0614103

, , traittarsus.2:traitbwt.1.animal

         traittarsus.1:traittarsus.1.animal traitbwt.1:traittarsus.1.animal
Lag 0                            0.43711841                       0.4680554
Lag 100                          0.38614287                       0.3822935
Lag 500                          0.32973015                       0.2828059
Lag 1000                         0.30898433                       0.3053279
Lag 5000                         0.06068506                       0.1038801
         traittarsus.2:traittarsus.1.animal traitbwt.2:traittarsus.1.animal
```

```
Lag 0                            0.71265304                       0.59763628
Lag 100                          0.64495665                       0.53517485
Lag 500                          0.56187680                       0.46435370
Lag 1000                         0.52770068                       0.43493174
Lag 5000                        -0.04596197                      -0.09919957
         traittarsus.1:traitbwt.1.animal traitbwt.1:traitbwt.1.animal
Lag 0                          0.4680554                   0.27897287
Lag 100                        0.3822935                   0.24804717
Lag 500                        0.2828059                   0.18131034
Lag 1000                       0.3053279                   0.20383689
Lag 5000                       0.1038801                   0.07466278
         traittarsus.2:traitbwt.1.animal traitbwt.2:traitbwt.1.animal
Lag 0                         1.00000000                   0.75320258
Lag 100                       0.84412396                   0.63847339
Lag 500                       0.63408467                   0.47179404
Lag 1000                      0.55041345                   0.40200369
Lag 5000                      0.07989653                   0.02863099
         traittarsus.1:traittarsus.2.animal traitbwt.1:traittarsus.2.animal
Lag 0                            0.71265304                      1.00000000
Lag 100                          0.64495665                      0.84412396
Lag 500                          0.56187680                      0.63408467
Lag 1000                         0.52770068                      0.55041345
Lag 5000                        -0.04596197                      0.07989653
         traittarsus.2:traittarsus.2.animal traitbwt.2:traittarsus.2.animal
Lag 0                            0.39609257                      0.50085427
Lag 100                          0.37249703                      0.45415166
Lag 500                          0.36147616                      0.41592880
Lag 1000                         0.38702161                      0.40262387
Lag 5000                         0.05902071                      0.05027704
         traittarsus.1:traitbwt.2.animal traitbwt.1:traitbwt.2.animal
Lag 0                         0.59763628                   0.75320258
Lag 100                       0.53517485                   0.63847339
Lag 500                       0.46435370                   0.47179404
```

```
Lag 1000                      0.43493174                   0.40200369
Lag 5000                     -0.09919957                   0.02863099
         traittarsus.2:traitbwt.2.animal traitbwt.2:traitbwt.2.animal
Lag 0                         0.50085427                   0.47574281
Lag 100                       0.45415166                   0.42373764
Lag 500                       0.41592880                   0.36577921
Lag 1000                      0.40262387                   0.31479935
Lag 5000                      0.05027704                   0.04228229
         traittarsus.1.byear traitbwt.1.byear traittarsus.2.byear
Lag 0            0.029421346      0.01370326          0.08861601
Lag 100          0.024425366      0.01320865          0.06508810
Lag 500          0.050837464      0.03060238          0.05880699
Lag 1000         0.065685010      0.04013922          0.02624809
Lag 5000        -0.006279369      0.01390888          0.06953734
         traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother
Lag 0         -0.06566102          0.010266822      -0.002921727
Lag 100       -0.05957647          0.001133316      -0.025849735
Lag 500       -0.03310752         -0.035302602      -0.011049599
Lag 1000      -0.01325750         -0.005132729      -0.030094999
Lag 5000       0.07737072          0.051936326       0.028222378
         traittarsus.2.mother traitbwt.2.mother
Lag 0             -0.01173970       0.004891297
Lag 100           -0.01984404       0.001495609
Lag 500           -0.01047992       0.019305497
Lag 1000          -0.06166849       0.035361493
Lag 5000          -0.03572076       0.037357859
         traittarsus.1:traittarsus.1.units traitbwt.1:traittarsus.1.units
Lag 0                           -0.3729388                     -0.3850991
Lag 100                         -0.3393916                     -0.3381615
Lag 500                         -0.2662669                     -0.2603097
Lag 1000                        -0.2581177                     -0.2862286
Lag 5000                        -0.1138844                     -0.1255711
         traittarsus.2:traittarsus.1.units traitbwt.2:traittarsus.1.units
```

```
Lag 0                          0.1304165                        0.1778597
Lag 100                        0.1523428                        0.1937314
Lag 500                        0.1726064                        0.2144724
Lag 1000                       0.1844905                        0.2275146
Lag 5000                       0.1876933                        0.1730132
         traittarsus.1:traitbwt.1.units traitbwt.1:traitbwt.1.units
Lag 0                       -0.3850991                  -0.2793636
Lag 100                     -0.3381615                  -0.2451230
Lag 500                     -0.2603097                  -0.1889420
Lag 1000                    -0.2862286                  -0.2310740
Lag 5000                    -0.1255711                  -0.1098246
         traittarsus.2:traitbwt.1.units traitbwt.2:traitbwt.1.units
Lag 0                        0.1142625                   0.1618783
Lag 100                      0.1516538                   0.1886145
Lag 500                      0.1942499                   0.2259939
Lag 1000                     0.1947749                   0.2314168
Lag 5000                     0.1938069                   0.1610221
         traittarsus.1:traittarsus.2.units traitbwt.1:traittarsus.2.units
Lag 0                          0.1304165                        0.1142625
Lag 100                        0.1523428                        0.1516538
Lag 500                        0.1726064                        0.1942499
Lag 1000                       0.1844905                        0.1947749
Lag 5000                       0.1876933                        0.1938069
         traittarsus.2:traittarsus.2.units traitbwt.2:traittarsus.2.units
Lag 0                        -0.41858410                      -0.47291409
Lag 100                      -0.40815749                      -0.45309828
Lag 500                      -0.38612479                      -0.40783101
Lag 1000                     -0.40349965                      -0.40278702
Lag 5000                     -0.06617356                      -0.06076514
         traittarsus.1:traitbwt.2.units traitbwt.1:traitbwt.2.units
Lag 0                        0.1778597                   0.1618783
Lag 100                      0.1937314                   0.1886145
Lag 500                      0.2144724                   0.2259939
```

```
Lag 1000                   0.2275146                  0.2314168
Lag 5000                   0.1730132                  0.1610221
         traittarsus.2:traitbwt.2.units traitbwt.2:traitbwt.2.units
Lag 0                    -0.47291409                 -0.4396042
Lag 100                  -0.45309828                 -0.4158969
Lag 500                  -0.40783101                 -0.3577962
Lag 1000                 -0.40278702                 -0.3301300
Lag 5000                 -0.06076514                 -0.0490055


, , traitbwt.2:traitbwt.1.animal


         traittarsus.1:traittarsus.1.animal traitbwt.1:traittarsus.1.animal
Lag 0                            0.23631479                      0.42935174
Lag 100                          0.19631829                      0.33111043
Lag 500                          0.13140023                      0.20166811
Lag 1000                         0.13084790                      0.23051272
Lag 5000                        -0.05046358                      0.04857134
         traittarsus.2:traittarsus.1.animal traitbwt.2:traittarsus.1.animal
Lag 0                             0.4651159                       0.6478170
Lag 100                           0.4250027                       0.5751741
Lag 500                           0.3644232                       0.4605468
Lag 1000                          0.3695356                       0.4130944
Lag 5000                         -0.0748654                      -0.1705451
         traittarsus.1:traitbwt.1.animal traitbwt.1:traitbwt.1.animal
Lag 0                         0.42935174                   0.50673141
Lag 100                       0.33111043                   0.36623376
Lag 500                       0.20166811                   0.24599792
Lag 1000                      0.23051272                   0.26598499
Lag 5000                      0.04857134                   0.06879203
         traittarsus.2:traitbwt.1.animal traitbwt.2:traitbwt.1.animal
Lag 0                         0.75320258                   1.00000000
Lag 100                       0.64643730                   0.80429897
Lag 500                       0.48359147                   0.55454840
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Lag 1000                      0.43668798                   0.44468678
Lag 5000                      0.08606661                  -0.01807979
         traittarsus.1:traittarsus.2.animal traitbwt.1:traittarsus.2.animal
Lag 0                             0.4651159                      0.75320258
Lag 100                           0.4250027                      0.64643730
Lag 500                           0.3644232                      0.48359147
Lag 1000                          0.3695356                      0.43668798
Lag 5000                         -0.0748654                      0.08606661
         traittarsus.2:traittarsus.2.animal traitbwt.2:traittarsus.2.animal
Lag 0                            0.35637772                     0.518702070
Lag 100                          0.34579510                     0.481108274
Lag 500                          0.32649959                     0.434843612
Lag 1000                         0.37931051                     0.436821292
Lag 5000                         0.03852246                     0.006399124
         traittarsus.1:traitbwt.2.animal traitbwt.1:traitbwt.2.animal
Lag 0                          0.6478170                   1.00000000
Lag 100                        0.5751741                   0.80429897
Lag 500                        0.4605468                   0.55454840
Lag 1000                       0.4130944                   0.44468678
Lag 5000                      -0.1705451                  -0.01807979
         traittarsus.2:traitbwt.2.animal traitbwt.2:traitbwt.2.animal
Lag 0                        0.518702070                   0.64907876
Lag 100                      0.481108274                   0.56161598
Lag 500                      0.434843612                   0.47984513
Lag 1000                     0.436821292                   0.40938531
Lag 5000                     0.006399124                  -0.01977366
         traittarsus.1.byear traitbwt.1.byear traittarsus.2.byear
Lag 0            0.034800266      0.007431509          0.10446126
Lag 100          0.051936557     -0.001493245          0.08007660
Lag 500          0.071129943      0.067797207          0.05478615
Lag 1000         0.103624443      0.063225351          0.01489821
Lag 5000        -0.000397122      0.008471637         -0.01350094
         traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother
```

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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
```

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Lag 1000                  0.19253125                 0.2644751
Lag 5000                  0.13671344                 0.1087463
         traittarsus.1:traittarsus.2.units traitbwt.1:traittarsus.2.units
Lag 0                        0.06808542                     0.09800038
Lag 100                      0.08333997                     0.12840120
Lag 500                      0.11004808                     0.17479984
Lag 1000                     0.13239890                     0.19253125
Lag 5000                     0.14121855                     0.13671344
         traittarsus.2:traittarsus.2.units traitbwt.2:traittarsus.2.units
Lag 0                       -0.38430674                    -0.49584021
Lag 100                     -0.36892511                    -0.47162690
Lag 500                     -0.35875583                    -0.43506761
Lag 1000                    -0.38190122                    -0.42199356
Lag 5000                    -0.04674851                    -0.01287201
         traittarsus.1:traitbwt.2.units traitbwt.1:traitbwt.2.units
Lag 0                         0.1473359                   0.1786089
Lag 100                       0.1644163                   0.2150929
Lag 500                       0.1967466                   0.2654006
Lag 1000                      0.2087490                   0.2644751
Lag 5000                      0.1213850                   0.1087463
         traittarsus.2:traitbwt.2.units traitbwt.2:traitbwt.2.units
Lag 0                       -0.49584021                 -0.56988609
Lag 100                     -0.47162690                 -0.53124887
Lag 500                     -0.43506761                 -0.45896948
Lag 1000                    -0.42199356                 -0.40139643
Lag 5000                    -0.01287201                  0.01366036

, , traittarsus.1:traittarsus.2.animal

         traittarsus.1:traittarsus.1.animal traitbwt.1:traittarsus.1.animal
Lag 0                           0.682164176                      0.38634307
Lag 100                         0.591700877                      0.34935277
Lag 500                         0.451559860                      0.32828629
```

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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
```

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Lag 0                          0.78206164                   0.46511587
Lag 100                        0.70110541                   0.41849123
Lag 500                        0.56910648                   0.35510793
Lag 1000                       0.44347532                   0.27846473
Lag 5000                       0.01712343                   0.08826768
         traittarsus.2:traitbwt.2.animal traitbwt.2:traitbwt.2.animal
Lag 0                          0.5613010                    0.4107260
Lag 100                        0.5141865                    0.3793894
Lag 500                        0.4619296                    0.3449678
Lag 1000                       0.3816713                    0.2731469
Lag 5000                       0.1489578                    0.1431489
         traittarsus.1.byear traitbwt.1.byear traittarsus.2.byear
Lag 0             0.01620495       0.04295234         0.052223393
Lag 100           0.02029711       0.05648775         0.034069858
Lag 500           0.04765917       0.03285861         0.007554307
Lag 1000          0.03767470       0.07587887         0.003191847
Lag 5000         -0.02249363       0.05599353         0.040862718
         traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother
Lag 0         -0.04161269         -0.102952660        0.04055573
Lag 100       -0.05474586         -0.077407539        0.03752540
Lag 500       -0.01536913         -0.009985327        0.02041393
Lag 1000      -0.02242552         -0.016880479        0.02095844
Lag 5000       0.05382429          0.093039192       -0.03853343
         traittarsus.2.mother traitbwt.2.mother
Lag 0             -0.15988076        0.11172969
Lag 100           -0.14920373        0.08235912
Lag 500           -0.10669450        0.07860308
Lag 1000          -0.09563279        0.04882603
Lag 5000          -0.03477033        0.03882608
         traittarsus.1:traittarsus.1.units traitbwt.1:traittarsus.1.units
Lag 0                          -0.48510213                    -0.35513667
Lag 100                        -0.43884380                    -0.32128424
Lag 500                        -0.37005382                    -0.29419691
```

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Lag 1000                       -0.29875897                    -0.25541065
Lag 5000                       -0.06651357                    -0.08518695
         traittarsus.2:traittarsus.1.units traitbwt.2:traittarsus.1.units
Lag 0                            0.1906441                      0.2159001
Lag 100                          0.2109187                      0.2292953
Lag 500                          0.2433902                      0.2525070
Lag 1000                         0.2670207                      0.2801991
Lag 5000                         0.2055428                      0.2202544
         traittarsus.1:traitbwt.1.units traitbwt.1:traitbwt.1.units
Lag 0                       -0.35513667                 -0.16353731
Lag 100                     -0.32128424                 -0.14737332
Lag 500                     -0.29419691                 -0.14406290
Lag 1000                    -0.25541065                 -0.15449858
Lag 5000                    -0.08518695                 -0.09726346
         traittarsus.2:traitbwt.1.units traitbwt.2:traitbwt.1.units
Lag 0                         0.1588923                   0.1751169
Lag 100                       0.1763493                   0.1863279
Lag 500                       0.2035612                   0.2019259
Lag 1000                      0.2408050                   0.2434815
Lag 5000                      0.2188271                   0.2190020
         traittarsus.1:traittarsus.2.units traitbwt.1:traittarsus.2.units
Lag 0                            0.1906441                      0.1588923
Lag 100                          0.2109187                      0.1763493
Lag 500                          0.2433902                      0.2035612
Lag 1000                         0.2670207                      0.2408050
Lag 5000                         0.2055428                      0.2188271
         traittarsus.2:traittarsus.2.units traitbwt.2:traittarsus.2.units
Lag 0                           -0.5600992                     -0.5208193
Lag 100                         -0.5263626                     -0.5010452
Lag 500                         -0.4620756                     -0.4434018
Lag 1000                        -0.4037773                     -0.3729971
Lag 5000                        -0.1493219                     -0.1529356
         traittarsus.1:traitbwt.2.units traitbwt.1:traitbwt.2.units
```

```
Lag 0                    0.2159001                   0.1751169
Lag 100                  0.2292953                   0.1863279
Lag 500                  0.2525070                   0.2019259
Lag 1000                 0.2801991                   0.2434815
Lag 5000                 0.2202544                   0.2190020
         traittarsus.2:traitbwt.2.units traitbwt.2:traitbwt.2.units
Lag 0                   -0.5208193                  -0.3939711
Lag 100                 -0.5010452                  -0.3851102
Lag 500                 -0.4434018                  -0.3487254
Lag 1000                -0.3729971                  -0.2846600
Lag 5000                -0.1529356                  -0.1449719

, , traitbwt.1:traittarsus.2.animal

         traittarsus.1:traittarsus.1.animal traitbwt.1:traittarsus.1.animal
Lag 0                            0.43711841                       0.4680554
Lag 100                          0.38614287                       0.3822935
Lag 500                          0.32973015                       0.2828059
Lag 1000                         0.30898433                       0.3053279
Lag 5000                         0.06068506                       0.1038801
         traittarsus.2:traittarsus.1.animal traitbwt.2:traittarsus.1.animal
Lag 0                            0.71265304                      0.59763628
Lag 100                          0.64495665                      0.53517485
Lag 500                          0.56187680                      0.46435370
Lag 1000                         0.52770068                      0.43493174
Lag 5000                        -0.04596197                     -0.09919957
         traittarsus.1:traitbwt.1.animal traitbwt.1:traitbwt.1.animal
Lag 0                          0.4680554                   0.27897287
Lag 100                        0.3822935                   0.24804717
Lag 500                        0.2828059                   0.18131034
Lag 1000                       0.3053279                   0.20383689
Lag 5000                       0.1038801                   0.07466278
         traittarsus.2:traitbwt.1.animal traitbwt.2:traitbwt.1.animal
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Lag 0                      1.00000000                   0.75320258
Lag 100                    0.84412396                   0.63847339
Lag 500                    0.63408467                   0.47179404
Lag 1000                   0.55041345                   0.40200369
Lag 5000                   0.07989653                   0.02863099
         traittarsus.1:traittarsus.2.animal traitbwt.1:traittarsus.2.animal
Lag 0                             0.71265304                      1.00000000
Lag 100                           0.64495665                      0.84412396
Lag 500                           0.56187680                      0.63408467
Lag 1000                          0.52770068                      0.55041345
Lag 5000                         -0.04596197                      0.07989653
         traittarsus.2:traittarsus.2.animal traitbwt.2:traittarsus.2.animal
Lag 0                             0.39609257                      0.50085427
Lag 100                           0.37249703                      0.45415166
Lag 500                           0.36147616                      0.41592880
Lag 1000                          0.38702161                      0.40262387
Lag 5000                          0.05902071                      0.05027704
         traittarsus.1:traitbwt.2.animal traitbwt.1:traitbwt.2.animal
Lag 0                         0.59763628                   0.75320258
Lag 100                       0.53517485                   0.63847339
Lag 500                       0.46435370                   0.47179404
Lag 1000                      0.43493174                   0.40200369
Lag 5000                     -0.09919957                   0.02863099
         traittarsus.2:traitbwt.2.animal traitbwt.2:traitbwt.2.animal
Lag 0                         0.50085427                   0.47574281
Lag 100                       0.45415166                   0.42373764
Lag 500                       0.41592880                   0.36577921
Lag 1000                      0.40262387                   0.31479935
Lag 5000                      0.05027704                   0.04228229
         traittarsus.1.byear traitbwt.1.byear traittarsus.2.byear
Lag 0            0.029421346       0.01370326          0.08861601
Lag 100          0.024425366       0.01320865          0.06508810
Lag 500          0.050837464       0.03060238          0.05880699
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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
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```
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
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Lag 0                         0.107806440                      0.09660116
Lag 100                       0.063335645                      0.07671143
Lag 500                       0.015199121                      0.08067887
Lag 1000                     -0.004286261                      0.05833877
Lag 5000                     -0.070723679                     -0.04217947
         traittarsus.2:traittarsus.1.animal traitbwt.2:traittarsus.1.animal
Lag 0                             0.5942621                       0.5635407
Lag 100                           0.5173844                       0.5077019
Lag 500                           0.4100415                       0.4261910
Lag 1000                          0.3053499                       0.3088610
Lag 5000                         -0.2062339                      -0.1851005
         traittarsus.1:traitbwt.1.animal traitbwt.1:traitbwt.1.animal
Lag 0                         0.09660116                   0.10548333
Lag 100                       0.07671143                   0.09974202
Lag 500                       0.08067887                   0.11354731
Lag 1000                      0.05833877                   0.12159525
Lag 5000                     -0.04217947                  -0.06338610
         traittarsus.2:traitbwt.1.animal traitbwt.2:traitbwt.1.animal
Lag 0                          0.3960926                    0.3563777
Lag 100                        0.3697695                    0.3333969
Lag 500                        0.3480333                    0.3176505
Lag 1000                       0.2823012                    0.2658600
Lag 5000                      -0.2062348                   -0.1460308
         traittarsus.1:traittarsus.2.animal traitbwt.1:traittarsus.2.animal
Lag 0                             0.5942621                       0.3960926
Lag 100                           0.5173844                       0.3697695
Lag 500                           0.4100415                       0.3480333
Lag 1000                          0.3053499                       0.2823012
Lag 5000                         -0.2062339                      -0.2062348
         traittarsus.2:traittarsus.2.animal traitbwt.2:traittarsus.2.animal
Lag 0                            1.00000000                      0.89913093
Lag 100                          0.90510783                      0.83322028
Lag 500                          0.73781155                      0.70412544
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```
Lag 1000                         0.57269345                      0.54745411
Lag 5000                        -0.03830606                     -0.09250669
         traittarsus.1:traitbwt.2.animal traitbwt.1:traitbwt.2.animal
Lag 0                          0.5635407                    0.3563777
Lag 100                        0.5077019                    0.3333969
Lag 500                        0.4261910                    0.3176505
Lag 1000                       0.3088610                    0.2658600
Lag 5000                      -0.1851005                   -0.1460308
         traittarsus.2:traitbwt.2.animal traitbwt.2:traitbwt.2.animal
Lag 0                         0.89913093                    0.6844205
Lag 100                       0.83322028                    0.6434324
Lag 500                       0.70412544                    0.5640206
Lag 1000                      0.54745411                    0.4452587
Lag 5000                     -0.09250669                   -0.0996112
         traittarsus.1.byear traitbwt.1.byear traittarsus.2.byear
Lag 0            0.035961574     -0.017469135         0.007171364
Lag 100          0.026817555     -0.002104493         0.011633070
Lag 500          0.008446146     -0.011130916         0.013837207
Lag 1000         0.029054326      0.040567400         0.023793648
Lag 5000        -0.032575030      0.020439004        -0.049218434
         traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother
Lag 0         -0.08333086           0.04651404       -0.06375729
Lag 100       -0.08053153           0.06577446       -0.05659105
Lag 500       -0.03847864           0.11200938       -0.07300512
Lag 1000      -0.04249559           0.08134977       -0.07101148
Lag 5000       0.07016400           0.02226530        0.03188352
         traittarsus.2.mother traitbwt.2.mother
Lag 0             -0.34477064        0.15871038
Lag 100           -0.31220276        0.12040861
Lag 500           -0.20777383        0.08824805
Lag 1000          -0.12481403        0.05105578
Lag 5000           0.01048624        0.01454861
         traittarsus.1:traittarsus.1.units traitbwt.1:traittarsus.1.units
```

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Lag 0                          -0.10376953                    -0.10398125
Lag 100                        -0.07294547                    -0.07699566
Lag 500                        -0.06977230                    -0.08979287
Lag 1000                       -0.03903802                    -0.06150263
Lag 5000                        0.09531506                     0.08613972
         traittarsus.2:traittarsus.1.units traitbwt.2:traittarsus.1.units
Lag 0                           0.18812698                     0.21480017
Lag 100                         0.19528250                     0.21914991
Lag 500                         0.19556551                     0.21256430
Lag 1000                        0.18892755                     0.20764610
Lag 5000                        0.06665558                     0.07468684
         traittarsus.1:traitbwt.1.units traitbwt.1:traitbwt.1.units
Lag 0                       -0.10398125                 -0.10182068
Lag 100                     -0.07699566                 -0.08777589
Lag 500                     -0.08979287                 -0.09511315
Lag 1000                    -0.06150263                 -0.09765668
Lag 5000                     0.08613972                  0.05634093
         traittarsus.2:traitbwt.1.units traitbwt.2:traitbwt.1.units
Lag 0                        0.22270138                  0.23393547
Lag 100                      0.22287169                  0.23382912
Lag 500                      0.20351827                  0.21079497
Lag 1000                     0.20537971                  0.21383439
Lag 5000                     0.03798515                  0.03641653
         traittarsus.1:traittarsus.2.units traitbwt.1:traittarsus.2.units
Lag 0                           0.18812698                     0.22270138
Lag 100                         0.19528250                     0.22287169
Lag 500                         0.19556551                     0.20351827
Lag 1000                        0.18892755                     0.20537971
Lag 5000                        0.06665558                     0.03798515
         traittarsus.2:traittarsus.2.units traitbwt.2:traittarsus.2.units
Lag 0                           -0.9107369                    -0.84107771
Lag 100                         -0.8633544                    -0.80717702
Lag 500                         -0.7252004                    -0.68217338
```

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Lag 1000                      -0.5917870                   -0.54946518
Lag 5000                       0.0476902                    0.09830838
         traittarsus.1:traitbwt.2.units traitbwt.1:traitbwt.2.units
Lag 0                       0.21480017                  0.23393547
Lag 100                     0.21914991                  0.23382912
Lag 500                     0.21256430                  0.21079497
Lag 1000                    0.20764610                  0.21383439
Lag 5000                    0.07468684                  0.03641653
         traittarsus.2:traitbwt.2.units traitbwt.2:traitbwt.2.units
Lag 0                      -0.84107771                  -0.6791085
Lag 100                    -0.80717702                  -0.6539764
Lag 500                    -0.68217338                  -0.5583969
Lag 1000                   -0.54946518                  -0.4464232
Lag 5000                    0.09830838                   0.1028304

, , traitbwt.2:traittarsus.2.animal

         traittarsus.1:traittarsus.1.animal traitbwt.1:traittarsus.1.animal
Lag 0                            0.12397199                      0.14997594
Lag 100                          0.08643519                      0.11314881
Lag 500                          0.03605225                      0.09323271
Lag 1000                         0.03084094                      0.10586940
Lag 5000                        -0.09632022                     -0.03936224
         traittarsus.2:traittarsus.1.animal traitbwt.2:traittarsus.1.animal
Lag 0                             0.5613010                       0.6729793
Lag 100                           0.5033508                       0.6010903
Lag 500                           0.4274531                       0.5133373
Lag 1000                          0.3517565                       0.4086869
Lag 5000                         -0.1677216                      -0.1581302
         traittarsus.1:traitbwt.1.animal traitbwt.1:traitbwt.1.animal
Lag 0                         0.14997594                   0.17131088
Lag 100                       0.11314881                   0.15721379
Lag 500                       0.09323271                   0.15933093
```

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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
```

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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
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Lag 1000                  -0.1076860                 -0.15700540
Lag 5000                   0.0712461                  0.01799705
         traittarsus.2:traitbwt.1.units traitbwt.2:traitbwt.1.units
Lag 0                     0.21778240                  0.25816273
Lag 100                   0.22684710                  0.26502282
Lag 500                   0.20506975                  0.23751874
Lag 1000                  0.19012136                  0.21960899
Lag 5000                  0.02816484                  0.03038383
         traittarsus.1:traittarsus.2.units traitbwt.1:traittarsus.2.units
Lag 0                        0.18051752                     0.21778240
Lag 100                      0.18953377                     0.22684710
Lag 500                      0.17920764                     0.20506975
Lag 1000                     0.16794260                     0.19012136
Lag 5000                     0.04389169                     0.02816484
         traittarsus.2:traittarsus.2.units traitbwt.2:traittarsus.2.units
Lag 0                     -0.8750125593                    -0.93853010
Lag 100                   -0.8368578282                    -0.89227332
Lag 500                   -0.7287281819                    -0.75764556
Lag 1000                  -0.6175608959                    -0.62307537
Lag 5000                  -0.0008665459                     0.04348967
         traittarsus.1:traitbwt.2.units traitbwt.1:traitbwt.2.units
Lag 0                     0.23807593                  0.25816273
Lag 100                   0.24534120                  0.26502282
Lag 500                   0.22900261                  0.23751874
Lag 1000                  0.21104881                  0.21960899
Lag 5000                  0.05181362                  0.03038383
         traittarsus.2:traitbwt.2.units traitbwt.2:traitbwt.2.units
Lag 0                    -0.93853010                 -0.85888343
Lag 100                  -0.89227332                 -0.81357341
Lag 500                  -0.75764556                 -0.67868373
Lag 1000                 -0.62307537                 -0.54366192
Lag 5000                  0.04348967                  0.05718606
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, , traittarsus.1:traitbwt.2.animal

         traittarsus.1:traittarsus.1.animal traitbwt.1:traittarsus.1.animal
Lag 0                            0.51576277                      0.52342220
Lag 100                          0.44159056                      0.43580048
Lag 500                          0.30785687                      0.33037079
Lag 1000                         0.24390874                      0.26926704
Lag 5000                        -0.05005481                      0.04687804
         traittarsus.2:traittarsus.1.animal traitbwt.2:traittarsus.1.animal
Lag 0                           0.782061640                      1.00000000
Lag 100                         0.696299215                      0.87453824
Lag 500                         0.538889846                      0.65219311
Lag 1000                        0.445389577                      0.48957859
Lag 5000                       -0.006519724                      0.01842864
         traittarsus.1:traitbwt.1.animal traitbwt.1:traitbwt.1.animal
Lag 0                         0.52342220                   0.32999449
Lag 100                       0.43580048                   0.28148773
Lag 500                       0.33037079                   0.26589289
Lag 1000                      0.26926704                   0.24323871
Lag 5000                      0.04687804                   0.09890983
         traittarsus.2:traitbwt.1.animal traitbwt.2:traitbwt.1.animal
Lag 0                         0.59763628                    0.6478170
Lag 100                       0.52643466                    0.5573055
Lag 500                       0.44551868                    0.4418750
Lag 1000                      0.37736602                    0.3442054
Lag 5000                      0.08285167                    0.1125165
         traittarsus.1:traittarsus.2.animal traitbwt.1:traittarsus.2.animal
Lag 0                           0.782061640                      0.59763628
Lag 100                         0.696299215                      0.52643466
Lag 500                         0.538889846                      0.44551868
Lag 1000                        0.445389577                      0.37736602
Lag 5000                       -0.006519724                      0.08285167
         traittarsus.2:traittarsus.2.animal traitbwt.2:traittarsus.2.animal
```

```
Lag 0                             0.5635407                       0.6729793
Lag 100                           0.5125673                       0.6052812
Lag 500                           0.4465910                       0.5277439
Lag 1000                          0.4070664                       0.4538221
Lag 5000                          0.1850370                       0.1792542
         traittarsus.1:traitbwt.2.animal traitbwt.1:traitbwt.2.animal
Lag 0                         1.00000000                    0.6478170
Lag 100                       0.87453824                    0.5573055
Lag 500                       0.65219311                    0.4418750
Lag 1000                      0.48957859                    0.3442054
Lag 5000                      0.01842864                    0.1125165
         traittarsus.2:traitbwt.2.animal traitbwt.2:traitbwt.2.animal
Lag 0                          0.6729793                    0.6191252
Lag 100                        0.6052812                    0.5529718
Lag 500                        0.5277439                    0.4729419
Lag 1000                       0.4538221                    0.3884032
Lag 5000                       0.1792542                    0.1542326
         traittarsus.1.byear traitbwt.1.byear traittarsus.2.byear
Lag 0            0.063463728       0.02730871         0.051964042
Lag 100          0.066558472       0.03961464         0.040967359
Lag 500          0.076728186       0.05374642        -0.012930939
Lag 1000         0.100842393       0.09752083        -0.062954038
Lag 5000        -0.006751012       0.04984406         0.002434151
         traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother
Lag 0         -0.09337461           0.02006907       -0.06942502
Lag 100       -0.09001277           0.02763705       -0.07262374
Lag 500       -0.04869538           0.02000750       -0.09505843
Lag 1000      -0.05831890           0.02560894       -0.08617648
Lag 5000       0.04246982           0.06392166       -0.03722137
         traittarsus.2.mother traitbwt.2.mother
Lag 0            -0.026436938         0.04826105
Lag 100          -0.041329867         0.04078039
Lag 500          -0.028290001         0.03056152
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Lag 1000         -0.036326123        0.04300492
Lag 5000         -0.008439906        0.00653221
         traittarsus.1:traittarsus.1.units traitbwt.1:traittarsus.1.units
Lag 0                        -0.3969629895                    -0.44235441
Lag 100                      -0.3457725771                    -0.37788435
Lag 500                      -0.2409128696                    -0.27612777
Lag 1000                     -0.2064627528                    -0.23939733
Lag 5000                     -0.0008284304                    -0.05932951
         traittarsus.2:traittarsus.1.units traitbwt.2:traittarsus.1.units
Lag 0                            0.1332860                      0.1894193
Lag 100                          0.1542105                      0.2129929
Lag 500                          0.1772766                      0.2426247
Lag 1000                         0.1956287                      0.2577964
Lag 5000                         0.1561845                      0.1623293
         traittarsus.1:traitbwt.1.units traitbwt.1:traitbwt.1.units
Lag 0                       -0.44235441                  -0.3300209
Lag 100                     -0.37788435                  -0.2868342
Lag 500                     -0.27612777                  -0.2200427
Lag 1000                    -0.23939733                  -0.2196364
Lag 5000                    -0.05932951                  -0.1105188
         traittarsus.2:traitbwt.1.units traitbwt.2:traitbwt.1.units
Lag 0                         0.1392793                   0.1845588
Lag 100                       0.1618837                   0.2068320
Lag 500                       0.1824833                   0.2322375
Lag 1000                      0.2062851                   0.2545405
Lag 5000                      0.1708879                   0.1679111
         traittarsus.1:traittarsus.2.units traitbwt.1:traittarsus.2.units
Lag 0                            0.1332860                      0.1392793
Lag 100                          0.1542105                      0.1618837
Lag 500                          0.1772766                      0.1824833
Lag 1000                         0.1956287                      0.2062851
Lag 5000                         0.1561845                      0.1708879
         traittarsus.2:traittarsus.2.units traitbwt.2:traittarsus.2.units
```

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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

, , traitbwt.1:traitbwt.2.animal

         traittarsus.1:traittarsus.1.animal traitbwt.1:traittarsus.1.animal
Lag 0                            0.23631479                      0.42935174
Lag 100                          0.19631829                      0.33111043
Lag 500                          0.13140023                      0.20166811
Lag 1000                         0.13084790                      0.23051272
Lag 5000                        -0.05046358                      0.04857134
         traittarsus.2:traittarsus.1.animal traitbwt.2:traittarsus.1.animal
Lag 0                             0.4651159                       0.6478170
Lag 100                           0.4250027                       0.5751741
Lag 500                           0.3644232                       0.4605468
Lag 1000                          0.3695356                       0.4130944
Lag 5000                         -0.0748654                      -0.1705451
         traittarsus.1:traitbwt.1.animal traitbwt.1:traitbwt.1.animal
```

```
Lag 0                     0.42935174                   0.50673141
Lag 100                   0.33111043                   0.36623376
Lag 500                   0.20166811                   0.24599792
Lag 1000                  0.23051272                   0.26598499
Lag 5000                  0.04857134                   0.06879203
         traittarsus.2:traitbwt.1.animal traitbwt.2:traitbwt.1.animal
Lag 0                     0.75320258                   1.00000000
Lag 100                   0.64643730                   0.80429897
Lag 500                   0.48359147                   0.55454840
Lag 1000                  0.43668798                   0.44468678
Lag 5000                  0.08606661                  -0.01807979
         traittarsus.1:traittarsus.2.animal traitbwt.1:traittarsus.2.animal
Lag 0                              0.4651159                      0.75320258
Lag 100                            0.4250027                      0.64643730
Lag 500                            0.3644232                      0.48359147
Lag 1000                           0.3695356                      0.43668798
Lag 5000                          -0.0748654                      0.08606661
         traittarsus.2:traittarsus.2.animal traitbwt.2:traittarsus.2.animal
Lag 0                             0.35637772                     0.518702070
Lag 100                           0.34579510                     0.481108274
Lag 500                           0.32649959                     0.434843612
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
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Lag 1000                     0.436821292                   0.40938531
Lag 5000                     0.006399124                  -0.01977366
         traittarsus.1.byear traitbwt.1.byear traittarsus.2.byear
Lag 0            0.034800266      0.007431509          0.10446126
Lag 100          0.051936557     -0.001493245          0.08007660
Lag 500          0.071129943      0.067797207          0.05478615
Lag 1000         0.103624443      0.063225351          0.01489821
Lag 5000        -0.000397122      0.008471637         -0.01350094
         traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother
Lag 0         -0.08333568          0.100888337       -0.21005355
Lag 100       -0.07762909          0.079323546       -0.17806133
Lag 500       -0.03825641         -0.007478373       -0.11051022
Lag 1000      -0.02784742          0.017077993       -0.10296388
Lag 5000       0.04558001          0.022598106        0.02483781
         traittarsus.2.mother traitbwt.2.mother
Lag 0             0.018470325      -0.095372303
Lag 100          -0.002048636      -0.029630368
Lag 500           0.014260425      -0.034300090
Lag 1000         -0.048567932       0.067004499
Lag 5000         -0.025983993       0.005631837
         traittarsus.1:traittarsus.1.units traitbwt.1:traittarsus.1.units
Lag 0                          -0.25474138                    -0.36301593
Lag 100                        -0.21067390                    -0.29399524
Lag 500                        -0.11042093                    -0.17823668
Lag 1000                       -0.13264168                    -0.21582496
Lag 5000                        0.02716341                    -0.03930422
         traittarsus.2:traittarsus.1.units traitbwt.2:traittarsus.1.units
Lag 0                           0.06808542                      0.1473359
Lag 100                         0.08333997                      0.1644163
Lag 500                         0.11004808                      0.1967466
Lag 1000                        0.13239890                      0.2087490
Lag 5000                        0.14121855                      0.1213850
         traittarsus.1:traitbwt.1.units traitbwt.1:traitbwt.1.units
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Lag 0                  -0.36301593                 -0.39024104
Lag 100                -0.29399524                 -0.30803165
Lag 500                -0.17823668                 -0.22428734
Lag 1000               -0.21582496                 -0.24800908
Lag 5000               -0.03930422                 -0.07900553
         traittarsus.2:traitbwt.1.units traitbwt.2:traitbwt.1.units
Lag 0                   0.09800038                   0.1786089
Lag 100                 0.12840120                   0.2150929
Lag 500                 0.17479984                   0.2654006
Lag 1000                0.19253125                   0.2644751
Lag 5000                0.13671344                   0.1087463
         traittarsus.1:traittarsus.2.units traitbwt.1:traittarsus.2.units
Lag 0                          0.06808542                     0.09800038
Lag 100                        0.08333997                     0.12840120
Lag 500                        0.11004808                     0.17479984
Lag 1000                       0.13239890                     0.19253125
Lag 5000                       0.14121855                     0.13671344
         traittarsus.2:traittarsus.2.units traitbwt.2:traittarsus.2.units
Lag 0                         -0.38430674                    -0.49584021
Lag 100                       -0.36892511                    -0.47162690
Lag 500                       -0.35875583                    -0.43506761
Lag 1000                      -0.38190122                    -0.42199356
Lag 5000                      -0.04674851                    -0.01287201
         traittarsus.1:traitbwt.2.units traitbwt.1:traitbwt.2.units
Lag 0                       0.1473359                   0.1786089
Lag 100                     0.1644163                   0.2150929
Lag 500                     0.1967466                   0.2654006
Lag 1000                    0.2087490                   0.2644751
Lag 5000                    0.1213850                   0.1087463
         traittarsus.2:traitbwt.2.units traitbwt.2:traitbwt.2.units
Lag 0                  -0.49584021                 -0.56988609
Lag 100                -0.47162690                 -0.53124887
Lag 500                -0.43506761                 -0.45896948
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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
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Lag 1000                          0.3517565                       0.3366895
Lag 5000                         -0.1677216                      -0.1140445
         traittarsus.2:traittarsus.2.animal traitbwt.2:traittarsus.2.animal
Lag 0                             0.8991309                      1.00000000
Lag 100                           0.8359176                      0.91646465
Lag 500                           0.7187715                      0.77900191
Lag 1000                          0.5982337                      0.63306113
Lag 5000                          0.0176654                     -0.03136451
         traittarsus.1:traitbwt.2.animal traitbwt.1:traitbwt.2.animal
Lag 0                          0.6729793                   0.51870207
Lag 100                        0.6010903                   0.46669360
Lag 500                        0.5133373                   0.41453930
Lag 1000                       0.4086869                   0.35501264
Lag 5000                      -0.1581302                  -0.07692479
         traittarsus.2:traitbwt.2.animal traitbwt.2:traitbwt.2.animal
Lag 0                         1.00000000                   0.89818763
Lag 100                       0.91646465                   0.82112793
Lag 500                       0.77900191                   0.69592684
Lag 1000                      0.63306113                   0.55065244
Lag 5000                     -0.03136451                  -0.04949222
         traittarsus.1.byear traitbwt.1.byear traittarsus.2.byear
Lag 0             0.05124741      0.001646162          0.04068399
Lag 100           0.04921037      0.008930910          0.03759685
Lag 500           0.03899327      0.015514352          0.02580930
Lag 1000          0.06406637      0.051682789          0.02147033
Lag 5000         -0.01137788      0.015052216         -0.04729885
         traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother
Lag 0         -0.12402916           0.08639137       -0.09704390
Lag 100       -0.10713277           0.09204331       -0.10427670
Lag 500       -0.07124572           0.09145340       -0.11605857
Lag 1000      -0.06554488           0.09437629       -0.10182520
Lag 5000       0.06888625           0.02727995        0.01776003
         traittarsus.2.mother traitbwt.2.mother
```

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Lag 0           -0.15610253        0.09891371
Lag 100         -0.16408367        0.08304541
Lag 500         -0.12517718        0.04261766
Lag 1000        -0.09948987        0.04824881
Lag 5000        -0.01179365       -0.01278893
         traittarsus.1:traittarsus.1.units traitbwt.1:traittarsus.1.units
Lag 0                          -0.14515627                     -0.1467921
Lag 100                        -0.11636785                     -0.1156256
Lag 500                        -0.08159624                     -0.1042741
Lag 1000                       -0.07861755                     -0.1076860
Lag 5000                        0.10186075                      0.0712461
         traittarsus.2:traittarsus.1.units traitbwt.2:traittarsus.1.units
Lag 0                           0.18051752                     0.23807593
Lag 100                         0.18953377                     0.24534120
Lag 500                         0.17920764                     0.22900261
Lag 1000                        0.16794260                     0.21104881
Lag 5000                        0.04389169                     0.05181362
         traittarsus.1:traitbwt.1.units traitbwt.1:traitbwt.1.units
Lag 0                        -0.1467921                 -0.14376430
Lag 100                      -0.1156256                 -0.12366939
Lag 500                      -0.1042741                 -0.12078005
Lag 1000                     -0.1076860                 -0.15700540
Lag 5000                      0.0712461                  0.01799705
         traittarsus.2:traitbwt.1.units traitbwt.2:traitbwt.1.units
Lag 0                        0.21778240                  0.25816273
Lag 100                      0.22684710                  0.26502282
Lag 500                      0.20506975                  0.23751874
Lag 1000                     0.19012136                  0.21960899
Lag 5000                     0.02816484                  0.03038383
         traittarsus.1:traittarsus.2.units traitbwt.1:traittarsus.2.units
Lag 0                           0.18051752                     0.21778240
Lag 100                         0.18953377                     0.22684710
Lag 500                         0.17920764                     0.20506975
```

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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
```

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Lag 1000                       0.3161080                        0.4110850
Lag 5000                      -0.1301409                       -0.1457415
         traittarsus.1:traitbwt.1.animal traitbwt.1:traitbwt.1.animal
Lag 0                       0.14180302                   0.21046169
Lag 100                     0.09666633                   0.16894953
Lag 500                     0.06603768                   0.16336058
Lag 1000                    0.11225922                   0.19977861
Lag 5000                   -0.02765292                   0.02292947
         traittarsus.2:traitbwt.1.animal traitbwt.2:traitbwt.1.animal
Lag 0                       0.47574281                   0.64907876
Lag 100                     0.42046513                   0.55150494
Lag 500                     0.36650261                   0.46465819
Lag 1000                    0.33756450                   0.39404623
Lag 5000                   -0.04573143                  -0.05021868
         traittarsus.1:traittarsus.2.animal traitbwt.1:traittarsus.2.animal
Lag 0                          0.4107260                      0.47574281
Lag 100                        0.3762287                      0.42046513
Lag 500                        0.3541228                      0.36650261
Lag 1000                       0.3161080                      0.33756450
Lag 5000                      -0.1301409                     -0.04573143
         traittarsus.2:traittarsus.2.animal traitbwt.2:traittarsus.2.animal
Lag 0                          0.6844205                      0.89818763
Lag 100                        0.6509791                      0.82577566
Lag 500                        0.5935139                      0.71300098
Lag 1000                       0.5428655                      0.62246323
Lag 5000                       0.0305572                     -0.02000725
         traittarsus.1:traitbwt.2.animal traitbwt.1:traitbwt.2.animal
Lag 0                        0.6191252                   0.64907876
Lag 100                      0.5533278                   0.55150494
Lag 500                      0.4906565                   0.46465819
Lag 1000                     0.4110850                   0.39404623
Lag 5000                    -0.1457415                  -0.05021868
         traittarsus.2:traitbwt.2.animal traitbwt.2:traitbwt.2.animal
```

```
Lag 0                      0.89818763                  1.00000000
Lag 100                    0.82577566                  0.87344161
Lag 500                    0.71300098                  0.71296418
Lag 1000                   0.62246323                  0.58027397
Lag 5000                  -0.02000725                 -0.05065402
         traittarsus.1.byear traitbwt.1.byear traittarsus.2.byear
Lag 0             0.05353374      0.007606345          0.07295919
Lag 100           0.05915538      0.016873424          0.06649764
Lag 500           0.05495199      0.034153584          0.05087275
Lag 1000          0.08867289      0.063336260          0.03210710
Lag 5000          0.01157646      0.010648297         -0.07267030
         traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother
Lag 0         -0.11303991           0.128729447      -0.162810059
Lag 100       -0.10682241           0.132664466      -0.165762472
Lag 500       -0.06622430           0.082749840      -0.142795999
Lag 1000      -0.06796661           0.092840268      -0.120838816
Lag 5000       0.07422776           0.007625067       0.007301082
         traittarsus.2.mother traitbwt.2.mother
Lag 0             -0.04298505      -0.033866092
Lag 100           -0.06870971       0.016347544
Lag 500           -0.06335390       0.003806205
Lag 1000          -0.06335680       0.042702082
Lag 5000          -0.03319016      -0.022982672
         traittarsus.1:traittarsus.1.units traitbwt.1:traittarsus.1.units
Lag 0                          -0.13106867                    -0.13241719
Lag 100                        -0.10278270                    -0.09227117
Lag 500                        -0.06959318                    -0.07769390
Lag 1000                       -0.08442761                    -0.10813364
Lag 5000                        0.12643968                     0.06443195
         traittarsus.2:traittarsus.1.units traitbwt.2:traittarsus.1.units
Lag 0                           0.13071885                     0.21162923
Lag 100                         0.13765665                     0.22039206
Lag 500                         0.12262833                     0.19792348
```

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Lag 1000                        0.11563474                     0.17509971
Lag 5000                        0.01775142                     0.02534375
         traittarsus.1:traitbwt.1.units traitbwt.1:traitbwt.1.units
Lag 0                       -0.13241719                  -0.1400636
Lag 100                     -0.09227117                  -0.1032594
Lag 500                     -0.07769390                  -0.1120628
Lag 1000                    -0.10813364                  -0.1695827
Lag 5000                     0.06443195                  -0.0137381
         traittarsus.2:traitbwt.1.units traitbwt.2:traitbwt.1.units
Lag 0                       0.172783869                  0.24161056
Lag 100                     0.184368154                  0.25618384
Lag 500                     0.169565117                  0.23188706
Lag 1000                    0.152615170                  0.20023901
Lag 5000                    0.008979599                  0.01431812
         traittarsus.1:traittarsus.2.units traitbwt.1:traittarsus.2.units
Lag 0                           0.13071885                    0.172783869
Lag 100                         0.13765665                    0.184368154
Lag 500                         0.12262833                    0.169565117
Lag 1000                        0.11563474                    0.152615170
Lag 5000                        0.01775142                    0.008979599
         traittarsus.2:traittarsus.2.units traitbwt.2:traittarsus.2.units
Lag 0                          -0.70436348                    -0.85484247
Lag 100                        -0.67503813                    -0.80874929
Lag 500                        -0.61496101                    -0.69869786
Lag 1000                       -0.55915090                    -0.60389172
Lag 5000                       -0.01252908                     0.03149869
         traittarsus.1:traitbwt.2.units traitbwt.1:traitbwt.2.units
Lag 0                        0.21162923                  0.24161056
Lag 100                      0.22039206                  0.25618384
Lag 500                      0.19792348                  0.23188706
Lag 1000                     0.17509971                  0.20023901
Lag 5000                     0.02534375                  0.01431812
         traittarsus.2:traitbwt.2.units traitbwt.2:traitbwt.2.units
```

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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
```

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Lag 0                               0.016204947                      0.02942135
Lag 100                             0.029428446                      0.02240012
Lag 500                             0.003988555                      0.02748906
Lag 1000                           -0.009687121                      0.01673477
Lag 5000                           -0.057748697                     -0.04116453
         traittarsus.2:traittarsus.2.animal traitbwt.2:traittarsus.2.animal
Lag 0                               0.035961574                      0.05124741
Lag 100                             0.039140531                      0.04519151
Lag 500                            -0.008894598                      0.03130914
Lag 1000                           -0.036681278                     -0.01447981
Lag 5000                           -0.088569223                     -0.10213928
         traittarsus.1:traitbwt.2.animal traitbwt.1:traitbwt.2.animal
Lag 0                         0.06346373                  0.034800266
Lag 100                       0.06520358                  0.032507546
Lag 500                       0.04831408                  0.041726424
Lag 1000                     -0.01510108                  0.007404418
Lag 5000                     -0.07984786                 -0.064540096
         traittarsus.2:traitbwt.2.animal traitbwt.2:traitbwt.2.animal
Lag 0                         0.05124741                   0.05353374
Lag 100                       0.04519151                   0.03671240
Lag 500                       0.03130914                   0.04212493
Lag 1000                     -0.01447981                  -0.01321894
Lag 5000                     -0.10213928                  -0.09784272
         traittarsus.1.byear traitbwt.1.byear traittarsus.2.byear
Lag 0             1.00000000     -0.011500754        -0.014207130
Lag 100           0.29498964      0.032775932         0.007424037
Lag 500           0.01534486     -0.007063004        -0.008141387
Lag 1000         -0.00531817      0.074940752        -0.088872220
Lag 5000         -0.04617778     -0.015458692        -0.020304988
         traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother
Lag 0       -0.0081906518          0.107143639       -0.06029833
Lag 100     -0.0458427594          0.096733446       -0.08150148
Lag 500      0.0004877642          0.068025342       -0.06046456
```

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Lag 1000     0.0105349484         -0.002189929       -0.01019378
Lag 5000    -0.0644916207         -0.020934152        0.04368155
         traittarsus.2.mother traitbwt.2.mother
Lag 0             -0.03378213       0.028992058
Lag 100           -0.04096317       0.005259162
Lag 500            0.04192974      -0.033349969
Lag 1000          -0.02480675      -0.011058052
Lag 5000           0.04747283      -0.001107231
         traittarsus.1:traittarsus.1.units traitbwt.1:traittarsus.1.units
Lag 0                         -0.145066040                   -0.104716754
Lag 100                       -0.089626633                   -0.078525674
Lag 500                       -0.055797909                   -0.064960700
Lag 1000                      -0.002415045                   -0.025253406
Lag 5000                       0.031464141                    0.006356867
         traittarsus.2:traittarsus.1.units traitbwt.2:traittarsus.1.units
Lag 0                         -0.038470154                    -0.03236997
Lag 100                       -0.037857054                    -0.03429257
Lag 500                       -0.023813333                    -0.02985769
Lag 1000                      -0.004466145                    -0.01855463
Lag 5000                       0.031916697                     0.01037899
         traittarsus.1:traitbwt.1.units traitbwt.1:traitbwt.1.units
Lag 0                      -0.104716754                -0.071954690
Lag 100                    -0.078525674                -0.071715488
Lag 500                    -0.064960700                -0.078535410
Lag 1000                   -0.025253406                -0.053257563
Lag 5000                    0.006356867                -0.008584678
         traittarsus.2:traitbwt.1.units traitbwt.2:traitbwt.1.units
Lag 0                       -0.02749973                 -0.02370119
Lag 100                     -0.02036580                 -0.01896999
Lag 500                     -0.02537270                 -0.03447923
Lag 1000                     0.01650965                  0.00885959
Lag 5000                     0.03965003                  0.01362772
         traittarsus.1:traittarsus.2.units traitbwt.1:traittarsus.2.units
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Lag 0                         -0.038470154                      -0.02749973
Lag 100                       -0.037857054                      -0.02036580
Lag 500                       -0.023813333                      -0.02537270
Lag 1000                      -0.004466145                       0.01650965
Lag 5000                       0.031916697                       0.03965003
         traittarsus.2:traittarsus.2.units traitbwt.2:traittarsus.2.units
Lag 0                         -0.029532571                      -0.04533921
Lag 100                       -0.006520508                      -0.01935854
Lag 500                        0.015074249                      -0.01914032
Lag 1000                       0.040326869                       0.01182073
Lag 5000                       0.077261030                       0.09163015
         traittarsus.1:traitbwt.2.units traitbwt.1:traitbwt.2.units
Lag 0                      -0.03236997                 -0.02370119
Lag 100                    -0.03429257                 -0.01896999
Lag 500                    -0.02985769                 -0.03447923
Lag 1000                   -0.01855463                  0.00885959
Lag 5000                    0.01037899                  0.01362772
         traittarsus.2:traitbwt.2.units traitbwt.2:traitbwt.2.units
Lag 0                      -0.04533921                -0.044815839
Lag 100                    -0.01935854                -0.018188105
Lag 500                    -0.01914032                -0.044430332
Lag 1000                    0.01182073                 0.006995154
Lag 5000                    0.09163015                 0.087372099

, , traitbwt.1.byear

         traittarsus.1:traittarsus.1.animal traitbwt.1:traittarsus.1.animal
Lag 0                            0.02533600                    -0.048571545
Lag 100                          0.04296781                    -0.011259967
Lag 500                          0.04385496                     0.001433897
Lag 1000                         0.00311012                    -0.028185947
Lag 5000                        -0.03791093                    -0.035032491
         traittarsus.2:traittarsus.1.animal traitbwt.2:traittarsus.1.animal
```

```
Lag 0                           0.042952342                     0.027308707
Lag 100                         0.053766787                     0.050479200
Lag 500                         0.061397390                     0.045799389
Lag 1000                        0.026376244                     0.045575916
Lag 5000                       -0.007467705                     0.004959177
         traittarsus.1:traitbwt.1.animal traitbwt.1:traitbwt.1.animal
Lag 0                       -0.048571545                 -0.054239888
Lag 100                     -0.011259967                 -0.013618719
Lag 500                      0.001433897                 -0.023666680
Lag 1000                    -0.028185947                 -0.035975542
Lag 5000                    -0.035032491                 -0.004849703
         traittarsus.2:traitbwt.1.animal traitbwt.2:traitbwt.1.animal
Lag 0                         0.01370326                  0.007431509
Lag 100                       0.02573311                  0.031124056
Lag 500                       0.01003935                 -0.020817482
Lag 1000                     -0.01201110                 -0.011831635
Lag 5000                     -0.03020983                  0.005318089
         traittarsus.1:traittarsus.2.animal traitbwt.1:traittarsus.2.animal
Lag 0                           0.042952342                      0.01370326
Lag 100                         0.053766787                      0.02573311
Lag 500                         0.061397390                      0.01003935
Lag 1000                        0.026376244                     -0.01201110
Lag 5000                       -0.007467705                     -0.03020983
         traittarsus.2:traittarsus.2.animal traitbwt.2:traittarsus.2.animal
Lag 0                           -0.01746914                     0.001646162
Lag 100                         -0.00918084                     0.014660207
Lag 500                          0.03727433                     0.029738658
Lag 1000                         0.05233753                     0.058558627
Lag 5000                         0.05442837                     0.036237222
         traittarsus.1:traitbwt.2.animal traitbwt.1:traitbwt.2.animal
Lag 0                        0.027308707                  0.007431509
Lag 100                      0.050479200                  0.031124056
Lag 500                      0.045799389                 -0.020817482
```

```
Lag 1000                      0.045575916                     -0.011831635
Lag 5000                      0.004959177                      0.005318089
         traittarsus.2:traitbwt.2.animal traitbwt.2:traitbwt.2.animal
Lag 0                         0.001646162                      0.007606345
Lag 100                       0.014660207                      0.025027029
Lag 500                       0.029738658                      0.007127126
Lag 1000                      0.058558627                      0.051997571
Lag 5000                      0.036237222                      0.030982100
         traittarsus.1.byear traitbwt.1.byear traittarsus.2.byear
Lag 0           -0.011500754       1.00000000        -0.032565228
Lag 100         -0.008778968       0.12997956        -0.003228198
Lag 500         -0.004505343       0.03863671        -0.017827698
Lag 1000         0.025463698      -0.01655625         0.013769326
Lag 5000         0.001254535      -0.04239004         0.001901775
         traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother
Lag 0        -0.039257246          -0.02879748       0.065880688
Lag 100       0.015007558          -0.03208555       0.058933430
Lag 500      -0.005393351           0.03210587       0.004743831
Lag 1000      0.043913747           0.05551756       0.012244934
Lag 5000     -0.026820593           0.05843803       0.010088100
         traittarsus.2.mother traitbwt.2.mother
Lag 0             0.008939011       0.059268463
Lag 100          -0.001571382       0.086064468
Lag 500          -0.023366713       0.008732966
Lag 1000          0.002165536      -0.002113612
Lag 5000         -0.038345540      -0.007683096
         traittarsus.1:traittarsus.1.units traitbwt.1:traittarsus.1.units
Lag 0                        -0.0435586501                    0.010219509
Lag 100                      -0.0505048908                   -0.031324102
Lag 500                      -0.0630828149                   -0.004357406
Lag 1000                      0.0199630207                    0.069957559
Lag 5000                      0.0005522977                   -0.005454216
         traittarsus.2:traittarsus.1.units traitbwt.2:traittarsus.1.units
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Lag 0                           0.05293519                     0.05768879
Lag 100                         0.04858011                     0.05892110
Lag 500                         0.05854491                     0.06372575
Lag 1000                        0.04969484                     0.03639502
Lag 5000                        0.02832954                     0.02784365
         traittarsus.1:traitbwt.1.units traitbwt.1:traitbwt.1.units
Lag 0                       0.010219509                -0.028183637
Lag 100                    -0.031324102                -0.040106071
Lag 500                    -0.004357406                 0.006591277
Lag 1000                    0.069957559                 0.063937711
Lag 5000                   -0.005454216                -0.027544320
         traittarsus.2:traitbwt.1.units traitbwt.2:traitbwt.1.units
Lag 0                        0.04996250                  0.04700881
Lag 100                      0.04397513                  0.04673808
Lag 500                      0.04695403                  0.04531904
Lag 1000                     0.03436998                  0.02563582
Lag 5000                     0.02256523                  0.02398399
         traittarsus.1:traittarsus.2.units traitbwt.1:traittarsus.2.units
Lag 0                           0.05293519                     0.04996250
Lag 100                         0.04858011                     0.04397513
Lag 500                         0.05854491                     0.04695403
Lag 1000                        0.04969484                     0.03436998
Lag 5000                        0.02832954                     0.02256523
         traittarsus.2:traittarsus.2.units traitbwt.2:traittarsus.2.units
Lag 0                           0.01013932                   -0.001638125
Lag 100                         0.01806400                    0.001129150
Lag 500                        -0.01420490                   -0.017077159
Lag 1000                       -0.04995245                   -0.056833617
Lag 5000                       -0.04322171                   -0.023913807
         traittarsus.1:traitbwt.2.units traitbwt.1:traitbwt.2.units
Lag 0                        0.05768879                  0.04700881
Lag 100                      0.05892110                  0.04673808
Lag 500                      0.06372575                  0.04531904
```

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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
```

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Lag 1000                      0.05734586                   0.08937241
Lag 5000                      0.08247995                   0.05423744
         traittarsus.1:traittarsus.2.animal traitbwt.1:traittarsus.2.animal
Lag 0                            0.05222339                      0.08861601
Lag 100                          0.07930026                      0.08291699
Lag 500                          0.04558008                      0.07447628
Lag 1000                         0.07097163                      0.05734586
Lag 5000                         0.06038135                      0.08247995
         traittarsus.2:traittarsus.2.animal traitbwt.2:traittarsus.2.animal
Lag 0                           0.007171364                      0.04068399
Lag 100                         0.043732946                      0.05987656
Lag 500                         0.015444417                      0.03370999
Lag 1000                        0.019544081                      0.04502976
Lag 5000                        0.006685864                     -0.01642810
         traittarsus.1:traitbwt.2.animal traitbwt.1:traitbwt.2.animal
Lag 0                         0.05196404                   0.10446126
Lag 100                       0.07496121                   0.08928353
Lag 500                       0.04893690                   0.09304440
Lag 1000                      0.08902753                   0.08937241
Lag 5000                      0.02474492                   0.05423744
         traittarsus.2:traitbwt.2.animal traitbwt.2:traitbwt.2.animal
Lag 0                         0.04068399                   0.07295919
Lag 100                       0.05987656                   0.07152626
Lag 500                       0.03370999                   0.07468887
Lag 1000                      0.04502976                   0.05593692
Lag 5000                     -0.01642810                  -0.02210630
         traittarsus.1.byear traitbwt.1.byear traittarsus.2.byear
Lag 0           -0.014207130      -0.03256523          1.00000000
Lag 100          0.004989327       0.01606065          0.26418064
Lag 500          0.044052804       0.03428138          0.09537772
Lag 1000        -0.001440518       0.01039861          0.10874833
Lag 5000         0.022958892      -0.01931981         -0.01473189
         traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother
```

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Lag 0        0.0396353651           0.00119313       0.009996629
Lag 100      0.0105436230           0.04327018       0.062928368
Lag 500     -0.0175690949           0.04625644       0.018026408
Lag 1000    -0.0005183552           0.06289415      -0.081508956
Lag 5000     0.0441472029          -0.04105115       0.035686320
         traittarsus.2.mother traitbwt.2.mother
Lag 0              0.04535223       0.002495676
Lag 100            0.02030029       0.045447997
Lag 500            0.02446377       0.009649222
Lag 1000           0.03899831       0.024762534
Lag 5000          -0.06415993       0.094134035
         traittarsus.1:traittarsus.1.units traitbwt.1:traittarsus.1.units
Lag 0                          -0.04924174                   0.0004983836
Lag 100                        -0.07260472                  -0.0274666354
Lag 500                        -0.08762084                  -0.0545545565
Lag 1000                       -0.11600745                  -0.0941075726
Lag 5000                       -0.01429942                  -0.0306094192
         traittarsus.2:traittarsus.1.units traitbwt.2:traittarsus.1.units
Lag 0                           0.06126409                     0.06054337
Lag 100                         0.06861858                     0.06794736
Lag 500                         0.06487160                     0.06219436
Lag 1000                        0.05154526                     0.06299063
Lag 5000                       -0.03961272                    -0.02077759
         traittarsus.1:traitbwt.1.units traitbwt.1:traitbwt.1.units
Lag 0                      0.0004983836                 0.045243199
Lag 100                   -0.0274666354                 0.002618325
Lag 500                   -0.0545545565                -0.045086068
Lag 1000                  -0.0941075726                -0.078265909
Lag 5000                  -0.0306094192                -0.039652118
         traittarsus.2:traitbwt.1.units traitbwt.2:traitbwt.1.units
Lag 0                        0.04569537                  0.05361674
Lag 100                      0.05790943                  0.06228633
Lag 500                      0.06629817                  0.07181673
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Lag 1000                     0.05677668                  0.07820270
Lag 5000                    -0.04900870                 -0.01725220
         traittarsus.1:traittarsus.2.units traitbwt.1:traittarsus.2.units
Lag 0                           0.06126409                     0.04569537
Lag 100                         0.06861858                     0.05790943
Lag 500                         0.06487160                     0.06629817
Lag 1000                        0.05154526                     0.05677668
Lag 5000                       -0.03961272                    -0.04900870
         traittarsus.2:traittarsus.2.units traitbwt.2:traittarsus.2.units
Lag 0                          -0.05907849                    -0.07410803
Lag 100                        -0.06985906                    -0.08123809
Lag 500                        -0.02440940                    -0.02862324
Lag 1000                       -0.03153841                    -0.04394287
Lag 5000                        0.01609465                     0.02558327
         traittarsus.1:traitbwt.2.units traitbwt.1:traitbwt.2.units
Lag 0                        0.06054337                  0.05361674
Lag 100                      0.06794736                  0.06228633
Lag 500                      0.06219436                  0.07181673
Lag 1000                     0.06299063                  0.07820270
Lag 5000                    -0.02077759                 -0.01725220
         traittarsus.2:traitbwt.2.units traitbwt.2:traitbwt.2.units
Lag 0                       -0.07410803                 -0.09539294
Lag 100                     -0.08123809                 -0.10192651
Lag 500                     -0.02862324                 -0.04787149
Lag 1000                    -0.04394287                 -0.05696449
Lag 5000                     0.02558327                  0.02318439

, , traitbwt.2.byear

         traittarsus.1:traittarsus.1.animal traitbwt.1:traittarsus.1.animal
Lag 0                          -0.012312644                    -0.026101857
Lag 100                         0.001679568                    -0.022719854
Lag 500                        -0.022095064                     0.036781391
```

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Lag 1000                  -0.044649058                 0.008440477
Lag 5000                   0.012471911                 0.017412057
         traittarsus.2:traittarsus.1.animal traitbwt.2:traittarsus.1.animal
Lag 0                     -0.041612693                -0.093374609
Lag 100                   -0.044670676                -0.085938138
Lag 500                   -0.073851310                -0.057467051
Lag 1000                  -0.112427556                -0.073729661
Lag 5000                  -0.002302422                -0.007211525
         traittarsus.1:traitbwt.1.animal traitbwt.1:traitbwt.1.animal
Lag 0                  -0.026101857                -0.024899884
Lag 100                -0.022719854                -0.008317247
Lag 500                 0.036781391                 0.041716499
Lag 1000                0.008440477                -0.015226273
Lag 5000                0.017412057                -0.007915616
         traittarsus.2:traitbwt.1.animal traitbwt.2:traitbwt.1.animal
Lag 0                   -0.06566102                 -0.08333568
Lag 100                 -0.07750349                 -0.08378159
Lag 500                 -0.08329811                 -0.05814502
Lag 1000                -0.08817705                 -0.08501262
Lag 5000                 0.01626488                 -0.01063817
         traittarsus.1:traittarsus.2.animal traitbwt.1:traittarsus.2.animal
Lag 0                     -0.041612693                 -0.06566102
Lag 100                   -0.044670676                 -0.07750349
Lag 500                   -0.073851310                 -0.08329811
Lag 1000                  -0.112427556                 -0.08817705
Lag 5000                  -0.002302422                  0.01626488
         traittarsus.2:traittarsus.2.animal traitbwt.2:traittarsus.2.animal
Lag 0                      -0.08333086                 -0.12402916
Lag 100                    -0.07538028                 -0.10747454
Lag 500                    -0.05024835                 -0.08333129
Lag 1000                   -0.08252216                 -0.09539109
Lag 5000                   -0.05270947                 -0.04030638
         traittarsus.1:traitbwt.2.animal traitbwt.1:traitbwt.2.animal
```

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Lag 0                        -0.093374609                  -0.08333568
Lag 100                      -0.085938138                  -0.08378159
Lag 500                      -0.057467051                  -0.05814502
Lag 1000                     -0.073729661                  -0.08501262
Lag 5000                     -0.007211525                  -0.01063817
         traittarsus.2:traitbwt.2.animal traitbwt.2:traitbwt.2.animal
Lag 0                         -0.12402916                  -0.11303991
Lag 100                       -0.10747454                  -0.09513886
Lag 500                       -0.08333129                  -0.08666156
Lag 1000                      -0.09539109                  -0.10675958
Lag 5000                      -0.04030638                  -0.02380443
         traittarsus.1.byear traitbwt.1.byear traittarsus.2.byear
Lag 0           -0.008190652     -0.039257246          0.03963537
Lag 100         -0.031080960     -0.037426765          0.00903900
Lag 500          0.006051004     -0.020419576         -0.06809153
Lag 1000         0.018314138     -0.002583670         -0.02323337
Lag 5000        -0.026798307     -0.007024901         -0.01177870
         traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother
Lag 0         1.000000000          -0.03484939       0.019595061
Lag 100       0.148773685          -0.05262924       0.013805361
Lag 500       0.023071337           0.01145834       0.001042167
Lag 1000      0.001235911           0.02017891       0.034032045
Lag 5000     -0.035993191          -0.01462895      -0.011384188
         traittarsus.2.mother traitbwt.2.mother
Lag 0             0.015981233      -0.007859673
Lag 100          -0.022156260      -0.004707385
Lag 500          -0.006728665      -0.029061201
Lag 1000         -0.021805472       0.003816387
Lag 5000         -0.009007212       0.012478432
         traittarsus.1:traittarsus.1.units traitbwt.1:traittarsus.1.units
Lag 0                           0.01051817                     0.02175859
Lag 100                         0.02304329                     0.01564866
Lag 500                         0.01520723                    -0.00804956
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Lag 1000                        0.04140673                     0.03546143
Lag 5000                       -0.01488195                    -0.01947941
        traittarsus.2:traittarsus.1.units traitbwt.2:traittarsus.1.units
Lag 0                          -0.04179855                    -0.03235648
Lag 100                        -0.04317226                    -0.03935256
Lag 500                        -0.03459143                    -0.04109499
Lag 1000                       -0.03581518                    -0.03377959
Lag 5000                       -0.04487869                    -0.06427439
        traittarsus.1:traitbwt.1.units traitbwt.1:traitbwt.1.units
Lag 0                        0.02175859                 0.008779544
Lag 100                      0.01564866                 0.004367987
Lag 500                     -0.00804956                -0.020584034
Lag 1000                     0.03546143                 0.024592354
Lag 5000                    -0.01947941                -0.008436479
        traittarsus.2:traitbwt.1.units traitbwt.2:traitbwt.1.units
Lag 0                       -0.05587517                 -0.03458419
Lag 100                     -0.04924453                 -0.03546666
Lag 500                     -0.03327777                 -0.03542884
Lag 1000                    -0.02872355                 -0.01384796
Lag 5000                    -0.05472119                 -0.06947879
        traittarsus.1:traittarsus.2.units traitbwt.1:traittarsus.2.units
Lag 0                          -0.04179855                    -0.05587517
Lag 100                        -0.04317226                    -0.04924453
Lag 500                        -0.03459143                    -0.03327777
Lag 1000                       -0.03581518                    -0.02872355
Lag 5000                       -0.04487869                    -0.05472119
        traittarsus.2:traittarsus.2.units traitbwt.2:traittarsus.2.units
Lag 0                           0.07499456                     0.09224924
Lag 100                         0.07208086                     0.09762890
Lag 500                         0.07251351                     0.09224810
Lag 1000                        0.08656386                     0.08963227
Lag 5000                        0.01938132                     0.01875251
        traittarsus.1:traitbwt.2.units traitbwt.1:traitbwt.2.units
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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
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Lag 0                     0.01026682                 0.10088834
Lag 100                   0.02777302                 0.10524313
Lag 500                  -0.02208151                 0.06189318
Lag 1000                 -0.03691548                 0.02840216
Lag 5000                 -0.05057754                -0.05628831
         traittarsus.1:traittarsus.2.animal traitbwt.1:traittarsus.2.animal
Lag 0                           -0.10295266                      0.01026682
Lag 100                         -0.08557369                      0.02777302
Lag 500                         -0.09200768                     -0.02208151
Lag 1000                        -0.07176616                     -0.03691548
Lag 5000                        -0.04022520                     -0.05057754
         traittarsus.2:traittarsus.2.animal traitbwt.2:traittarsus.2.animal
Lag 0                           0.046514036                     0.086391373
Lag 100                         0.041591585                     0.092682345
Lag 500                         0.014159903                     0.054749349
Lag 1000                       -0.006046443                     0.037148101
Lag 5000                        0.023770495                    -0.002799893
         traittarsus.1:traitbwt.2.animal traitbwt.1:traitbwt.2.animal
Lag 0                        0.020069065                   0.10088834
Lag 100                      0.024944654                   0.10524313
Lag 500                     -0.007032787                   0.06189318
Lag 1000                    -0.035638619                   0.02840216
Lag 5000                    -0.053311401                  -0.05628831
         traittarsus.2:traitbwt.2.animal traitbwt.2:traitbwt.2.animal
Lag 0                        0.086391373                  0.128729447
Lag 100                      0.092682345                  0.137837082
Lag 500                      0.054749349                  0.091445074
Lag 1000                     0.037148101                  0.065510680
Lag 5000                    -0.002799893                 -0.009892994
         traittarsus.1.byear traitbwt.1.byear traittarsus.2.byear
Lag 0             0.10714364     -0.028797482         0.001193130
Lag 100           0.12475726     -0.002859105         0.017423692
Lag 500           0.05635178      0.024729770         0.044602685
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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
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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
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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
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Lag 1000                       -0.051714924                     -0.09839159
Lag 5000                        0.004416861                      0.02809940
         traittarsus.1:traitbwt.2.animal traitbwt.1:traitbwt.2.animal
Lag 0                        -0.06942502                   -0.21005355
Lag 100                      -0.06694784                   -0.17453411
Lag 500                      -0.04628001                   -0.13167639
Lag 1000                     -0.02832344                   -0.06743430
Lag 5000                      0.06116511                    0.06036364
         traittarsus.2:traitbwt.2.animal traitbwt.2:traitbwt.2.animal
Lag 0                        -0.09704390                   -0.16281006
Lag 100                      -0.11278771                   -0.15402583
Lag 500                      -0.13102396                   -0.18417663
Lag 1000                     -0.09839159                   -0.13265931
Lag 5000                      0.02809940                    0.06774942
         traittarsus.1.byear traitbwt.1.byear traittarsus.2.byear
Lag 0            -0.06029833      0.065880688         0.009996629
Lag 100          -0.06060175      0.002155759         0.013541244
Lag 500           0.02852613     -0.001260087         0.019839054
Lag 1000         -0.02910626      0.001290157         0.048245645
Lag 5000         -0.01024266      0.050399045         0.056737041
         traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother
Lag 0        0.0195950614        -0.2712137958       1.000000000
Lag 100     -0.0008933777        -0.1720110752       0.379551682
Lag 500      0.0366638614        -0.0393624856       0.041329213
Lag 1000    -0.0151426446         0.0476618317       0.002159042
Lag 5000     0.0123140414         0.0001252644      -0.018222262
         traittarsus.2.mother traitbwt.2.mother
Lag 0             0.031492934        0.14519001
Lag 100           0.002534347        0.07587057
Lag 500          -0.013284762        0.04165749
Lag 1000         -0.031081556       -0.02212041
Lag 5000          0.013850724       -0.02074787
         traittarsus.1:traittarsus.1.units traitbwt.1:traittarsus.1.units
```

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Lag 0                        0.01973629                       0.03665672
Lag 100                     -0.02293101                       0.01498518
Lag 500                     -0.11066356                      -0.05474960
Lag 1000                    -0.09135360                      -0.03226117
Lag 5000                    -0.07860493                      -0.07560389
         traittarsus.2:traittarsus.1.units traitbwt.2:traittarsus.1.units
Lag 0                        0.04294093                      0.012376673
Lag 100                      0.03955764                      0.010683501
Lag 500                      0.01752126                     -0.006221666
Lag 1000                     0.02219142                     -0.001297180
Lag 5000                     0.01239642                      0.030951874
         traittarsus.1:traitbwt.1.units traitbwt.1:traitbwt.1.units
Lag 0                     0.03665672                -0.007047622
Lag 100                   0.01498518                 0.037977225
Lag 500                  -0.05474960                 0.019970710
Lag 1000                 -0.03226117                -0.007739455
Lag 5000                 -0.07560389                -0.062919612
         traittarsus.2:traitbwt.1.units traitbwt.2:traitbwt.1.units
Lag 0                   -0.002752353                 -0.03097991
Lag 100                 -0.003093096                 -0.03192449
Lag 500                 -0.009027187                 -0.04102552
Lag 1000                -0.020527419                 -0.03483856
Lag 5000                 0.006886321                  0.02535835
         traittarsus.1:traittarsus.2.units traitbwt.1:traittarsus.2.units
Lag 0                        0.04294093                     -0.002752353
Lag 100                      0.03955764                     -0.003093096
Lag 500                      0.01752126                     -0.009027187
Lag 1000                     0.02219142                     -0.020527419
Lag 5000                     0.01239642                      0.006886321
         traittarsus.2:traittarsus.2.units traitbwt.2:traittarsus.2.units
Lag 0                        0.08205572                       0.11704839
Lag 100                      0.07607819                       0.11403531
Lag 500                      0.10265484                       0.14762922
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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
```

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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
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Lag 1000                   -0.037570106                -0.014564806
Lag 5000                   -0.018285255                -0.019587618
         traittarsus.2:traitbwt.1.units traitbwt.2:traitbwt.1.units
Lag 0                      -0.044767110                -0.050917805
Lag 100                    -0.038505551                -0.046892201
Lag 500                    -0.026544619                -0.030053092
Lag 1000                   -0.047964926                -0.058484565
Lag 5000                    0.005513663                 0.008103974
         traittarsus.1:traittarsus.2.units traitbwt.1:traittarsus.2.units
Lag 0                         -0.032394558                   -0.044767110
Lag 100                       -0.025527001                   -0.038505551
Lag 500                       -0.026572307                   -0.026544619
Lag 1000                      -0.039244262                   -0.047964926
Lag 5000                      -0.005888125                    0.005513663
         traittarsus.2:traittarsus.2.units traitbwt.2:traittarsus.2.units
Lag 0                            0.1360740                      0.1159929
Lag 100                          0.1741515                      0.1418886
Lag 500                          0.1700049                      0.1445076
Lag 1000                         0.1777767                      0.1521923
Lag 5000                        -0.1463666                     -0.1686025
         traittarsus.1:traitbwt.2.units traitbwt.1:traitbwt.2.units
Lag 0                      -0.038463991                -0.050917805
Lag 100                    -0.031296257                -0.046892201
Lag 500                    -0.025766415                -0.030053092
Lag 1000                   -0.042965449                -0.058484565
Lag 5000                   -0.008787816                 0.008103974
         traittarsus.2:traitbwt.2.units traitbwt.2:traitbwt.2.units
Lag 0                         0.1159929                   0.0979877
Lag 100                       0.1418886                   0.1021546
Lag 500                       0.1445076                   0.1134636
Lag 1000                      0.1521923                   0.1278208
Lag 5000                     -0.1686025                  -0.1687524
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, , 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
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Lag 0                            0.15871038                      0.09891371
Lag 100                          0.13316302                      0.07837814
Lag 500                          0.10976919                      0.06061434
Lag 1000                         0.08100730                      0.06929365
Lag 5000                        -0.02040836                     -0.01741179
         traittarsus.1:traitbwt.2.animal traitbwt.1:traitbwt.2.animal
Lag 0                         0.04826105                 -0.095372303
Lag 100                       0.03784269                 -0.050527725
Lag 500                       0.03087286                 -0.018316704
Lag 1000                      0.03858511                 -0.004218270
Lag 5000                      0.02719676                  0.008525728
         traittarsus.2:traitbwt.2.animal traitbwt.2:traitbwt.2.animal
Lag 0                         0.09891371                 -0.033866092
Lag 100                       0.07837814                 -0.011360083
Lag 500                       0.06061434                  0.012969192
Lag 1000                      0.06929365                  0.045752648
Lag 5000                     -0.01741179                 -0.001193243
         traittarsus.1.byear traitbwt.1.byear traittarsus.2.byear
Lag 0             0.02899206       0.05926846        0.0024956756
Lag 100          -0.01583481       0.05520016        0.0239528518
Lag 500           0.03917478       0.01148328        0.0002419691
Lag 1000         -0.03694049       0.02504159        0.0667961149
Lag 5000         -0.06196001       0.02957462        0.0049061407
         traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother
Lag 0        -0.007859673          -0.05622667        0.14519001
Lag 100       0.010189964          -0.05585546        0.13743423
Lag 500       0.007357905           0.02124383        0.03427438
Lag 1000      0.029340288           0.06934074       -0.01797194
Lag 5000      0.011164278           0.01230641        0.01184408
         traittarsus.2.mother traitbwt.2.mother
Lag 0             -0.329182837       1.000000000
Lag 100           -0.235728358       0.284175599
Lag 500           -0.148665968       0.029162936
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Lag 1000         -0.007592145      -0.008559910
Lag 5000          0.006615767       0.006917489
         traittarsus.1:traittarsus.1.units traitbwt.1:traittarsus.1.units
Lag 0                          -0.04849521                    -0.01247903
Lag 100                        -0.04229095                    -0.01179876
Lag 500                        -0.06190225                    -0.03479262
Lag 1000                       -0.06244621                    -0.01333269
Lag 5000                       -0.04472803                    -0.03405548
         traittarsus.2:traittarsus.1.units traitbwt.2:traittarsus.1.units
Lag 0                           0.06299708                     0.07575889
Lag 100                         0.05582189                     0.06465068
Lag 500                         0.05304268                     0.04802379
Lag 1000                        0.07638864                     0.07282218
Lag 5000                        0.04062409                     0.05791562
         traittarsus.1:traitbwt.1.units traitbwt.1:traitbwt.1.units
Lag 0                       -0.01247903                -0.009223763
Lag 100                     -0.01179876                -0.004801511
Lag 500                     -0.03479262                -0.021159851
Lag 1000                    -0.01333269                -0.005423005
Lag 5000                    -0.03405548                -0.040128813
         traittarsus.2:traitbwt.1.units traitbwt.2:traitbwt.1.units
Lag 0                        0.07595500                  0.08248472
Lag 100                      0.06741840                  0.07062568
Lag 500                      0.04493967                  0.04348999
Lag 1000                     0.05963657                  0.06140170
Lag 5000                     0.05397711                  0.06956257
         traittarsus.1:traittarsus.2.units traitbwt.1:traittarsus.2.units
Lag 0                           0.06299708                     0.07595500
Lag 100                         0.05582189                     0.06741840
Lag 500                         0.05304268                     0.04493967
Lag 1000                        0.07638864                     0.05963657
Lag 5000                        0.04062409                     0.05397711
         traittarsus.2:traittarsus.2.units traitbwt.2:traittarsus.2.units
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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

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         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
```

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Lag 0                     -0.53741563                   -0.2245265
Lag 100                   -0.47900505                   -0.1935129
Lag 500                   -0.35990127                   -0.1387130
Lag 1000                  -0.24167598                   -0.1103208
Lag 5000                  -0.08362331                   -0.1059888
         traittarsus.2:traitbwt.1.animal traitbwt.2:traitbwt.1.animal
Lag 0                      -0.3729388                   -0.2547414
Lag 100                    -0.3377067                   -0.2223712
Lag 500                    -0.2941086                   -0.2173660
Lag 1000                   -0.2338232                   -0.1759256
Lag 5000                   -0.1733008                   -0.1754188
         traittarsus.1:traittarsus.2.animal traitbwt.1:traittarsus.2.animal
Lag 0                         -0.4851021                      -0.3729388
Lag 100                       -0.4391087                      -0.3377067
Lag 500                       -0.3514192                      -0.2941086
Lag 1000                      -0.2817756                      -0.2338232
Lag 5000                      -0.1379797                      -0.1733008
         traittarsus.2:traittarsus.2.animal traitbwt.2:traittarsus.2.animal
Lag 0                        -0.10376953                      -0.1451563
Lag 100                      -0.07852837                      -0.1303753
Lag 500                      -0.06730801                      -0.1313359
Lag 1000                     -0.06713014                      -0.1425029
Lag 5000                     -0.15697371                      -0.2346428
         traittarsus.1:traitbwt.2.animal traitbwt.1:traitbwt.2.animal
Lag 0                      -0.3969630                   -0.2547414
Lag 100                    -0.3672331                   -0.2223712
Lag 500                    -0.3303341                   -0.2173660
Lag 1000                   -0.2606715                   -0.1759256
Lag 5000                   -0.1850268                   -0.1754188
         traittarsus.2:traitbwt.2.animal traitbwt.2:traitbwt.2.animal
Lag 0                      -0.1451563                   -0.1310687
Lag 100                    -0.1303753                   -0.1210976
Lag 500                    -0.1313359                   -0.1454273
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Lag 1000                      -0.1425029                   -0.1484290
Lag 5000                      -0.2346428                   -0.2608162
         traittarsus.1.byear traitbwt.1.byear traittarsus.2.byear
Lag 0            -0.14506604     -0.043558650         -0.04924174
Lag 100          -0.12498034     -0.053994536         -0.03871946
Lag 500          -0.05225308     -0.005205432         -0.05590755
Lag 1000         -0.05643316     -0.037921140          0.00532337
Lag 5000         -0.01904738     -0.070857345          0.03761236
         traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother
Lag 0          0.01051817          -0.28511353        0.01973629
Lag 100        0.03224747          -0.21849925        0.02374680
Lag 500        0.03546917          -0.12897815        0.01858679
Lag 1000       0.01230618          -0.03335119        0.03274960
Lag 5000       0.02825979          -0.05125552        0.04540862
         traittarsus.2.mother traitbwt.2.mother
Lag 0            -0.003303414      -0.048495208
Lag 100          -0.027103529      -0.040346222
Lag 500          -0.025758939       0.002369226
Lag 1000         -0.025407178      -0.024008377
Lag 5000         -0.010658268       0.012747460
         traittarsus.1:traittarsus.1.units traitbwt.1:traittarsus.1.units
Lag 0                           1.00000000                     0.71266479
Lag 100                         0.69601632                     0.48602800
Lag 500                         0.44391095                     0.33331074
Lag 1000                        0.32879898                     0.24626220
Lag 5000                        0.09190517                     0.09278524
         traittarsus.2:traittarsus.1.units traitbwt.2:traittarsus.1.units
Lag 0                           -0.2592850                     -0.2645685
Lag 100                         -0.2655767                     -0.2702771
Lag 500                         -0.2886811                     -0.2950022
Lag 1000                        -0.2858651                     -0.3159051
Lag 5000                        -0.2005196                     -0.2351461
         traittarsus.1:traitbwt.1.units traitbwt.1:traitbwt.1.units
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Lag 0                        0.71266479                   0.3606694
Lag 100                      0.48602800                   0.2474550
Lag 500                      0.33331074                   0.1595171
Lag 1000                     0.24626220                   0.1323001
Lag 5000                     0.09278524                   0.1142750
         traittarsus.2:traitbwt.1.units traitbwt.2:traitbwt.1.units
Lag 0                        -0.2009925                  -0.1971901
Lag 100                      -0.2133808                  -0.2127295
Lag 500                      -0.2513257                  -0.2534202
Lag 1000                     -0.2644654                  -0.2860502
Lag 5000                     -0.2208762                  -0.2453635
         traittarsus.1:traittarsus.2.units traitbwt.1:traittarsus.2.units
Lag 0                           -0.2592850                     -0.2009925
Lag 100                         -0.2655767                     -0.2133808
Lag 500                         -0.2886811                     -0.2513257
Lag 1000                        -0.2858651                     -0.2644654
Lag 5000                        -0.2005196                     -0.2208762
         traittarsus.2:traittarsus.2.units traitbwt.2:traittarsus.2.units
Lag 0                           0.09543017                     0.11602826
Lag 100                         0.06131639                     0.09650511
Lag 500                         0.06137108                     0.11179013
Lag 1000                        0.08079826                     0.13634360
Lag 5000                        0.18979188                     0.24893895
         traittarsus.1:traitbwt.2.units traitbwt.1:traitbwt.2.units
Lag 0                        -0.2645685                  -0.1971901
Lag 100                      -0.2702771                  -0.2127295
Lag 500                      -0.2950022                  -0.2534202
Lag 1000                     -0.3159051                  -0.2860502
Lag 5000                     -0.2351461                  -0.2453635
         traittarsus.2:traitbwt.2.units traitbwt.2:traitbwt.2.units
Lag 0                        0.11602826                  0.10062986
Lag 100                      0.09650511                  0.09093566
Lag 500                      0.11179013                  0.12421446
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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
```

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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
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Lag 0             -0.03359578      -0.012479028
Lag 100           -0.04488434      -0.002934766
Lag 500           -0.06697376       0.021613573
Lag 1000          -0.08457909       0.019481160
Lag 5000          -0.08600099       0.051485249
         traittarsus.1:traittarsus.1.units traitbwt.1:traittarsus.1.units
Lag 0                            0.7126648                      1.0000000
Lag 100                          0.4891102                      0.6680602
Lag 500                          0.3020606                      0.3997173
Lag 1000                         0.2345067                      0.2999511
Lag 5000                         0.1759098                      0.1561292
         traittarsus.2:traittarsus.1.units traitbwt.2:traittarsus.1.units
Lag 0                           -0.1706739                     -0.1801399
Lag 100                         -0.1802375                     -0.1994176
Lag 500                         -0.2103921                     -0.2440747
Lag 1000                        -0.2087782                     -0.2510893
Lag 5000                        -0.1812853                     -0.1905911
         traittarsus.1:traitbwt.1.units traitbwt.1:traitbwt.1.units
Lag 0                         1.0000000                   0.8197350
Lag 100                       0.6680602                   0.5536026
Lag 500                       0.3997173                   0.3326177
Lag 1000                      0.2999511                   0.2334663
Lag 5000                      0.1561292                   0.1202757
         traittarsus.2:traitbwt.1.units traitbwt.2:traitbwt.1.units
Lag 0                        -0.1666030                  -0.1700866
Lag 100                      -0.1812316                  -0.1939150
Lag 500                      -0.2194596                  -0.2430469
Lag 1000                     -0.2384353                  -0.2743602
Lag 5000                     -0.2008085                  -0.2014312
         traittarsus.1:traittarsus.2.units traitbwt.1:traittarsus.2.units
Lag 0                           -0.1706739                     -0.1666030
Lag 100                         -0.1802375                     -0.1812316
Lag 500                         -0.2103921                     -0.2194596
```

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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

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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
         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
         traittarsus.1:traitbwt.1.animal traitbwt.1:traitbwt.1.animal
Lag 0                        0.124710076                   0.08095300
Lag 100                      0.130500544                   0.07950890
Lag 500                      0.139328738                   0.07894049
Lag 1000                     0.142277480                   0.08409986
Lag 5000                     0.009474997                  -0.03476503
         traittarsus.2:traitbwt.1.animal traitbwt.2:traitbwt.1.animal
Lag 0                         0.13041646                   0.06808542
Lag 100                       0.13619199                   0.07439607
Lag 500                       0.15236746                   0.10133254
Lag 1000                      0.16354531                   0.12513909
Lag 5000                      0.09727094                   0.09702098
         traittarsus.1:traittarsus.2.animal traitbwt.1:traittarsus.2.animal
Lag 0                             0.1906441                      0.13041646
Lag 100                           0.2063827                      0.13619199
Lag 500                           0.2249905                      0.15236746
Lag 1000                          0.2243627                      0.16354531
Lag 5000                          0.1612708                      0.09727094
         traittarsus.2:traittarsus.2.animal traitbwt.2:traittarsus.2.animal
Lag 0                             0.1881270                       0.1805175
Lag 100                           0.2019192                       0.1895957
Lag 500                           0.2143083                       0.2038416
Lag 1000                          0.2049762                       0.2031078
Lag 5000                          0.2015150                       0.2236163
         traittarsus.1:traitbwt.2.animal traitbwt.1:traitbwt.2.animal
Lag 0                         0.13328596                   0.06808542
Lag 100                       0.13989222                   0.07439607
Lag 500                       0.15953298                   0.10133254
Lag 1000                      0.17422740                   0.12513909
Lag 5000                      0.09845918                   0.09702098
         traittarsus.2:traitbwt.2.animal traitbwt.2:traitbwt.2.animal
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Lag 0                          0.1805175                    0.1307188
Lag 100                        0.1895957                    0.1387545
Lag 500                        0.2038416                    0.1596754
Lag 1000                       0.2031078                    0.1718471
Lag 5000                       0.2236163                    0.2388384
         traittarsus.1.byear traitbwt.1.byear traittarsus.2.byear
Lag 0            -0.03847015       0.05293519          0.06126409
Lag 100          -0.03144044       0.04956734          0.06250612
Lag 500          -0.01780154       0.05591029          0.07921148
Lag 1000         -0.02643841       0.04337011          0.09113494
Lag 5000         -0.01140358       0.03031863         -0.02594409
         traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother
Lag 0        -0.041798551            0.1697424        0.04294093
Lag 100      -0.034073821            0.1688986        0.04145441
Lag 500      -0.048890409            0.1720568        0.02794912
Lag 1000     -0.040999443            0.1790535        0.02144402
Lag 5000     -0.002784642            0.1836021       -0.02796491
         traittarsus.2.mother traitbwt.2.mother
Lag 0             -0.03239456        0.06299708
Lag 100           -0.03271179        0.06442310
Lag 500           -0.02932124        0.06841853
Lag 1000          -0.01370787        0.05547883
Lag 5000          -0.04156138        0.02258640
         traittarsus.1:traittarsus.1.units traitbwt.1:traittarsus.1.units
Lag 0                           -0.2592850                    -0.17067395
Lag 100                         -0.2666810                    -0.16983312
Lag 500                         -0.2761829                    -0.17499382
Lag 1000                        -0.2748628                    -0.18004636
Lag 5000                        -0.2185399                    -0.04226407
         traittarsus.2:traittarsus.1.units traitbwt.2:traittarsus.1.units
Lag 0                            1.0000000                      0.9603400
Lag 100                          0.9783825                      0.9444274
Lag 500                          0.9365031                      0.9054416
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Lag 1000                         0.8964880                      0.8617258
Lag 5000                         0.6039003                      0.6022291
         traittarsus.1:traitbwt.1.units traitbwt.1:traitbwt.1.units
Lag 0                       -0.17067395                 -0.12741602
Lag 100                     -0.16983312                 -0.12362277
Lag 500                     -0.17499382                 -0.11972769
Lag 1000                    -0.18004636                 -0.12502460
Lag 5000                    -0.04226407                  0.01790192
         traittarsus.2:traitbwt.1.units traitbwt.2:traitbwt.1.units
Lag 0                         0.9609935                   0.9034487
Lag 100                       0.9411829                   0.8893146
Lag 500                       0.8990207                   0.8539291
Lag 1000                      0.8622161                   0.8157349
Lag 5000                      0.5753236                   0.5773694
         traittarsus.1:traittarsus.2.units traitbwt.1:traittarsus.2.units
Lag 0                            1.0000000                      0.9609935
Lag 100                          0.9783825                      0.9411829
Lag 500                          0.9365031                      0.8990207
Lag 1000                         0.8964880                      0.8622161
Lag 5000                         0.6039003                      0.5753236
         traittarsus.2:traittarsus.2.units traitbwt.2:traittarsus.2.units
Lag 0                           -0.1856903                     -0.1801544
Lag 100                         -0.1921763                     -0.1830867
Lag 500                         -0.2110415                     -0.2009371
Lag 1000                        -0.2033807                     -0.1989511
Lag 5000                        -0.1866476                     -0.2075534
         traittarsus.1:traitbwt.2.units traitbwt.1:traitbwt.2.units
Lag 0                         0.9603400                   0.9034487
Lag 100                       0.9444274                   0.8893146
Lag 500                       0.9054416                   0.8539291
Lag 1000                      0.8617258                   0.8157349
Lag 5000                      0.6022291                   0.5773694
         traittarsus.2:traitbwt.2.units traitbwt.2:traitbwt.2.units
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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
```

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Lag 0                             0.2159001                       0.1778597
Lag 100                           0.2292097                       0.1832967
Lag 500                           0.2470830                       0.2035349
Lag 1000                          0.2430281                       0.2085231
Lag 5000                          0.1564420                       0.1096782
         traittarsus.2:traittarsus.2.animal traitbwt.2:traittarsus.2.animal
Lag 0                             0.2148002                       0.2380759
Lag 100                           0.2260582                       0.2490150
Lag 500                           0.2434250                       0.2659527
Lag 1000                          0.2396319                       0.2621966
Lag 5000                          0.2311987                       0.2321063
         traittarsus.1:traitbwt.2.animal traitbwt.1:traitbwt.2.animal
Lag 0                         0.18941930                    0.1473359
Lag 100                       0.19756460                    0.1558541
Lag 500                       0.21294438                    0.1829320
Lag 1000                      0.21181509                    0.1947599
Lag 5000                      0.09549646                    0.1076230
         traittarsus.2:traitbwt.2.animal traitbwt.2:traitbwt.2.animal
Lag 0                          0.2380759                    0.2116292
Lag 100                        0.2490150                    0.2231338
Lag 500                        0.2659527                    0.2429222
Lag 1000                       0.2621966                    0.2441661
Lag 5000                       0.2321063                    0.2236298
         traittarsus.1.byear traitbwt.1.byear traittarsus.2.byear
Lag 0           -0.032369970       0.05768879          0.06054337
Lag 100         -0.031641858       0.05864059          0.06580478
Lag 500         -0.001530924       0.04503326          0.07399288
Lag 1000        -0.016005519       0.03161375          0.08585903
Lag 5000         0.010619935       0.01730446         -0.02417570
         traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother
Lag 0        -0.032356483            0.1703875       0.012376673
Lag 100      -0.034654911            0.1647608       0.013581085
Lag 500      -0.052597308            0.1600416       0.005553001
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Lag 1000     -0.039591608            0.1872703      -0.009042770
Lag 5000      0.004455343            0.1972374      -0.027185781
         traittarsus.2.mother traitbwt.2.mother
Lag 0             -0.03846399        0.07575889
Lag 100           -0.03390447        0.06853459
Lag 500           -0.02862102        0.06274714
Lag 1000          -0.01799649        0.06065063
Lag 5000          -0.05555704        0.02202828
         traittarsus.1:traittarsus.1.units traitbwt.1:traittarsus.1.units
Lag 0                           -0.2645685                    -0.18013988
Lag 100                         -0.2616234                    -0.17607364
Lag 500                         -0.2652457                    -0.18034511
Lag 1000                        -0.2671219                    -0.17702256
Lag 5000                        -0.2093233                    -0.06028968
         traittarsus.2:traittarsus.1.units traitbwt.2:traittarsus.1.units
Lag 0                            0.9603400                      1.0000000
Lag 100                          0.9432077                      0.9762869
Lag 500                          0.9124477                      0.9252632
Lag 1000                         0.8838890                      0.8792611
Lag 5000                         0.6117319                      0.6007465
         traittarsus.1:traitbwt.1.units traitbwt.1:traitbwt.1.units
Lag 0                       -0.18013988                 -0.15026999
Lag 100                     -0.17607364                 -0.14749648
Lag 500                     -0.18034511                 -0.15145709
Lag 1000                    -0.17702256                 -0.15538707
Lag 5000                    -0.06028968                 -0.02621414
         traittarsus.2:traitbwt.1.units traitbwt.2:traitbwt.1.units
Lag 0                         0.9303986                   0.9527160
Lag 100                       0.9147001                   0.9321247
Lag 500                       0.8850543                   0.8884276
Lag 1000                      0.8576398                   0.8431799
Lag 5000                      0.5876791                   0.5807055
         traittarsus.1:traittarsus.2.units traitbwt.1:traittarsus.2.units
```

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Lag 0                           0.9603400                      0.9303986
Lag 100                         0.9432077                      0.9147001
Lag 500                         0.9124477                      0.8850543
Lag 1000                        0.8838890                      0.8576398
Lag 5000                        0.6117319                      0.5876791
         traittarsus.2:traittarsus.2.units traitbwt.2:traittarsus.2.units
Lag 0                          -0.2006563                     -0.2276707
Lag 100                        -0.2124295                     -0.2354203
Lag 500                        -0.2379446                     -0.2556157
Lag 1000                       -0.2389714                     -0.2561306
Lag 5000                       -0.2130152                     -0.2137306
         traittarsus.1:traitbwt.2.units traitbwt.1:traitbwt.2.units
Lag 0                         1.0000000                   0.9527160
Lag 100                       0.9762869                   0.9321247
Lag 500                       0.9252632                   0.8884276
Lag 1000                      0.8792611                   0.8431799
Lag 5000                      0.6007465                   0.5807055
         traittarsus.2:traitbwt.2.units traitbwt.2:traitbwt.2.units
Lag 0                        -0.2276707                  -0.2128094
Lag 100                      -0.2354203                  -0.2168142
Lag 500                      -0.2556157                  -0.2324758
Lag 1000                     -0.2561306                  -0.2373888
Lag 5000                     -0.2137306                  -0.1974646

, , traittarsus.1:traitbwt.1.units


         traittarsus.1:traittarsus.1.animal traitbwt.1:traittarsus.1.animal
Lag 0                           -0.5806661                      -0.7822168
Lag 100                         -0.5195230                      -0.6845208
Lag 500                         -0.3880444                      -0.4391722
Lag 1000                        -0.2850697                      -0.3219049
Lag 5000                        -0.1858774                      -0.1615545
         traittarsus.2:traittarsus.1.animal traitbwt.2:traittarsus.1.animal
```

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Lag 0                              -0.3551367                      -0.4423544
Lag 100                            -0.3116917                      -0.4053917
Lag 500                            -0.2504438                      -0.3222535
Lag 1000                           -0.2164808                      -0.2714011
Lag 5000                           -0.1964028                      -0.1739972
         traittarsus.1:traitbwt.1.animal traitbwt.1:traitbwt.1.animal
Lag 0                         -0.7822168                   -0.5785722
Lag 100                       -0.6845208                   -0.5036377
Lag 500                       -0.4391722                   -0.3105590
Lag 1000                      -0.3219049                   -0.2500610
Lag 5000                      -0.1615545                   -0.1051180
         traittarsus.2:traitbwt.1.animal traitbwt.2:traitbwt.1.animal
Lag 0                         -0.3850991                   -0.3630159
Lag 100                       -0.3306453                   -0.3097920
Lag 500                       -0.2840530                   -0.2549302
Lag 1000                      -0.2403468                   -0.2124423
Lag 5000                      -0.2587649                   -0.2036370
         traittarsus.1:traittarsus.2.animal traitbwt.1:traittarsus.2.animal
Lag 0                            -0.3551367                      -0.3850991
Lag 100                          -0.3116917                      -0.3306453
Lag 500                          -0.2504438                      -0.2840530
Lag 1000                         -0.2164808                      -0.2403468
Lag 5000                         -0.1964028                      -0.2587649
         traittarsus.2:traittarsus.2.animal traitbwt.2:traittarsus.2.animal
Lag 0                           -0.10398125                      -0.1467921
Lag 100                         -0.07656994                      -0.1228344
Lag 500                         -0.05666776                      -0.1265197
Lag 1000                        -0.08628503                      -0.1605079
Lag 5000                        -0.11080574                      -0.1945688
         traittarsus.1:traitbwt.2.animal traitbwt.1:traitbwt.2.animal
Lag 0                         -0.4423544                   -0.3630159
Lag 100                       -0.4053917                   -0.3097920
Lag 500                       -0.3222535                   -0.2549302
```

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Lag 1000                      -0.2714011                   -0.2124423
Lag 5000                      -0.1739972                   -0.2036370
         traittarsus.2:traitbwt.2.animal traitbwt.2:traitbwt.2.animal
Lag 0                         -0.1467921                   -0.1324172
Lag 100                       -0.1228344                   -0.1123196
Lag 500                       -0.1265197                   -0.1443413
Lag 1000                      -0.1605079                   -0.1717954
Lag 5000                      -0.1945688                   -0.2243561
         traittarsus.1.byear traitbwt.1.byear traittarsus.2.byear
Lag 0            -0.10471675       0.01021951        0.0004983836
Lag 100          -0.08194667       0.01380504       -0.0044687157
Lag 500          -0.01278894       0.03290932       -0.0005650915
Lag 1000         -0.06407190      -0.02170329        0.0530406940
Lag 5000         -0.07516029      -0.06130238       -0.0224119290
         traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother
Lag 0          0.02175859         -0.039522955        0.03665672
Lag 100        0.03477326         -0.019056605        0.05315654
Lag 500       -0.01973469         -0.002626844        0.03028858
Lag 1000       0.04003712          0.003169525        0.06449203
Lag 5000       0.02550062         -0.010727363        0.04503907
         traittarsus.2.mother traitbwt.2.mother
Lag 0             -0.03359578      -0.012479028
Lag 100           -0.04488434      -0.002934766
Lag 500           -0.06697376       0.021613573
Lag 1000          -0.08457909       0.019481160
Lag 5000          -0.08600099       0.051485249
         traittarsus.1:traittarsus.1.units traitbwt.1:traittarsus.1.units
Lag 0                            0.7126648                      1.0000000
Lag 100                          0.4891102                      0.6680602
Lag 500                          0.3020606                      0.3997173
Lag 1000                         0.2345067                      0.2999511
Lag 5000                         0.1759098                      0.1561292
         traittarsus.2:traittarsus.1.units traitbwt.2:traittarsus.1.units
```

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Lag 0                         -0.1706739                    -0.1801399
Lag 100                       -0.1802375                    -0.1994176
Lag 500                       -0.2103921                    -0.2440747
Lag 1000                      -0.2087782                    -0.2510893
Lag 5000                      -0.1812853                    -0.1905911
         traittarsus.1:traitbwt.1.units traitbwt.1:traitbwt.1.units
Lag 0                         1.0000000                   0.8197350
Lag 100                       0.6680602                   0.5536026
Lag 500                       0.3997173                   0.3326177
Lag 1000                      0.2999511                   0.2334663
Lag 5000                      0.1561292                   0.1202757
         traittarsus.2:traitbwt.1.units traitbwt.2:traitbwt.1.units
Lag 0                        -0.1666030                  -0.1700866
Lag 100                      -0.1812316                  -0.1939150
Lag 500                      -0.2194596                  -0.2430469
Lag 1000                     -0.2384353                  -0.2743602
Lag 5000                     -0.2008085                  -0.2014312
         traittarsus.1:traittarsus.2.units traitbwt.1:traittarsus.2.units
Lag 0                         -0.1706739                    -0.1666030
Lag 100                       -0.1802375                    -0.1812316
Lag 500                       -0.2103921                    -0.2194596
Lag 1000                      -0.2087782                    -0.2384353
Lag 5000                      -0.1812853                    -0.2008085
         traittarsus.2:traittarsus.2.units traitbwt.2:traittarsus.2.units
Lag 0                         0.10875399                    0.13276682
Lag 100                       0.05904373                    0.09500984
Lag 500                       0.06612909                    0.11639092
Lag 1000                      0.10572947                    0.15285062
Lag 5000                      0.15545551                    0.20383203
         traittarsus.1:traitbwt.2.units traitbwt.1:traitbwt.2.units
Lag 0                        -0.1801399                  -0.1700866
Lag 100                      -0.1994176                  -0.1939150
Lag 500                      -0.2440747                  -0.2430469
```

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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
```

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Lag 1000                      -0.1803300                   -0.2025644
Lag 5000                      -0.2243905                   -0.1275516
         traittarsus.1:traittarsus.2.animal traitbwt.1:traittarsus.2.animal
Lag 0                        -0.16353731                      -0.2793636
Lag 100                      -0.13444098                      -0.2441693
Lag 500                      -0.07860312                      -0.1881361
Lag 1000                     -0.07437860                      -0.1803300
Lag 5000                     -0.15240021                      -0.2243905
         traittarsus.2:traittarsus.2.animal traitbwt.2:traittarsus.2.animal
Lag 0                        -0.10182068                     -0.14376430
Lag 100                      -0.07461870                     -0.12129614
Lag 500                      -0.03475445                     -0.09690301
Lag 1000                     -0.07582375                     -0.13287333
Lag 5000                     -0.06172035                     -0.10552070
         traittarsus.1:traitbwt.2.animal traitbwt.1:traitbwt.2.animal
Lag 0                     -0.33002093                   -0.3902410
Lag 100                   -0.30242196                   -0.3411243
Lag 500                   -0.20182430                   -0.2431591
Lag 1000                  -0.16489835                   -0.2025644
Lag 5000                  -0.07855392                   -0.1275516
         traittarsus.2:traitbwt.2.animal traitbwt.2:traitbwt.2.animal
Lag 0                     -0.14376430                   -0.1400636
Lag 100                   -0.12129614                   -0.1267043
Lag 500                   -0.09690301                   -0.1357567
Lag 1000                  -0.13287333                   -0.1570152
Lag 5000                  -0.10552070                   -0.1203712
         traittarsus.1.byear traitbwt.1.byear traittarsus.2.byear
Lag 0           -0.071954690     -0.028183637          0.04524320
Lag 100         -0.044770596      0.002882978          0.03767827
Lag 500         -0.005911696      0.003838461          0.01619977
Lag 1000        -0.056263708      0.008443638          0.05346543
Lag 5000        -0.087263536     -0.023015448         -0.01948411
         traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother
```

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Lag 0         0.008779544          0.028265685      -0.007047622
Lag 100       0.013764785          0.026135300       0.054993361
Lag 500      -0.033989612          0.002688467       0.096589744
Lag 1000      0.025220721          0.005441149       0.099042795
Lag 5000      0.047628522         -0.007718921       0.047775710
         traittarsus.2.mother traitbwt.2.mother
Lag 0             -0.04785615      -0.009223763
Lag 100           -0.05001172       0.003907093
Lag 500           -0.07099090       0.044036802
Lag 1000          -0.05777658       0.037746309
Lag 5000          -0.09694236       0.069793617
         traittarsus.1:traittarsus.1.units traitbwt.1:traittarsus.1.units
Lag 0                           0.36066940                       0.8197350
Lag 100                         0.25257032                       0.5640460
Lag 500                         0.11373127                       0.3085415
Lag 1000                        0.07190253                       0.2121382
Lag 5000                        0.13152446                       0.1159014
         traittarsus.2:traittarsus.1.units traitbwt.2:traittarsus.1.units
Lag 0                           -0.1274160                      -0.1502700
Lag 100                         -0.1314926                      -0.1663342
Lag 500                         -0.1561690                      -0.2058338
Lag 1000                        -0.1493199                      -0.1963753
Lag 5000                        -0.1353839                      -0.1194476
         traittarsus.1:traitbwt.1.units traitbwt.1:traitbwt.1.units
Lag 0                         0.8197350                   1.00000000
Lag 100                       0.5640460                   0.66059880
Lag 500                       0.3085415                   0.35457689
Lag 1000                      0.2121382                   0.23677816
Lag 5000                      0.1159014                   0.06278176
         traittarsus.2:traitbwt.1.units traitbwt.2:traitbwt.1.units
Lag 0                        -0.1670809                   -0.1902055
Lag 100                      -0.1716919                   -0.2107271
Lag 500                      -0.1984597                   -0.2462995
```

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Lag 1000                    -0.2124167                  -0.2635936
Lag 5000                    -0.1444361                  -0.1252641
         traittarsus.1:traittarsus.2.units traitbwt.1:traittarsus.2.units
Lag 0                          -0.1274160                     -0.1670809
Lag 100                        -0.1314926                     -0.1716919
Lag 500                        -0.1561690                     -0.1984597
Lag 1000                       -0.1493199                     -0.2124167
Lag 5000                       -0.1353839                     -0.1444361
         traittarsus.2:traittarsus.2.units traitbwt.2:traittarsus.2.units
Lag 0                          0.11081955                     0.13741353
Lag 100                        0.06249231                     0.09952814
Lag 500                        0.04779758                     0.10118050
Lag 1000                       0.09619023                     0.13533567
Lag 5000                       0.09963826                     0.10989738
         traittarsus.1:traitbwt.2.units traitbwt.1:traitbwt.2.units
Lag 0                       -0.1502700                  -0.1902055
Lag 100                     -0.1663342                  -0.2107271
Lag 500                     -0.2058338                  -0.2462995
Lag 1000                    -0.1963753                  -0.2635936
Lag 5000                    -0.1194476                  -0.1252641
         traittarsus.2:traitbwt.2.units traitbwt.2:traitbwt.2.units
Lag 0                       0.13741353                   0.1314508
Lag 100                     0.09952814                   0.1030693
Lag 500                     0.10118050                   0.1373268
Lag 1000                    0.13533567                   0.1500819
Lag 5000                    0.10989738                   0.1138216

, , traittarsus.2:traitbwt.1.units


         traittarsus.1:traittarsus.1.animal traitbwt.1:traittarsus.1.animal
Lag 0                             0.1148525                      0.10037928
Lag 100                           0.1303566                      0.10703233
Lag 500                           0.1453432                      0.12751184
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Lag 1000                      0.1449075                      0.12663225
Lag 5000                      0.1652756                      0.03681818
         traittarsus.2:traittarsus.1.animal traitbwt.2:traittarsus.1.animal
Lag 0                         0.1588923                       0.1392793
Lag 100                       0.1783256                       0.1463284
Lag 500                       0.2040736                       0.1612874
Lag 1000                      0.2230315                       0.1896293
Lag 5000                      0.1750420                       0.0827739
         traittarsus.1:traitbwt.1.animal traitbwt.1:traitbwt.1.animal
Lag 0                        0.10037928                  0.12062597
Lag 100                      0.10703233                  0.11559443
Lag 500                      0.12751184                  0.11837717
Lag 1000                     0.12663225                  0.10630852
Lag 5000                     0.03681818                 -0.04309778
         traittarsus.2:traitbwt.1.animal traitbwt.2:traitbwt.1.animal
Lag 0                         0.1142625                  0.09800038
Lag 100                       0.1363961                  0.11259128
Lag 500                       0.1781857                  0.14358029
Lag 1000                      0.1973172                  0.16595148
Lag 5000                      0.1261037                  0.08832747
         traittarsus.1:traittarsus.2.animal traitbwt.1:traittarsus.2.animal
Lag 0                         0.1588923                       0.1142625
Lag 100                       0.1783256                       0.1363961
Lag 500                       0.2040736                       0.1781857
Lag 1000                      0.2230315                       0.1973172
Lag 5000                      0.1750420                       0.1261037
         traittarsus.2:traittarsus.2.animal traitbwt.2:traittarsus.2.animal
Lag 0                         0.2227014                       0.2177824
Lag 100                       0.2383512                       0.2331011
Lag 500                       0.2644369                       0.2625082
Lag 1000                      0.2577927                       0.2670893
Lag 5000                      0.1772736                       0.1885761
         traittarsus.1:traitbwt.2.animal traitbwt.1:traitbwt.2.animal
```

```
Lag 0                        0.1392793                 0.09800038
Lag 100                      0.1463284                 0.11259128
Lag 500                      0.1612874                 0.14358029
Lag 1000                     0.1896293                 0.16595148
Lag 5000                     0.0827739                 0.08832747
         traittarsus.2:traitbwt.2.animal traitbwt.2:traitbwt.2.animal
Lag 0                        0.2177824                  0.1727839
Lag 100                      0.2331011                  0.1869982
Lag 500                      0.2625082                  0.2195418
Lag 1000                     0.2670893                  0.2381230
Lag 5000                     0.1885761                  0.1980800
         traittarsus.1.byear traitbwt.1.byear traittarsus.2.byear
Lag 0           -0.027499725       0.04996250          0.04569537
Lag 100         -0.023937020       0.05747431          0.04863214
Lag 500         -0.009997799       0.05757848          0.05649481
Lag 1000        -0.028336813       0.03932991          0.08794045
Lag 5000        -0.028421868       0.02850733         -0.02604903
         traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother
Lag 0        -0.0558751650            0.1570314      -0.002752353
Lag 100      -0.0390036691            0.1577619      -0.005577721
Lag 500      -0.0604361094            0.1762753      -0.008689304
Lag 1000     -0.0544777158            0.1711484      -0.003879605
Lag 5000      0.0009703848            0.1611550       0.001378773
         traittarsus.2.mother traitbwt.2.mother
Lag 0             -0.04476711        0.07595500
Lag 100           -0.04782246        0.07837204
Lag 500           -0.04024464        0.07773574
Lag 1000          -0.01332984        0.04580976
Lag 5000          -0.03731338        0.02497852
         traittarsus.1:traittarsus.1.units traitbwt.1:traittarsus.1.units
Lag 0                           -0.2009925                    -0.16660301
Lag 100                         -0.2135650                    -0.16581994
Lag 500                         -0.2387289                    -0.17888627
```

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Lag 1000                        -0.2382720                    -0.17175572
Lag 5000                        -0.2290178                    -0.06304922
         traittarsus.2:traittarsus.1.units traitbwt.2:traittarsus.1.units
Lag 0                            0.9609935                      0.9303986
Lag 100                          0.9414150                      0.9167945
Lag 500                          0.9016587                      0.8805530
Lag 1000                         0.8646228                      0.8343108
Lag 5000                         0.5874768                      0.5773601
         traittarsus.1:traitbwt.1.units traitbwt.1:traitbwt.1.units
Lag 0                       -0.16660301                -0.167080898
Lag 100                     -0.16581994                -0.156138622
Lag 500                     -0.17888627                -0.151199166
Lag 1000                    -0.17175572                -0.139083793
Lag 5000                    -0.06304922                 0.007994506
         traittarsus.2:traitbwt.1.units traitbwt.2:traitbwt.1.units
Lag 0                         1.0000000                   0.9457989
Lag 100                       0.9647777                   0.9182192
Lag 500                       0.8967026                   0.8587466
Lag 1000                      0.8499110                   0.8058180
Lag 5000                      0.5555747                   0.5516644
         traittarsus.1:traittarsus.2.units traitbwt.1:traittarsus.2.units
Lag 0                            0.9609935                      1.0000000
Lag 100                          0.9414150                      0.9647777
Lag 500                          0.9016587                      0.8967026
Lag 1000                         0.8646228                      0.8499110
Lag 5000                         0.5874768                      0.5555747
         traittarsus.2:traittarsus.2.units traitbwt.2:traittarsus.2.units
Lag 0                           -0.2146171                     -0.2167857
Lag 100                         -0.2184104                     -0.2221790
Lag 500                         -0.2572470                     -0.2584745
Lag 1000                        -0.2569503                     -0.2596379
Lag 5000                        -0.1645148                     -0.1699811
         traittarsus.1:traitbwt.2.units traitbwt.1:traitbwt.2.units
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```
Lag 0                     0.9303986                   0.9457989
Lag 100                   0.9167945                   0.9182192
Lag 500                   0.8805530                   0.8587466
Lag 1000                  0.8343108                   0.8058180
Lag 5000                  0.5773601                   0.5516644
         traittarsus.2:traitbwt.2.units traitbwt.2:traitbwt.2.units
Lag 0                    -0.2167857                  -0.1800172
Lag 100                  -0.2221790                  -0.1849007
Lag 500                  -0.2584745                  -0.2183863
Lag 1000                 -0.2596379                  -0.2235166
Lag 5000                 -0.1699811                  -0.1684397

, , traitbwt.2:traitbwt.1.units

         traittarsus.1:traittarsus.1.animal traitbwt.1:traittarsus.1.animal
Lag 0                         0.1045202                      0.10675486
Lag 100                       0.1144301                      0.10909010
Lag 500                       0.1244192                      0.13415361
Lag 1000                      0.1101292                      0.11544191
Lag 5000                      0.1331335                      0.04367713
         traittarsus.2:traittarsus.1.animal traitbwt.2:traittarsus.1.animal
Lag 0                         0.1751169                      0.18455878
Lag 100                       0.1936998                      0.19497627
Lag 500                       0.2199790                      0.20989089
Lag 1000                      0.2292872                      0.21238609
Lag 5000                      0.1693953                      0.06254965
         traittarsus.1:traitbwt.1.animal traitbwt.1:traitbwt.1.animal
Lag 0                     0.10675486                   0.15466547
Lag 100                   0.10909010                   0.15753844
Lag 500                   0.13415361                   0.17187977
Lag 1000                  0.11544191                   0.14889411
Lag 5000                  0.04367713                  -0.01393939
         traittarsus.2:traitbwt.1.animal traitbwt.2:traitbwt.1.animal
```

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Lag 0                          0.1618783                   0.17860886
Lag 100                        0.1807130                   0.20406604
Lag 500                        0.2315550                   0.24587070
Lag 1000                       0.2433453                   0.24000705
Lag 5000                       0.1313066                   0.07959284
         traittarsus.1:traittarsus.2.animal traitbwt.1:traittarsus.2.animal
Lag 0                             0.1751169                       0.1618783
Lag 100                           0.1936998                       0.1807130
Lag 500                           0.2199790                       0.2315550
Lag 1000                          0.2292872                       0.2433453
Lag 5000                          0.1693953                       0.1313066
         traittarsus.2:traittarsus.2.animal traitbwt.2:traittarsus.2.animal
Lag 0                             0.2339355                       0.2581627
Lag 100                           0.2476485                       0.2736295
Lag 500                           0.2790724                       0.3078386
Lag 1000                          0.2842308                       0.3166841
Lag 5000                          0.2101542                       0.1923682
         traittarsus.1:traitbwt.2.animal traitbwt.1:traitbwt.2.animal
Lag 0                         0.18455878                   0.17860886
Lag 100                       0.19497627                   0.20406604
Lag 500                       0.20989089                   0.24587070
Lag 1000                      0.21238609                   0.24000705
Lag 5000                      0.06254965                   0.07959284
         traittarsus.2:traitbwt.2.animal traitbwt.2:traitbwt.2.animal
Lag 0                          0.2581627                    0.2416106
Lag 100                        0.2736295                    0.2608676
Lag 500                        0.3078386                    0.2963880
Lag 1000                       0.3166841                    0.3068141
Lag 5000                       0.1923682                    0.1712560
         traittarsus.1.byear traitbwt.1.byear traittarsus.2.byear
Lag 0           -0.023701193       0.04700881          0.05361674
Lag 100         -0.021944414       0.05837761          0.06114321
Lag 500         -0.004019018       0.04124133          0.05472308
```

```
Lag 1000        -0.014592442       0.02897141          0.08299624
Lag 5000        -0.001455363       0.01713092         -0.03330245
         traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother
Lag 0         -0.03458419            0.1501420      -0.030979909
Lag 100       -0.02882752            0.1495980      -0.034573917
Lag 500       -0.05044049            0.1542703      -0.037881298
Lag 1000      -0.04326520            0.1753867      -0.049179995
Lag 5000       0.01976572            0.1700994      -0.002621514
         traittarsus.2.mother traitbwt.2.mother
Lag 0             -0.05091781        0.08248472
Lag 100           -0.04612708        0.07643625
Lag 500           -0.04592155        0.07211789
Lag 1000          -0.02428388        0.04810929
Lag 5000          -0.05454058        0.02230047
         traittarsus.1:traittarsus.1.units traitbwt.1:traittarsus.1.units
Lag 0                           -0.1971901                    -0.17008659
Lag 100                         -0.2006748                    -0.16466175
Lag 500                         -0.2146434                    -0.17764629
Lag 1000                        -0.2152829                    -0.15594317
Lag 5000                        -0.2163189                    -0.07951097
         traittarsus.2:traittarsus.1.units traitbwt.2:traittarsus.1.units
Lag 0                            0.9034487                      0.9527160
Lag 100                          0.8867034                      0.9318204
Lag 500                          0.8558412                      0.8820862
Lag 1000                         0.8281770                      0.8332104
Lag 5000                         0.5777198                      0.5582022
         traittarsus.1:traitbwt.1.units traitbwt.1:traitbwt.1.units
Lag 0                       -0.17008659                  -0.1902055
Lag 100                     -0.16466175                  -0.1881759
Lag 500                     -0.17764629                  -0.1918480
Lag 1000                    -0.15594317                  -0.1592987
Lag 5000                    -0.07951097                  -0.0307547
         traittarsus.2:traitbwt.1.units traitbwt.2:traitbwt.1.units
```

```
Lag 0                        0.9457989                   1.0000000
Lag 100                      0.9171312                   0.9591397
Lag 500                      0.8650556                   0.8846934
Lag 1000                     0.8286470                   0.8252821
Lag 5000                     0.5520607                   0.5384118
         traittarsus.1:traittarsus.2.units traitbwt.1:traittarsus.2.units
Lag 0                           0.9034487                      0.9457989
Lag 100                         0.8867034                      0.9171312
Lag 500                         0.8558412                      0.8650556
Lag 1000                        0.8281770                      0.8286470
Lag 5000                        0.5777198                      0.5520607
         traittarsus.2:traittarsus.2.units traitbwt.2:traittarsus.2.units
Lag 0                          -0.2187484                     -0.2507033
Lag 100                        -0.2283894                     -0.2593514
Lag 500                        -0.2686154                     -0.2983604
Lag 1000                       -0.2818961                     -0.3082824
Lag 5000                       -0.1951997                     -0.1732268
         traittarsus.1:traitbwt.2.units traitbwt.1:traitbwt.2.units
Lag 0                        0.9527160                   1.0000000
Lag 100                      0.9318204                   0.9591397
Lag 500                      0.8820862                   0.8846934
Lag 1000                     0.8332104                   0.8252821
Lag 5000                     0.5582022                   0.5384118
         traittarsus.2:traitbwt.2.units traitbwt.2:traitbwt.2.units
Lag 0                       -0.2507033                  -0.2443613
Lag 100                     -0.2593514                  -0.2551879
Lag 500                     -0.2983604                  -0.2884325
Lag 1000                    -0.3082824                  -0.2942164
Lag 5000                    -0.1732268                  -0.1455134

, , traittarsus.1:traittarsus.2.units

         traittarsus.1:traittarsus.1.animal traitbwt.1:traittarsus.1.animal
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```
Lag 0                     0.1834123                     0.124710076
Lag 100                   0.1968309                     0.130500544
Lag 500                   0.2068864                     0.139328738
Lag 1000                  0.1939570                     0.142277480
Lag 5000                  0.1325680                     0.009474997
         traittarsus.2:traittarsus.1.animal traitbwt.2:traittarsus.1.animal
Lag 0                     0.1906441                      0.13328596
Lag 100                   0.2063827                      0.13989222
Lag 500                   0.2249905                      0.15953298
Lag 1000                  0.2243627                      0.17422740
Lag 5000                  0.1612708                      0.09845918
         traittarsus.1:traitbwt.1.animal traitbwt.1:traitbwt.1.animal
Lag 0                        0.124710076                   0.08095300
Lag 100                      0.130500544                   0.07950890
Lag 500                      0.139328738                   0.07894049
Lag 1000                     0.142277480                   0.08409986
Lag 5000                     0.009474997                  -0.03476503
         traittarsus.2:traitbwt.1.animal traitbwt.2:traitbwt.1.animal
Lag 0                         0.13041646                   0.06808542
Lag 100                       0.13619199                   0.07439607
Lag 500                       0.15236746                   0.10133254
Lag 1000                      0.16354531                   0.12513909
Lag 5000                      0.09727094                   0.09702098
         traittarsus.1:traittarsus.2.animal traitbwt.1:traittarsus.2.animal
Lag 0                     0.1906441                      0.13041646
Lag 100                   0.2063827                      0.13619199
Lag 500                   0.2249905                      0.15236746
Lag 1000                  0.2243627                      0.16354531
Lag 5000                  0.1612708                      0.09727094
         traittarsus.2:traittarsus.2.animal traitbwt.2:traittarsus.2.animal
Lag 0                     0.1881270                       0.1805175
Lag 100                   0.2019192                       0.1895957
Lag 500                   0.2143083                       0.2038416
```

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Lag 1000                          0.2049762                      0.2031078
Lag 5000                          0.2015150                      0.2236163
         traittarsus.1:traitbwt.2.animal traitbwt.1:traitbwt.2.animal
Lag 0                         0.13328596                   0.06808542
Lag 100                       0.13989222                   0.07439607
Lag 500                       0.15953298                   0.10133254
Lag 1000                      0.17422740                   0.12513909
Lag 5000                      0.09845918                   0.09702098
         traittarsus.2:traitbwt.2.animal traitbwt.2:traitbwt.2.animal
Lag 0                          0.1805175                    0.1307188
Lag 100                        0.1895957                    0.1387545
Lag 500                        0.2038416                    0.1596754
Lag 1000                       0.2031078                    0.1718471
Lag 5000                       0.2236163                    0.2388384
         traittarsus.1.byear traitbwt.1.byear traittarsus.2.byear
Lag 0            -0.03847015       0.05293519          0.06126409
Lag 100          -0.03144044       0.04956734          0.06250612
Lag 500          -0.01780154       0.05591029          0.07921148
Lag 1000         -0.02643841       0.04337011          0.09113494
Lag 5000         -0.01140358       0.03031863         -0.02594409
         traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother
Lag 0        -0.041798551            0.1697424        0.04294093
Lag 100      -0.034073821            0.1688986        0.04145441
Lag 500      -0.048890409            0.1720568        0.02794912
Lag 1000     -0.040999443            0.1790535        0.02144402
Lag 5000     -0.002784642            0.1836021       -0.02796491
         traittarsus.2.mother traitbwt.2.mother
Lag 0             -0.03239456        0.06299708
Lag 100           -0.03271179        0.06442310
Lag 500           -0.02932124        0.06841853
Lag 1000          -0.01370787        0.05547883
Lag 5000          -0.04156138        0.02258640
         traittarsus.1:traittarsus.1.units traitbwt.1:traittarsus.1.units
```

```
Lag 0                           -0.2592850                    -0.17067395
Lag 100                         -0.2666810                    -0.16983312
Lag 500                         -0.2761829                    -0.17499382
Lag 1000                        -0.2748628                    -0.18004636
Lag 5000                        -0.2185399                    -0.04226407
         traittarsus.2:traittarsus.1.units traitbwt.2:traittarsus.1.units
Lag 0                            1.0000000                      0.9603400
Lag 100                          0.9783825                      0.9444274
Lag 500                          0.9365031                      0.9054416
Lag 1000                         0.8964880                      0.8617258
Lag 5000                         0.6039003                      0.6022291
         traittarsus.1:traitbwt.1.units traitbwt.1:traitbwt.1.units
Lag 0                       -0.17067395                 -0.12741602
Lag 100                     -0.16983312                 -0.12362277
Lag 500                     -0.17499382                 -0.11972769
Lag 1000                    -0.18004636                 -0.12502460
Lag 5000                    -0.04226407                  0.01790192
         traittarsus.2:traitbwt.1.units traitbwt.2:traitbwt.1.units
Lag 0                          0.9609935                   0.9034487
Lag 100                        0.9411829                   0.8893146
Lag 500                        0.8990207                   0.8539291
Lag 1000                       0.8622161                   0.8157349
Lag 5000                       0.5753236                   0.5773694
         traittarsus.1:traittarsus.2.units traitbwt.1:traittarsus.2.units
Lag 0                            1.0000000                      0.9609935
Lag 100                          0.9783825                      0.9411829
Lag 500                          0.9365031                      0.8990207
Lag 1000                         0.8964880                      0.8622161
Lag 5000                         0.6039003                      0.5753236
         traittarsus.2:traittarsus.2.units traitbwt.2:traittarsus.2.units
Lag 0                           -0.1856903                     -0.1801544
Lag 100                         -0.1921763                     -0.1830867
Lag 500                         -0.2110415                     -0.2009371
```

```
Lag 1000                        -0.2033807                     -0.1989511
Lag 5000                        -0.1866476                     -0.2075534
         traittarsus.1:traitbwt.2.units traitbwt.1:traitbwt.2.units
Lag 0                         0.9603400                   0.9034487
Lag 100                       0.9444274                   0.8893146
Lag 500                       0.9054416                   0.8539291
Lag 1000                      0.8617258                   0.8157349
Lag 5000                      0.6022291                   0.5773694
         traittarsus.2:traitbwt.2.units traitbwt.2:traitbwt.2.units
Lag 0                        -0.1801544                  -0.1345421
Lag 100                      -0.1830867                  -0.1370653
Lag 500                      -0.2009371                  -0.1566901
Lag 1000                     -0.1989511                  -0.1643648
Lag 5000                     -0.2075534                  -0.2123302

, , traitbwt.1:traittarsus.2.units

         traittarsus.1:traittarsus.1.animal traitbwt.1:traittarsus.1.animal
Lag 0                             0.1148525                      0.10037928
Lag 100                           0.1303566                      0.10703233
Lag 500                           0.1453432                      0.12751184
Lag 1000                          0.1449075                      0.12663225
Lag 5000                          0.1652756                      0.03681818
         traittarsus.2:traittarsus.1.animal traitbwt.2:traittarsus.1.animal
Lag 0                             0.1588923                       0.1392793
Lag 100                           0.1783256                       0.1463284
Lag 500                           0.2040736                       0.1612874
Lag 1000                          0.2230315                       0.1896293
Lag 5000                          0.1750420                       0.0827739
         traittarsus.1:traitbwt.1.animal traitbwt.1:traitbwt.1.animal
Lag 0                         0.10037928                   0.12062597
Lag 100                       0.10703233                   0.11559443
Lag 500                       0.12751184                   0.11837717
```

```
Lag 1000                      0.12663225                   0.10630852
Lag 5000                      0.03681818                  -0.04309778
         traittarsus.2:traitbwt.1.animal traitbwt.2:traitbwt.1.animal
Lag 0                          0.1142625                   0.09800038
Lag 100                        0.1363961                   0.11259128
Lag 500                        0.1781857                   0.14358029
Lag 1000                       0.1973172                   0.16595148
Lag 5000                       0.1261037                   0.08832747
         traittarsus.1:traittarsus.2.animal traitbwt.1:traittarsus.2.animal
Lag 0                                 0.1588923                       0.1142625
Lag 100                               0.1783256                       0.1363961
Lag 500                               0.2040736                       0.1781857
Lag 1000                              0.2230315                       0.1973172
Lag 5000                              0.1750420                       0.1261037
         traittarsus.2:traittarsus.2.animal traitbwt.2:traittarsus.2.animal
Lag 0                                 0.2227014                       0.2177824
Lag 100                               0.2383512                       0.2331011
Lag 500                               0.2644369                       0.2625082
Lag 1000                              0.2577927                       0.2670893
Lag 5000                              0.1772736                       0.1885761
         traittarsus.1:traitbwt.2.animal traitbwt.1:traitbwt.2.animal
Lag 0                          0.1392793                   0.09800038
Lag 100                        0.1463284                   0.11259128
Lag 500                        0.1612874                   0.14358029
Lag 1000                       0.1896293                   0.16595148
Lag 5000                       0.0827739                   0.08832747
         traittarsus.2:traitbwt.2.animal traitbwt.2:traitbwt.2.animal
Lag 0                          0.2177824                    0.1727839
Lag 100                        0.2331011                    0.1869982
Lag 500                        0.2625082                    0.2195418
Lag 1000                       0.2670893                    0.2381230
Lag 5000                       0.1885761                    0.1980800
         traittarsus.1.byear traitbwt.1.byear traittarsus.2.byear
```

```
Lag 0           -0.027499725       0.04996250          0.04569537
Lag 100         -0.023937020       0.05747431          0.04863214
Lag 500         -0.009997799       0.05757848          0.05649481
Lag 1000        -0.028336813       0.03932991          0.08794045
Lag 5000        -0.028421868       0.02850733         -0.02604903
         traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother
Lag 0       -0.0558751650            0.1570314      -0.002752353
Lag 100     -0.0390036691            0.1577619      -0.005577721
Lag 500     -0.0604361094            0.1762753      -0.008689304
Lag 1000    -0.0544777158            0.1711484      -0.003879605
Lag 5000     0.0009703848            0.1611550       0.001378773
         traittarsus.2.mother traitbwt.2.mother
Lag 0             -0.04476711        0.07595500
Lag 100           -0.04782246        0.07837204
Lag 500           -0.04024464        0.07773574
Lag 1000          -0.01332984        0.04580976
Lag 5000          -0.03731338        0.02497852
         traittarsus.1:traittarsus.1.units traitbwt.1:traittarsus.1.units
Lag 0                           -0.2009925                    -0.16660301
Lag 100                         -0.2135650                    -0.16581994
Lag 500                         -0.2387289                    -0.17888627
Lag 1000                        -0.2382720                    -0.17175572
Lag 5000                        -0.2290178                    -0.06304922
         traittarsus.2:traittarsus.1.units traitbwt.2:traittarsus.1.units
Lag 0                            0.9609935                      0.9303986
Lag 100                          0.9414150                      0.9167945
Lag 500                          0.9016587                      0.8805530
Lag 1000                         0.8646228                      0.8343108
Lag 5000                         0.5874768                      0.5773601
         traittarsus.1:traitbwt.1.units traitbwt.1:traitbwt.1.units
Lag 0                       -0.16660301                -0.167080898
Lag 100                     -0.16581994                -0.156138622
Lag 500                     -0.17888627                -0.151199166
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Lag 1000                    -0.17175572                -0.139083793
Lag 5000                    -0.06304922                 0.007994506
         traittarsus.2:traitbwt.1.units traitbwt.2:traitbwt.1.units
Lag 0                         1.0000000                   0.9457989
Lag 100                       0.9647777                   0.9182192
Lag 500                       0.8967026                   0.8587466
Lag 1000                      0.8499110                   0.8058180
Lag 5000                      0.5555747                   0.5516644
         traittarsus.1:traittarsus.2.units traitbwt.1:traittarsus.2.units
Lag 0                                0.9609935                      1.0000000
Lag 100                              0.9414150                      0.9647777
Lag 500                              0.9016587                      0.8967026
Lag 1000                             0.8646228                      0.8499110
Lag 5000                             0.5874768                      0.5555747
         traittarsus.2:traittarsus.2.units traitbwt.2:traittarsus.2.units
Lag 0                               -0.2146171                     -0.2167857
Lag 100                             -0.2184104                     -0.2221790
Lag 500                             -0.2572470                     -0.2584745
Lag 1000                            -0.2569503                     -0.2596379
Lag 5000                            -0.1645148                     -0.1699811
         traittarsus.1:traitbwt.2.units traitbwt.1:traitbwt.2.units
Lag 0                         0.9303986                   0.9457989
Lag 100                       0.9167945                   0.9182192
Lag 500                       0.8805530                   0.8587466
Lag 1000                      0.8343108                   0.8058180
Lag 5000                      0.5773601                   0.5516644
         traittarsus.2:traitbwt.2.units traitbwt.2:traitbwt.2.units
Lag 0                        -0.2167857                  -0.1800172
Lag 100                      -0.2221790                  -0.1849007
Lag 500                      -0.2584745                  -0.2183863
Lag 1000                     -0.2596379                  -0.2235166
Lag 5000                     -0.1699811                  -0.1684397
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, , traittarsus.2:traittarsus.2.units

         traittarsus.1:traittarsus.1.animal traitbwt.1:traittarsus.1.animal
Lag 0                           -0.09279221                     -0.09677793
Lag 100                         -0.06813005                     -0.09295582
Lag 500                         -0.02512501                     -0.08099239
Lag 1000                        -0.02287160                     -0.08741368
Lag 5000                         0.07141747                      0.05570893
         traittarsus.2:traittarsus.1.animal traitbwt.2:traittarsus.1.animal
Lag 0                            -0.5600992                      -0.5541670
Lag 100                          -0.5121175                      -0.5169149
Lag 500                          -0.4106125                      -0.4295480
Lag 1000                         -0.3066655                      -0.3332778
Lag 5000                          0.2026604                       0.1966380
         traittarsus.1:traitbwt.1.animal traitbwt.1:traitbwt.1.animal
Lag 0                        -0.09677793                  -0.11346055
Lag 100                      -0.09295582                  -0.11622763
Lag 500                      -0.08099239                  -0.09958123
Lag 1000                     -0.08741368                  -0.12997232
Lag 5000                      0.05570893                   0.07322980
         traittarsus.2:traitbwt.1.animal traitbwt.2:traitbwt.1.animal
Lag 0                         -0.4185841                   -0.3843067
Lag 100                       -0.3914286                   -0.3603585
Lag 500                       -0.3364209                   -0.3074805
Lag 1000                      -0.2650097                   -0.2595029
Lag 5000                       0.1809913                    0.1272979
         traittarsus.1:traittarsus.2.animal traitbwt.1:traittarsus.2.animal
Lag 0                            -0.5600992                      -0.4185841
Lag 100                          -0.5121175                      -0.3914286
Lag 500                          -0.4106125                      -0.3364209
Lag 1000                         -0.3066655                      -0.2650097
Lag 5000                          0.2026604                       0.1809913
         traittarsus.2:traittarsus.2.animal traitbwt.2:traittarsus.2.animal
```

```
Lag 0                           -0.91073694                     -0.87501256
Lag 100                         -0.86504036                     -0.83310883
Lag 500                         -0.70973046                     -0.68729285
Lag 1000                        -0.55757696                     -0.54103224
Lag 5000                         0.02356453                      0.08002102
         traittarsus.1:traitbwt.2.animal traitbwt.1:traitbwt.2.animal
Lag 0                         -0.5541670                   -0.3843067
Lag 100                       -0.5169149                   -0.3603585
Lag 500                       -0.4295480                   -0.3074805
Lag 1000                      -0.3332778                   -0.2595029
Lag 5000                       0.1966380                    0.1272979
         traittarsus.2:traitbwt.2.animal traitbwt.2:traitbwt.2.animal
Lag 0                        -0.87501256                  -0.70436348
Lag 100                      -0.83310883                  -0.67114014
Lag 500                      -0.68729285                  -0.55786587
Lag 1000                     -0.54103224                  -0.43429408
Lag 5000                      0.08002102                   0.08588843
         traittarsus.1.byear traitbwt.1.byear traittarsus.2.byear
Lag 0          -0.0295325711       0.01013932         -0.05907849
Lag 100        -0.0258002546       0.01023903         -0.03799824
Lag 500        -0.0008409219       0.01222834         -0.02632830
Lag 1000       -0.0645850913      -0.04476975         -0.04078215
Lag 5000        0.0499883850      -0.01870262          0.03463537
         traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother
Lag 0          0.07499456          -0.05365944        0.08205572
Lag 100        0.07846166          -0.07198121        0.07982740
Lag 500        0.06122895          -0.08239796        0.07480035
Lag 1000       0.04893466          -0.08171638        0.06996265
Lag 5000      -0.05752959          -0.01133586       -0.02071995
         traittarsus.2.mother traitbwt.2.mother
Lag 0              0.13607402      -0.063098741
Lag 100            0.16280409      -0.056620767
Lag 500            0.14111652      -0.077496866
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Lag 1000           0.12664216      -0.055395330
Lag 5000           0.01649277      -0.003196996
         traittarsus.1:traittarsus.1.units traitbwt.1:traittarsus.1.units
Lag 0                           0.09543017                     0.10875399
Lag 100                         0.06598285                     0.08293245
Lag 500                         0.05295587                     0.08321338
Lag 1000                        0.06481928                     0.08697241
Lag 5000                       -0.09911194                    -0.09382365
         traittarsus.2:traittarsus.1.units traitbwt.2:traittarsus.1.units
Lag 0                          -0.18569026                    -0.20065634
Lag 100                        -0.19134621                    -0.20598290
Lag 500                        -0.19158726                    -0.20439959
Lag 1000                       -0.17346895                    -0.18874412
Lag 5000                       -0.04965337                    -0.05447094
         traittarsus.1:traitbwt.1.units traitbwt.1:traitbwt.1.units
Lag 0                        0.10875399                  0.11081955
Lag 100                      0.08293245                  0.09377309
Lag 500                      0.08321338                  0.07955802
Lag 1000                     0.08697241                  0.10737966
Lag 5000                    -0.09382365                 -0.07165472
         traittarsus.2:traitbwt.1.units traitbwt.2:traitbwt.1.units
Lag 0                       -0.21461708                  -0.2187484
Lag 100                     -0.21502402                  -0.2194216
Lag 500                     -0.20000700                  -0.2023328
Lag 1000                    -0.19364240                  -0.1958537
Lag 5000                    -0.02836013                  -0.0258784
         traittarsus.1:traittarsus.2.units traitbwt.1:traittarsus.2.units
Lag 0                          -0.18569026                    -0.21461708
Lag 100                        -0.19134621                    -0.21502402
Lag 500                        -0.19158726                    -0.20000700
Lag 1000                       -0.17346895                    -0.19364240
Lag 5000                       -0.04965337                    -0.02836013
         traittarsus.2:traittarsus.2.units traitbwt.2:traittarsus.2.units
```

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Lag 0                         1.0000000                    0.92685734
Lag 100                       0.8892164                    0.83343965
Lag 500                       0.7197831                    0.67640907
Lag 1000                      0.5723349                    0.53670401
Lag 5000                     -0.0393405                   -0.08858763
         traittarsus.1:traitbwt.2.units traitbwt.1:traitbwt.2.units
Lag 0                       -0.20065634                  -0.2187484
Lag 100                     -0.20598290                  -0.2194216
Lag 500                     -0.20439959                  -0.2023328
Lag 1000                    -0.18874412                  -0.1958537
Lag 5000                    -0.05447094                  -0.0258784
         traittarsus.2:traitbwt.2.units traitbwt.2:traitbwt.2.units
Lag 0                        0.92685734                  0.75421487
Lag 100                      0.83343965                  0.68043059
Lag 500                      0.67640907                  0.55259827
Lag 1000                     0.53670401                  0.43176584
Lag 5000                    -0.08858763                 -0.08998996

, , traitbwt.2:traittarsus.2.units


         traittarsus.1:traittarsus.1.animal traitbwt.1:traittarsus.1.animal
Lag 0                           -0.09066377                     -0.12847847
Lag 100                         -0.06791265                     -0.11660390
Lag 500                         -0.02813480                     -0.08793510
Lag 1000                        -0.02464042                     -0.10829057
Lag 5000                         0.09059977                      0.04232726
         traittarsus.2:traittarsus.1.animal traitbwt.2:traittarsus.1.animal
Lag 0                            -0.5208193                      -0.6200400
Lag 100                          -0.4814739                      -0.5760115
Lag 500                          -0.4160646                      -0.4939845
Lag 1000                         -0.3309504                      -0.3961937
Lag 5000                          0.1719378                       0.1704323
         traittarsus.1:traitbwt.1.animal traitbwt.1:traitbwt.1.animal
```

```
Lag 0                        -0.12847847                -0.16728073
Lag 100                      -0.11660390                -0.16431801
Lag 500                      -0.08793510                -0.14580635
Lag 1000                     -0.10829057                -0.17627597
Lag 5000                      0.04232726                 0.02621324
         traittarsus.2:traitbwt.1.animal traitbwt.2:traitbwt.1.animal
Lag 0                         -0.4729141                -0.49584021
Lag 100                       -0.4400289                -0.46178772
Lag 500                       -0.3667218                -0.38855190
Lag 1000                      -0.3075053                -0.32632756
Lag 5000                       0.1176403                 0.08762877
         traittarsus.1:traittarsus.2.animal traitbwt.1:traittarsus.2.animal
Lag 0                            -0.5208193                      -0.4729141
Lag 100                          -0.4814739                      -0.4400289
Lag 500                          -0.4160646                      -0.3667218
Lag 1000                         -0.3309504                      -0.3075053
Lag 5000                          0.1719378                       0.1176403
         traittarsus.2:traittarsus.2.animal traitbwt.2:traittarsus.2.animal
Lag 0                           -0.84107771                     -0.93853010
Lag 100                         -0.80537663                     -0.88900373
Lag 500                         -0.70011206                     -0.74957513
Lag 1000                        -0.58965340                     -0.62094832
Lag 5000                        -0.01326034                      0.04348338
         traittarsus.1:traitbwt.2.animal traitbwt.1:traitbwt.2.animal
Lag 0                         -0.6200400                -0.49584021
Lag 100                       -0.5760115                -0.46178772
Lag 500                       -0.4939845                -0.38855190
Lag 1000                      -0.3961937                -0.32632756
Lag 5000                       0.1704323                 0.08762877
         traittarsus.2:traitbwt.2.animal traitbwt.2:traitbwt.2.animal
Lag 0                        -0.93853010                -0.85484247
Lag 100                      -0.88900373                -0.80629890
Lag 500                      -0.74957513                -0.66699739
```

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Lag 1000                     -0.62094832                 -0.53588327
Lag 5000                      0.04348338                  0.06798066
         traittarsus.1.byear traitbwt.1.byear traittarsus.2.byear
Lag 0            -0.04533921     -0.001638125         -0.07410803
Lag 100          -0.04526568      0.002752216         -0.05435921
Lag 500          -0.02361959     -0.010266769         -0.04066778
Lag 1000         -0.08661480     -0.055915794         -0.03404716
Lag 5000          0.02028860     -0.015718402          0.05000555
         traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother
Lag 0         0.09224924          -0.08507034       0.117048388
Lag 100       0.09712475          -0.09090158       0.119562799
Lag 500       0.06704383          -0.06950074       0.093258667
Lag 1000      0.06946025          -0.09719184       0.091569829
Lag 5000     -0.05957284          -0.01506617      -0.004965446
         traittarsus.2.mother traitbwt.2.mother
Lag 0              0.11599294       -0.06384447
Lag 100            0.12644815       -0.06061567
Lag 500            0.12233108       -0.05933391
Lag 1000           0.11302925       -0.05409993
Lag 5000           0.02623229        0.01443371
         traittarsus.1:traittarsus.1.units traitbwt.1:traittarsus.1.units
Lag 0                           0.11602826                     0.13276682
Lag 100                         0.08412251                     0.10350782
Lag 500                         0.06419072                     0.10039070
Lag 1000                        0.08359941                     0.11689682
Lag 5000                       -0.10317497                    -0.07583069
         traittarsus.2:traittarsus.1.units traitbwt.2:traittarsus.1.units
Lag 0                           -0.1801544                     -0.2276707
Lag 100                         -0.1866591                     -0.2347923
Lag 500                         -0.1769783                     -0.2196866
Lag 1000                        -0.1617965                     -0.1997778
Lag 5000                        -0.0380065                     -0.0414611
         traittarsus.1:traitbwt.1.units traitbwt.1:traitbwt.1.units
```

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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
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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
```

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Lag 1000                          0.2430281                       0.2085231
Lag 5000                          0.1564420                       0.1096782
         traittarsus.2:traittarsus.2.animal traitbwt.2:traittarsus.2.animal
Lag 0                             0.2148002                       0.2380759
Lag 100                           0.2260582                       0.2490150
Lag 500                           0.2434250                       0.2659527
Lag 1000                          0.2396319                       0.2621966
Lag 5000                          0.2311987                       0.2321063
         traittarsus.1:traitbwt.2.animal traitbwt.1:traitbwt.2.animal
Lag 0                         0.18941930                    0.1473359
Lag 100                       0.19756460                    0.1558541
Lag 500                       0.21294438                    0.1829320
Lag 1000                      0.21181509                    0.1947599
Lag 5000                      0.09549646                    0.1076230
         traittarsus.2:traitbwt.2.animal traitbwt.2:traitbwt.2.animal
Lag 0                          0.2380759                    0.2116292
Lag 100                        0.2490150                    0.2231338
Lag 500                        0.2659527                    0.2429222
Lag 1000                       0.2621966                    0.2441661
Lag 5000                       0.2321063                    0.2236298
         traittarsus.1.byear traitbwt.1.byear traittarsus.2.byear
Lag 0           -0.032369970       0.05768879          0.06054337
Lag 100         -0.031641858       0.05864059          0.06580478
Lag 500         -0.001530924       0.04503326          0.07399288
Lag 1000        -0.016005519       0.03161375          0.08585903
Lag 5000         0.010619935       0.01730446         -0.02417570
         traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother
Lag 0        -0.032356483            0.1703875       0.012376673
Lag 100      -0.034654911            0.1647608       0.013581085
Lag 500      -0.052597308            0.1600416       0.005553001
Lag 1000     -0.039591608            0.1872703      -0.009042770
Lag 5000      0.004455343            0.1972374      -0.027185781
         traittarsus.2.mother traitbwt.2.mother
```

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Lag 0             -0.03846399        0.07575889
Lag 100           -0.03390447        0.06853459
Lag 500           -0.02862102        0.06274714
Lag 1000          -0.01799649        0.06065063
Lag 5000          -0.05555704        0.02202828
         traittarsus.1:traittarsus.1.units traitbwt.1:traittarsus.1.units
Lag 0                           -0.2645685                    -0.18013988
Lag 100                         -0.2616234                    -0.17607364
Lag 500                         -0.2652457                    -0.18034511
Lag 1000                        -0.2671219                    -0.17702256
Lag 5000                        -0.2093233                    -0.06028968
         traittarsus.2:traittarsus.1.units traitbwt.2:traittarsus.1.units
Lag 0                            0.9603400                      1.0000000
Lag 100                          0.9432077                      0.9762869
Lag 500                          0.9124477                      0.9252632
Lag 1000                         0.8838890                      0.8792611
Lag 5000                         0.6117319                      0.6007465
         traittarsus.1:traitbwt.1.units traitbwt.1:traitbwt.1.units
Lag 0                       -0.18013988                 -0.15026999
Lag 100                     -0.17607364                 -0.14749648
Lag 500                     -0.18034511                 -0.15145709
Lag 1000                    -0.17702256                 -0.15538707
Lag 5000                    -0.06028968                 -0.02621414
         traittarsus.2:traitbwt.1.units traitbwt.2:traitbwt.1.units
Lag 0                         0.9303986                   0.9527160
Lag 100                       0.9147001                   0.9321247
Lag 500                       0.8850543                   0.8884276
Lag 1000                      0.8576398                   0.8431799
Lag 5000                      0.5876791                   0.5807055
         traittarsus.1:traittarsus.2.units traitbwt.1:traittarsus.2.units
Lag 0                            0.9603400                      0.9303986
Lag 100                          0.9432077                      0.9147001
Lag 500                          0.9124477                      0.8850543
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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
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Lag 1000                          0.2292872                      0.21238609
Lag 5000                          0.1693953                      0.06254965
         traittarsus.1:traitbwt.1.animal traitbwt.1:traitbwt.1.animal
Lag 0                         0.10675486                   0.15466547
Lag 100                       0.10909010                   0.15753844
Lag 500                       0.13415361                   0.17187977
Lag 1000                      0.11544191                   0.14889411
Lag 5000                      0.04367713                  -0.01393939
         traittarsus.2:traitbwt.1.animal traitbwt.2:traitbwt.1.animal
Lag 0                          0.1618783                   0.17860886
Lag 100                        0.1807130                   0.20406604
Lag 500                        0.2315550                   0.24587070
Lag 1000                       0.2433453                   0.24000705
Lag 5000                       0.1313066                   0.07959284
         traittarsus.1:traittarsus.2.animal traitbwt.1:traittarsus.2.animal
Lag 0                             0.1751169                       0.1618783
Lag 100                           0.1936998                       0.1807130
Lag 500                           0.2199790                       0.2315550
Lag 1000                          0.2292872                       0.2433453
Lag 5000                          0.1693953                       0.1313066
         traittarsus.2:traittarsus.2.animal traitbwt.2:traittarsus.2.animal
Lag 0                             0.2339355                       0.2581627
Lag 100                           0.2476485                       0.2736295
Lag 500                           0.2790724                       0.3078386
Lag 1000                          0.2842308                       0.3166841
Lag 5000                          0.2101542                       0.1923682
         traittarsus.1:traitbwt.2.animal traitbwt.1:traitbwt.2.animal
Lag 0                         0.18455878                   0.17860886
Lag 100                       0.19497627                   0.20406604
Lag 500                       0.20989089                   0.24587070
Lag 1000                      0.21238609                   0.24000705
Lag 5000                      0.06254965                   0.07959284
         traittarsus.2:traitbwt.2.animal traitbwt.2:traitbwt.2.animal
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Lag 0                          0.2581627                    0.2416106
Lag 100                        0.2736295                    0.2608676
Lag 500                        0.3078386                    0.2963880
Lag 1000                       0.3166841                    0.3068141
Lag 5000                       0.1923682                    0.1712560
         traittarsus.1.byear traitbwt.1.byear traittarsus.2.byear
Lag 0           -0.023701193       0.04700881          0.05361674
Lag 100         -0.021944414       0.05837761          0.06114321
Lag 500         -0.004019018       0.04124133          0.05472308
Lag 1000        -0.014592442       0.02897141          0.08299624
Lag 5000        -0.001455363       0.01713092         -0.03330245
         traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother
Lag 0         -0.03458419            0.1501420      -0.030979909
Lag 100       -0.02882752            0.1495980      -0.034573917
Lag 500       -0.05044049            0.1542703      -0.037881298
Lag 1000      -0.04326520            0.1753867      -0.049179995
Lag 5000       0.01976572            0.1700994      -0.002621514
         traittarsus.2.mother traitbwt.2.mother
Lag 0             -0.05091781        0.08248472
Lag 100           -0.04612708        0.07643625
Lag 500           -0.04592155        0.07211789
Lag 1000          -0.02428388        0.04810929
Lag 5000          -0.05454058        0.02230047
         traittarsus.1:traittarsus.1.units traitbwt.1:traittarsus.1.units
Lag 0                           -0.1971901                    -0.17008659
Lag 100                         -0.2006748                    -0.16466175
Lag 500                         -0.2146434                    -0.17764629
Lag 1000                        -0.2152829                    -0.15594317
Lag 5000                        -0.2163189                    -0.07951097
         traittarsus.2:traittarsus.1.units traitbwt.2:traittarsus.1.units
Lag 0                            0.9034487                      0.9527160
Lag 100                          0.8867034                      0.9318204
Lag 500                          0.8558412                      0.8820862
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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
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Lag 0                        -0.2507033                  -0.2443613
Lag 100                      -0.2593514                  -0.2551879
Lag 500                      -0.2983604                  -0.2884325
Lag 1000                     -0.3082824                  -0.2942164
Lag 5000                     -0.1732268                  -0.1455134

, , traittarsus.2:traitbwt.2.units

         traittarsus.1:traittarsus.1.animal traitbwt.1:traittarsus.1.animal
Lag 0                           -0.09066377                     -0.12847847
Lag 100                         -0.06791265                     -0.11660390
Lag 500                         -0.02813480                     -0.08793510
Lag 1000                        -0.02464042                     -0.10829057
Lag 5000                         0.09059977                      0.04232726
         traittarsus.2:traittarsus.1.animal traitbwt.2:traittarsus.1.animal
Lag 0                            -0.5208193                      -0.6200400
Lag 100                          -0.4814739                      -0.5760115
Lag 500                          -0.4160646                      -0.4939845
Lag 1000                         -0.3309504                      -0.3961937
Lag 5000                          0.1719378                       0.1704323
         traittarsus.1:traitbwt.1.animal traitbwt.1:traitbwt.1.animal
Lag 0                        -0.12847847                  -0.16728073
Lag 100                      -0.11660390                  -0.16431801
Lag 500                      -0.08793510                  -0.14580635
Lag 1000                     -0.10829057                  -0.17627597
Lag 5000                      0.04232726                   0.02621324
         traittarsus.2:traitbwt.1.animal traitbwt.2:traitbwt.1.animal
Lag 0                         -0.4729141                  -0.49584021
Lag 100                       -0.4400289                  -0.46178772
Lag 500                       -0.3667218                  -0.38855190
Lag 1000                      -0.3075053                  -0.32632756
Lag 5000                       0.1176403                   0.08762877
         traittarsus.1:traittarsus.2.animal traitbwt.1:traittarsus.2.animal
```

```
Lag 0                            -0.5208193                       -0.4729141
Lag 100                          -0.4814739                       -0.4400289
Lag 500                          -0.4160646                       -0.3667218
Lag 1000                         -0.3309504                       -0.3075053
Lag 5000                          0.1719378                        0.1176403
         traittarsus.2:traittarsus.2.animal traitbwt.2:traittarsus.2.animal
Lag 0                           -0.84107771                      -0.93853010
Lag 100                         -0.80537663                      -0.88900373
Lag 500                         -0.70011206                      -0.74957513
Lag 1000                        -0.58965340                      -0.62094832
Lag 5000                        -0.01326034                       0.04348338
         traittarsus.1:traitbwt.2.animal traitbwt.1:traitbwt.2.animal
Lag 0                         -0.6200400                  -0.49584021
Lag 100                       -0.5760115                  -0.46178772
Lag 500                       -0.4939845                  -0.38855190
Lag 1000                      -0.3961937                  -0.32632756
Lag 5000                       0.1704323                   0.08762877
         traittarsus.2:traitbwt.2.animal traitbwt.2:traitbwt.2.animal
Lag 0                        -0.93853010                  -0.85484247
Lag 100                      -0.88900373                  -0.80629890
Lag 500                      -0.74957513                  -0.66699739
Lag 1000                     -0.62094832                  -0.53588327
Lag 5000                      0.04348338                   0.06798066
         traittarsus.1.byear traitbwt.1.byear traittarsus.2.byear
Lag 0            -0.04533921     -0.001638125         -0.07410803
Lag 100          -0.04526568      0.002752216         -0.05435921
Lag 500          -0.02361959     -0.010266769         -0.04066778
Lag 1000         -0.08661480     -0.055915794         -0.03404716
Lag 5000          0.02028860     -0.015718402          0.05000555
         traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother
Lag 0          0.09224924          -0.08507034       0.117048388
Lag 100        0.09712475          -0.09090158       0.119562799
Lag 500        0.06704383          -0.06950074       0.093258667
```

```
Lag 1000       0.06946025          -0.09719184       0.091569829
Lag 5000      -0.05957284          -0.01506617      -0.004965446
         traittarsus.2.mother traitbwt.2.mother
Lag 0              0.11599294       -0.06384447
Lag 100            0.12644815       -0.06061567
Lag 500            0.12233108       -0.05933391
Lag 1000           0.11302925       -0.05409993
Lag 5000           0.02623229        0.01443371
         traittarsus.1:traittarsus.1.units traitbwt.1:traittarsus.1.units
Lag 0                           0.11602826                     0.13276682
Lag 100                         0.08412251                     0.10350782
Lag 500                         0.06419072                     0.10039070
Lag 1000                        0.08359941                     0.11689682
Lag 5000                       -0.10317497                    -0.07583069
         traittarsus.2:traittarsus.1.units traitbwt.2:traittarsus.1.units
Lag 0                           -0.1801544                     -0.2276707
Lag 100                         -0.1866591                     -0.2347923
Lag 500                         -0.1769783                     -0.2196866
Lag 1000                        -0.1617965                     -0.1997778
Lag 5000                        -0.0380065                     -0.0414611
         traittarsus.1:traitbwt.1.units traitbwt.1:traitbwt.1.units
Lag 0                        0.13276682                  0.13741353
Lag 100                      0.10350782                  0.11641231
Lag 500                      0.10039070                  0.12001620
Lag 1000                     0.11689682                  0.15480317
Lag 5000                    -0.07583069                 -0.03093518
         traittarsus.2:traitbwt.1.units traitbwt.2:traitbwt.1.units
Lag 0                       -0.21678569                  -0.2507033
Lag 100                     -0.22198433                  -0.2562972
Lag 500                     -0.20689452                  -0.2323026
Lag 1000                    -0.19261030                  -0.2149386
Lag 5000                    -0.02955808                  -0.0282441
         traittarsus.1:traittarsus.2.units traitbwt.1:traittarsus.2.units
```

```
Lag 0                         -0.1801544                       -0.21678569
Lag 100                       -0.1866591                       -0.22198433
Lag 500                       -0.1769783                       -0.20689452
Lag 1000                      -0.1617965                       -0.19261030
Lag 5000                      -0.0380065                       -0.02955808
         traittarsus.2:traittarsus.2.units traitbwt.2:traittarsus.2.units
Lag 0                        0.926857338                        1.00000000
Lag 100                      0.838930228                        0.89252017
Lag 500                      0.714319171                        0.73419722
Lag 1000                     0.601447081                        0.60685285
Lag 5000                    -0.005767447                       -0.05722557
         traittarsus.1:traitbwt.2.units traitbwt.1:traitbwt.2.units
Lag 0                         -0.2276707                  -0.2507033
Lag 100                       -0.2347923                  -0.2562972
Lag 500                       -0.2196866                  -0.2323026
Lag 1000                      -0.1997778                  -0.2149386
Lag 5000                      -0.0414611                  -0.0282441
         traittarsus.2:traitbwt.2.units traitbwt.2:traitbwt.2.units
Lag 0                         1.00000000                  0.92347712
Lag 100                       0.89252017                  0.81767393
Lag 500                       0.73419722                  0.65250913
Lag 1000                      0.60685285                  0.52632018
Lag 5000                     -0.05722557                 -0.07523754

, , traitbwt.2:traitbwt.2.units

         traittarsus.1:traittarsus.1.animal traitbwt.1:traittarsus.1.animal
Lag 0                          -0.043059890                      -0.10947233
Lag 100                        -0.021006970                      -0.08947374
Lag 500                        -0.001331729                      -0.06046211
Lag 1000                       -0.008677951                      -0.10284705
Lag 5000                        0.111890868                       0.03101996
         traittarsus.2:traittarsus.1.animal traitbwt.2:traittarsus.1.animal
```

```
Lag 0                            -0.3939711                      -0.5649761
Lag 100                          -0.3674489                      -0.5248935
Lag 500                          -0.3564907                      -0.4716725
Lag 1000                         -0.3026255                      -0.3959870
Lag 5000                          0.1392553                       0.1506927
         traittarsus.1:traitbwt.1.animal traitbwt.1:traitbwt.1.animal
Lag 0                       -0.10947233                 -0.187811354
Lag 100                     -0.08947374                 -0.167609258
Lag 500                     -0.06046211                 -0.153207032
Lag 1000                    -0.10284705                 -0.191376283
Lag 5000                     0.03101996                 -0.009266993
         traittarsus.2:traitbwt.1.animal traitbwt.2:traitbwt.1.animal
Lag 0                       -0.43960419                  -0.56988609
Lag 100                     -0.41008412                  -0.52185804
Lag 500                     -0.34705550                  -0.43385778
Lag 1000                    -0.31152313                  -0.36023626
Lag 5000                     0.07052962                   0.07222864
         traittarsus.1:traittarsus.2.animal traitbwt.1:traittarsus.2.animal
Lag 0                            -0.3939711                     -0.43960419
Lag 100                          -0.3674489                     -0.41008412
Lag 500                          -0.3564907                     -0.34705550
Lag 1000                         -0.3026255                     -0.31152313
Lag 5000                          0.1392553                      0.07052962
         traittarsus.2:traittarsus.2.animal traitbwt.2:traittarsus.2.animal
Lag 0                           -0.67910852                     -0.85888343
Lag 100                         -0.65466001                     -0.81238323
Lag 500                         -0.60647885                     -0.70052835
Lag 1000                        -0.54835587                     -0.61884830
Lag 5000                        -0.02772098                      0.03373215
         traittarsus.1:traitbwt.2.animal traitbwt.1:traitbwt.2.animal
Lag 0                        -0.5649761                  -0.56988609
Lag 100                      -0.5248935                  -0.52185804
Lag 500                      -0.4716725                  -0.43385778
```

```
Lag 1000                      -0.3959870                  -0.36023626
Lag 5000                       0.1506927                   0.07222864
         traittarsus.2:traitbwt.2.animal traitbwt.2:traitbwt.2.animal
Lag 0                        -0.85888343                  -0.90703776
Lag 100                      -0.81238323                  -0.83971454
Lag 500                      -0.70052835                  -0.68420955
Lag 1000                     -0.61884830                  -0.57020879
Lag 5000                      0.03373215                   0.07361913
         traittarsus.1.byear traitbwt.1.byear traittarsus.2.byear
Lag 0           -0.044815839     -0.007601342         -0.09539294
Lag 100         -0.046632422     -0.009618828         -0.07733270
Lag 500         -0.039749429     -0.026455434         -0.05466463
Lag 1000        -0.096232932     -0.063248471         -0.04859295
Lag 5000        -0.007307801     -0.011838332          0.07303267
         traitbwt.2.byear traittarsus.1.mother traitbwt.1.mother
Lag 0          0.07926090          -0.11755479      0.1533639724
Lag 100        0.09525987          -0.11193096      0.1505628703
Lag 500        0.05998165          -0.06092327      0.1143539752
Lag 1000       0.06572238          -0.09798980      0.1117926423
Lag 5000      -0.05632018          -0.00703712      0.0007242137
         traittarsus.2.mother traitbwt.2.mother
Lag 0              0.09798770       -0.07912857
Lag 100            0.09530597       -0.05178227
Lag 500            0.10285009       -0.03607903
Lag 1000           0.08664286       -0.05475142
Lag 5000           0.03594017        0.03608548
         traittarsus.1:traittarsus.1.units traitbwt.1:traittarsus.1.units
Lag 0                           0.10062986                     0.11344391
Lag 100                         0.07039582                     0.08507484
Lag 500                         0.04998573                     0.08084299
Lag 1000                        0.07979248                     0.11040825
Lag 5000                       -0.11441105                    -0.06475361
         traittarsus.2:traittarsus.1.units traitbwt.2:traittarsus.1.units
```

```
Lag 0                          -0.13454205                    -0.21280936
Lag 100                        -0.14136050                    -0.21928247
Lag 500                        -0.12646869                    -0.19382371
Lag 1000                       -0.12162967                    -0.17751558
Lag 5000                       -0.02590274                    -0.02880894
         traittarsus.1:traitbwt.1.units traitbwt.1:traitbwt.1.units
Lag 0                        0.11344391                 0.131450832
Lag 100                      0.08507484                 0.105602349
Lag 500                      0.08084299                 0.125553514
Lag 1000                     0.11040825                 0.165398766
Lag 5000                    -0.06475361                 0.003312387
         traittarsus.2:traitbwt.1.units traitbwt.2:traitbwt.1.units
Lag 0                       -0.18001725                 -0.24436125
Lag 100                     -0.18862947                 -0.25750569
Lag 500                     -0.17962012                 -0.23342183
Lag 1000                    -0.16368716                 -0.20650410
Lag 5000                    -0.02638416                 -0.02742457
         traittarsus.1:traittarsus.2.units traitbwt.1:traittarsus.2.units
Lag 0                          -0.13454205                    -0.18001725
Lag 100                        -0.14136050                    -0.18862947
Lag 500                        -0.12646869                    -0.17962012
Lag 1000                       -0.12162967                    -0.16368716
Lag 5000                       -0.02590274                    -0.02638416
         traittarsus.2:traittarsus.2.units traitbwt.2:traittarsus.2.units
Lag 0                           0.75421487                     0.92347712
Lag 100                         0.68911416                     0.81697064
Lag 500                         0.62438762                     0.68932883
Lag 1000                        0.56071503                     0.60055861
Lag 5000                        0.01204694                    -0.04603239
         traittarsus.1:traitbwt.2.units traitbwt.1:traitbwt.2.units
Lag 0                       -0.21280936                 -0.24436125
Lag 100                     -0.21928247                 -0.25750569
Lag 500                     -0.19382371                 -0.23342183
```

```
Lag 1000                   -0.17751558                  -0.20650410
Lag 5000                   -0.02880894                  -0.02742457
         traittarsus.2:traitbwt.2.units traitbwt.2:traitbwt.2.units
Lag 0                       0.92347712                   1.00000000
Lag 100                     0.81697064                   0.84520133
Lag 500                     0.68932883                   0.66116525
Lag 1000                    0.60055861                   0.55204450
Lag 5000                   -0.04603239                  -0.08094849
```

Chapitre 7

brms

First load brms:

```r
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
```

```r
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 = "r-obj/brms_m2_1.rda")
```

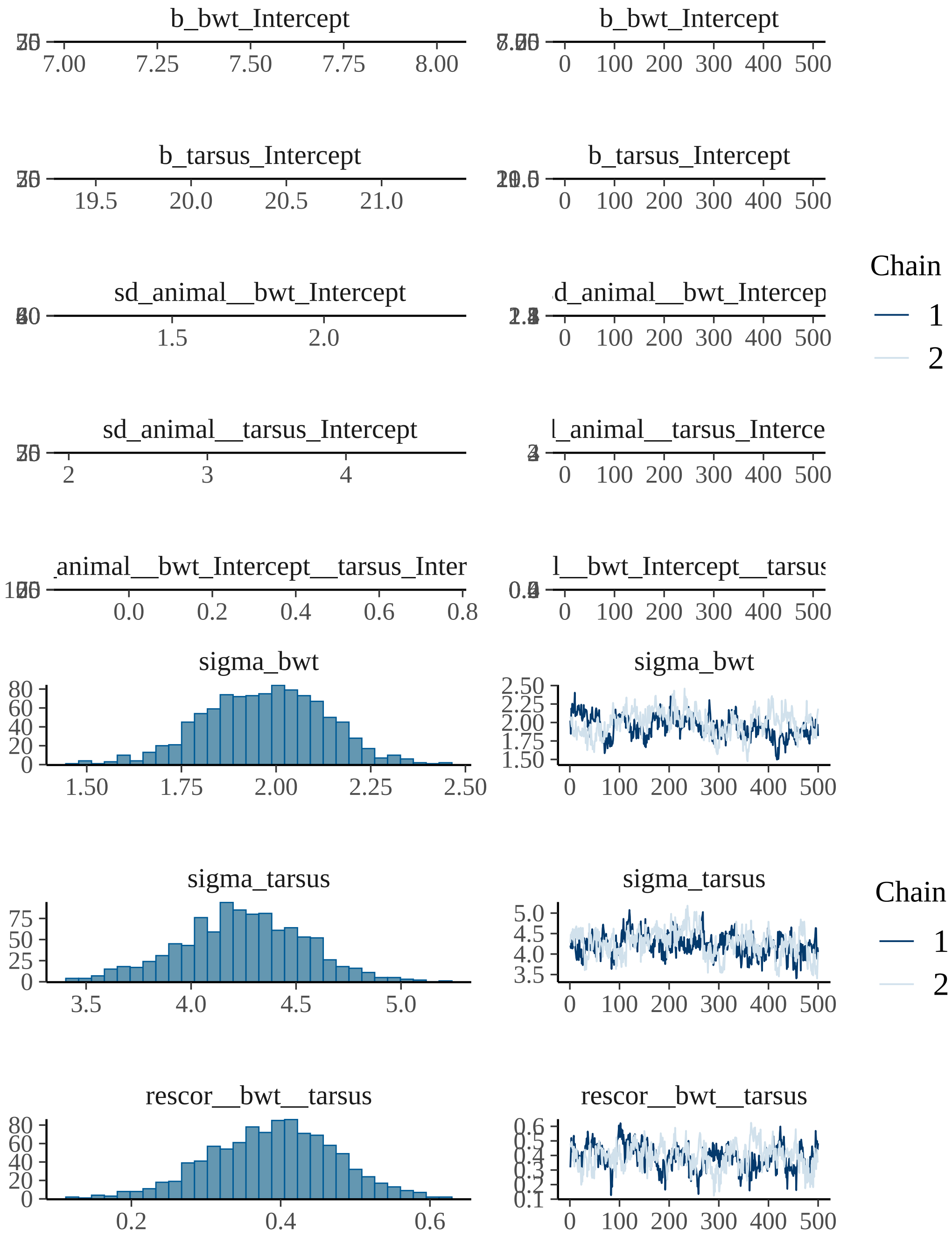
Again we have provided the data from one such run. It can be accessed using the code:

```
load("r-obj/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).
```

```r
plot(brms_m2.1, ask = FALSE)
```



```r
VarCorr(brms_m2.1)
```

```
$animal
$animal$sd
                  Estimate Est.Error     Q2.5    Q97.5
bwt_Intercept     1.808171 0.2050233 1.412824 2.204805
tarsus_Intercept 3.438368 0.4283612 2.491218 4.245264
```

```
$animal$cor
, , bwt_Intercept

                 Estimate Est.Error      Q2.5     Q97.5
bwt_Intercept   1.0000000 0.0000000 1.00000000 1.0000000
tarsus_Intercept 0.3814062 0.1380014 0.07581464 0.6209038

, , tarsus_Intercept

                 Estimate Est.Error      Q2.5     Q97.5
bwt_Intercept   0.3814062 0.1380014 0.07581464 0.6209038
tarsus_Intercept 1.0000000 0.0000000 1.00000000 1.0000000


$animal$cov
, , bwt_Intercept

                Estimate Est.Error      Q2.5    Q97.5
bwt_Intercept   3.311473 0.7430185 1.9960721 4.861167
tarsus_Intercept 2.440166 1.0901689 0.3870783 4.668720

, , tarsus_Intercept

                 Estimate Est.Error      Q2.5    Q97.5
bwt_Intercept     2.440166  1.090169 0.3870783  4.66872
tarsus_Intercept 12.005688  2.918741 6.2061701 18.02226



$residual__
$residual__$sd
       Estimate Est.Error     Q2.5    Q97.5
bwt    1.970532 0.1597581 1.658782 2.276074
```

```
tarsus 4.244704 0.2984518 3.632824 4.820109


$residual__$cor
, , bwt

        Estimate  Est.Error     Q2.5     Q97.5
bwt    1.0000000 0.00000000 1.0000000 1.0000000
tarsus 0.3888754 0.08510488 0.2127907 0.5526631

, , tarsus

        Estimate  Est.Error     Q2.5     Q97.5
bwt    0.3888754 0.08510488 0.2127907 0.5526631
tarsus 1.0000000 0.00000000 1.0000000 1.0000000



$residual__$cov
, , bwt

       Estimate Est.Error     Q2.5    Q97.5
bwt    3.908493 0.6282892 2.751557 5.180511
tarsus 3.289995 0.9305960 1.572647 5.147133

, , tarsus

        Estimate Est.Error      Q2.5     Q97.5
bwt     3.289995  0.930596  1.572647  5.147133
tarsus 18.106495  2.530138 13.197409 23.233452
```

It is also possible to calculate the heritability for each trait using the function ‘as.mcmc’

```r
v_animal <- (VarCorr(brms_m2.1, summary = FALSE)$animal$sd)^2
v_r <- (VarCorr(brms_m2.1, summary = FALSE)$residual$sd)^2
```

```r
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)
```

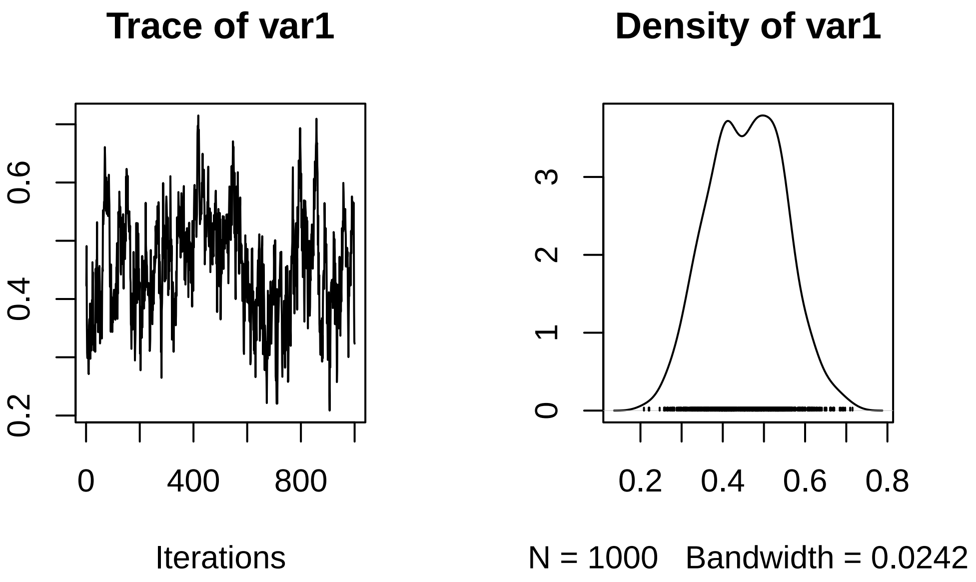
```


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
```

```r
summary(h.tarsus.2)
```

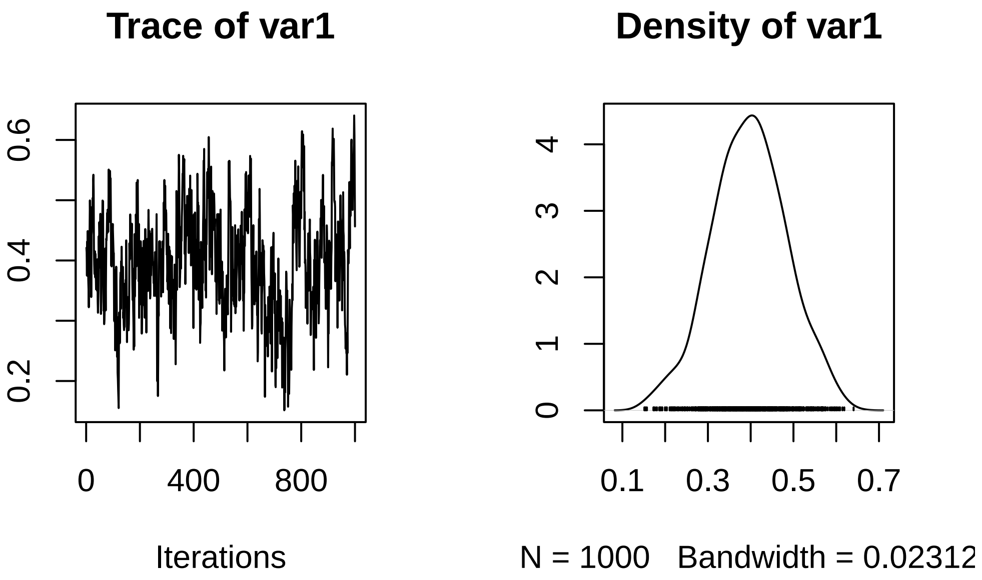
```


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

```r
cor_g <- as.mcmc((VarCorr(brms_m2.1, summary = FALSE)$animal$cor[, 1, 2]))
cor_res <- as.mcmc((VarCorr(brms_m2.1, summary = FALSE)$residual$cor[, 1, 2]))

summary(cor_g)
```

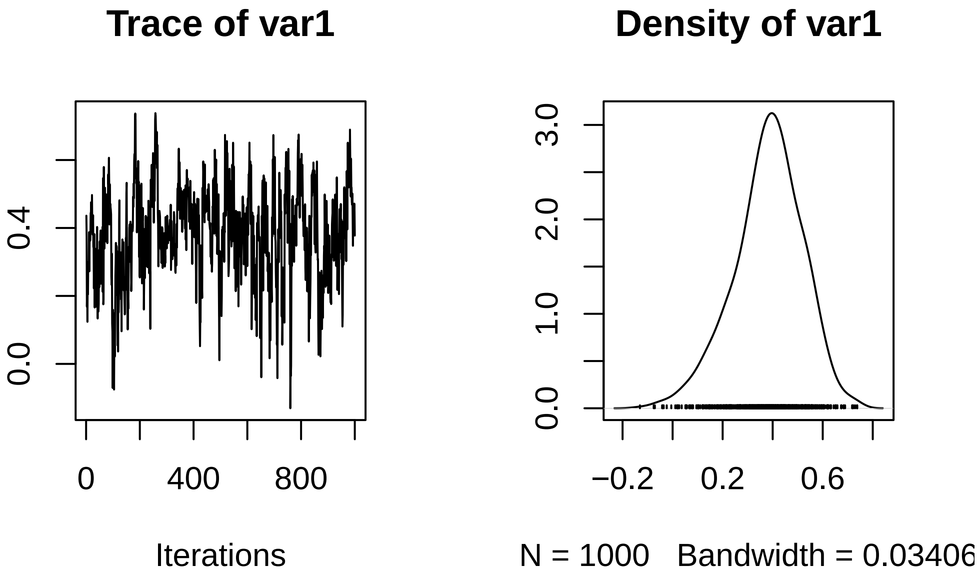
```

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

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

          Mean             SD       Naive SE Time-series SE
      0.381406       0.138001       0.004364       0.014946

2. Quantiles for each variable:

   2.5%     25%     50%     75%   97.5%
0.07581 0.30354 0.39041 0.47497 0.62090
```

```r
summary(cor_res)
```

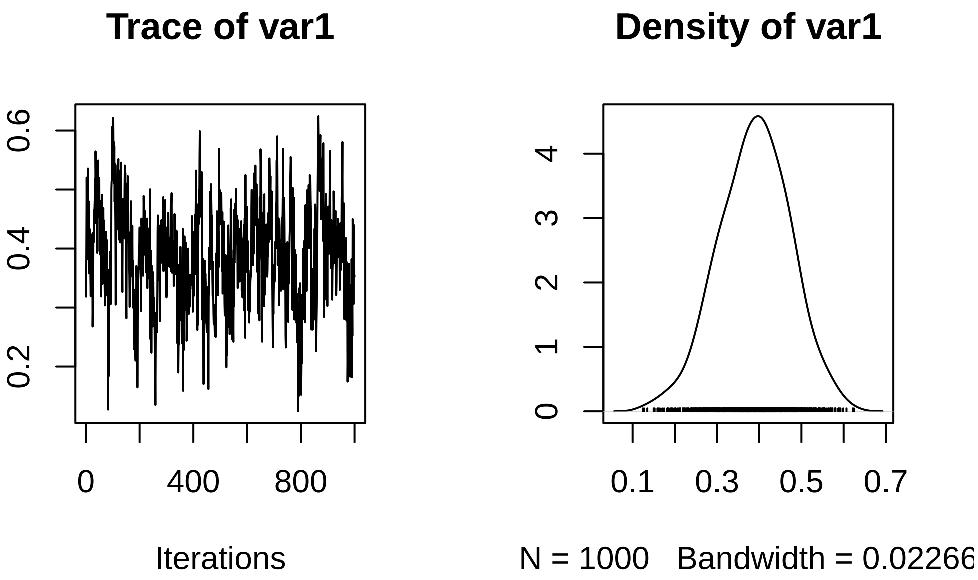
```

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

1. Empirical mean and standard deviation for each variable,
```

```
   plus standard error of the mean:


          Mean             SD       Naive SE Time-series SE

      0.388875       0.085105       0.002691       0.009215


2. Quantiles for each variable:


  2.5%    25%    50%    75%  97.5%

0.2128 0.3319 0.3913 0.4484 0.5527
```

```
plot(cor_g)
```



```
plot(cor_res)
```



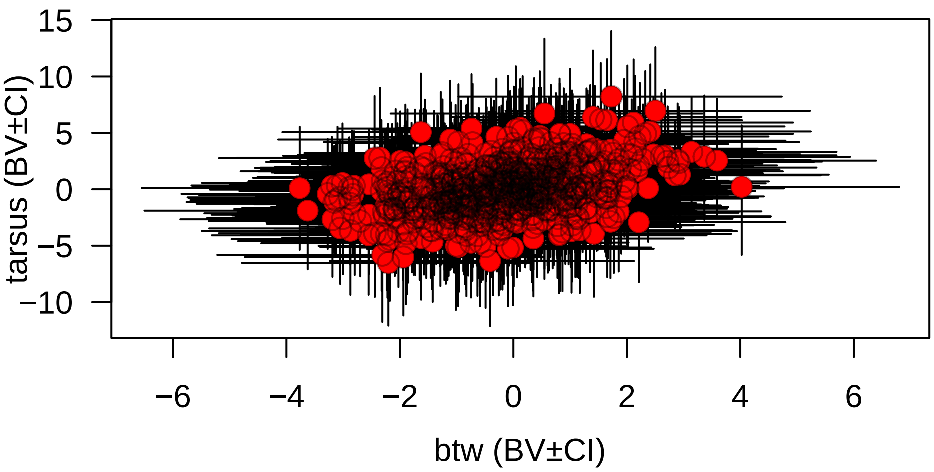
Here we can plot the genetic correlation by extraction the breeding values or BLUP.

```
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

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 = "r-obj/brms_m2_2.rda")
```

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

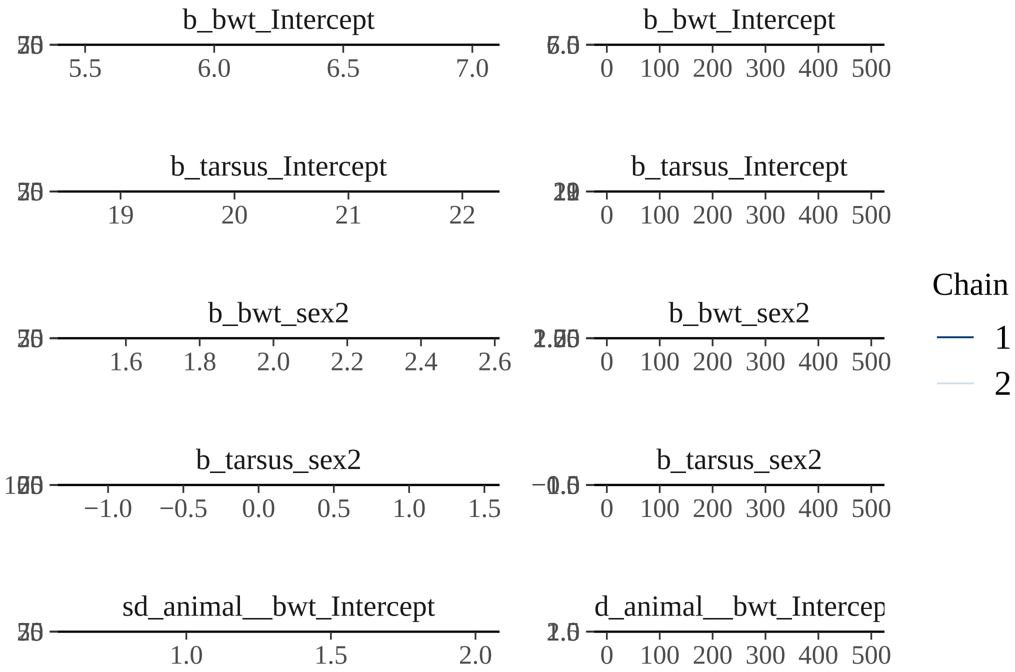
```
load("r-obj/brms_m2_2.rda")
summary(brms_m2.2)
```

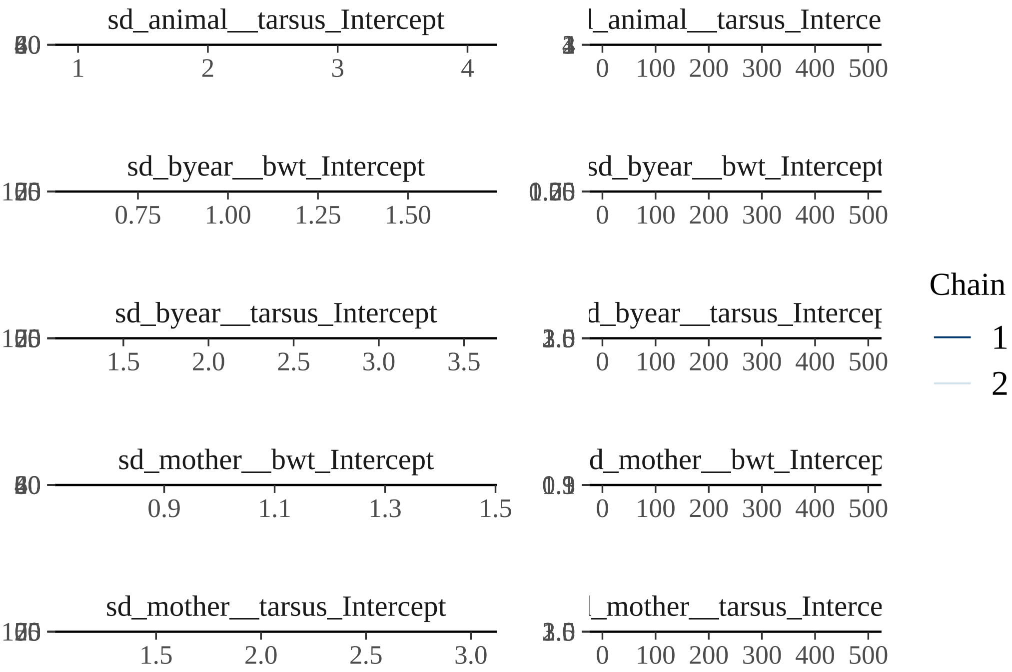
```
Warning: Parts of the model have not converged (some Rhats are > 1.05). Be
careful when analysing the results! We recommend running more iterations and/or
setting stronger priors.

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
```

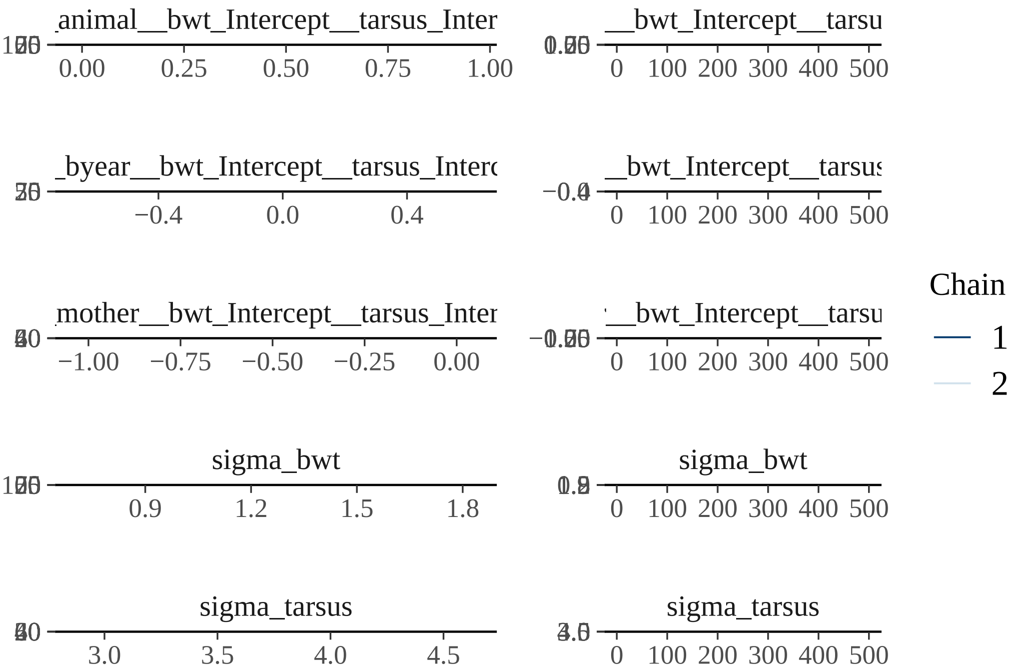
```
sd(tarsus_Intercept)                      52      162
cor(bwt_Intercept,tarsus_Intercept)       25       30

~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
```

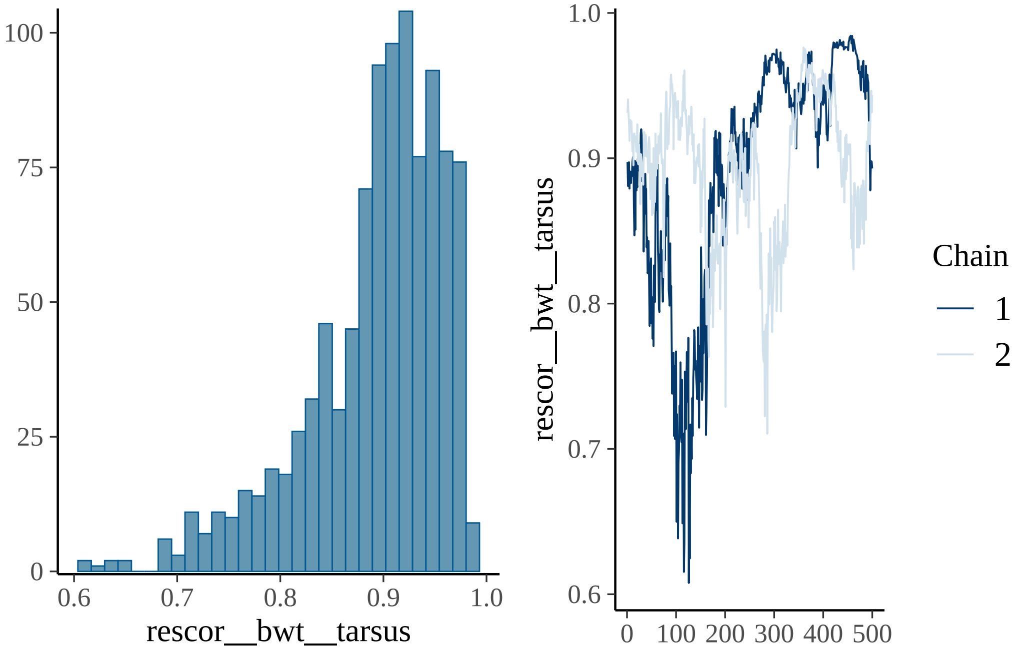
```
sigma_tarsus     3.73      0.32     3.14     4.32 1.00       55      176

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).
```

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




sd_animal__tarsus_Intercept
1
2
3
4
l_animal__tarsus_Interce
0 100 200 300 400 500
sd_byear__bwt_Intercept
0.75
1.00
1.25
1.50
sd_byear__bwt_Intercept
0 100 200 300 400 500
sd_byear__tarsus_Intercept
1.5
2.0
2.5
3.0
3.5
d_byear__tarsus_Intercep
0 100 200 300 400 500
sd_mother__bwt_Intercept
0.9
1.1
1.3
1.5
d_mother__bwt_Intercep
0 100 200 300 400 500
sd_mother__tarsus_Intercept
1.5
2.0
2.5
3.0
_mother__tarsus_Interce
0 100 200 300 400 500
Chain
1
2


animal__bwt_Intercept__tarsus_Inter
0.00
0.25
0.50
0.75
1.00
__bwt_Intercept__tarsu
0 100 200 300 400 500
_byear__bwt_Intercept__tarsus_Interc
−0.4
0.0
0.4
__bwt_Intercept__tarsus
0 100 200 300 400 500
mother__bwt_Intercept__tarsus_Inter
−1.00
−0.75
−0.50
−0.25
0.00
__bwt_Intercept__tarsu
0 100 200 300 400 500
sigma_bwt
0.9
1.2
1.5
1.8
sigma_bwt
0 100 200 300 400 500
sigma_tarsus
3.0
3.5
4.0
4.5
sigma_tarsus
0 100 200 300 400 500
Chain
1
2



```r
VarCorr(brms_m2.2)
```

```
$animal
$animal$sd
                 Estimate Est.Error      Q2.5    Q97.5
bwt_Intercept    1.306921 0.2109780 0.8555702 1.687254
tarsus_Intercept 2.876731 0.4718524 1.8827128 3.699873

$animal$cor
, , bwt_Intercept

                  Estimate Est.Error      Q2.5     Q97.5
bwt_Intercept    1.0000000 0.0000000 1.0000000 1.0000000
tarsus_Intercept 0.5961514 0.1727943 0.1849725 0.8929607

, , tarsus_Intercept

                  Estimate Est.Error      Q2.5     Q97.5
bwt_Intercept    0.5961514 0.1727943 0.1849725 0.8929607
tarsus_Intercept 1.0000000 0.0000000 1.0000000 1.0000000
```

```
$animal$cov
, , bwt_Intercept

                 Estimate Est.Error      Q2.5    Q97.5
bwt_Intercept    1.752510 0.5433004 0.7320013 2.846827
tarsus_Intercept 2.357852 1.0462644 0.3960956 4.526731

, , tarsus_Intercept

                 Estimate Est.Error      Q2.5     Q97.5
bwt_Intercept    2.357852  1.046264 0.3960956  4.526731
tarsus_Intercept 8.498003  2.672465 3.5446115 13.689062



$byear
$byear$sd
                  Estimate Est.Error      Q2.5    Q97.5
bwt_Intercept    0.9904858 0.1696752 0.7102391 1.390260
tarsus_Intercept 2.0166804 0.3366954 1.4463862 2.777005

$byear$cor
, , bwt_Intercept

                   Estimate Est.Error       Q2.5     Q97.5
bwt_Intercept    1.00000000 0.0000000  1.0000000 1.0000000
tarsus_Intercept 0.01351405 0.2206186 -0.4367809 0.4412319

, , tarsus_Intercept

                   Estimate Est.Error       Q2.5     Q97.5
bwt_Intercept    0.01351405 0.2206186 -0.4367809 0.4412319
```

```
tarsus_Intercept 1.00000000 0.0000000  1.0000000 1.0000000



$byear$cov
, , bwt_Intercept


                   Estimate Est.Error       Q2.5    Q97.5
bwt_Intercept    1.00982294 0.3583697  0.5044397 1.932823
tarsus_Intercept 0.06412895 0.4880116 -0.8559486 1.092317


, , tarsus_Intercept


                   Estimate Est.Error       Q2.5    Q97.5
bwt_Intercept    0.06412895 0.4880116 -0.8559486 1.092317
tarsus_Intercept 4.18025049 1.4249595  2.0920330 7.711755




$mother
$mother$sd
                 Estimate Est.Error      Q2.5    Q97.5
bwt_Intercept    1.137249 0.1175495 0.8968349 1.358078
tarsus_Intercept 2.088602 0.2865291 1.5425683 2.673791


$mother$cor
, , bwt_Intercept


                   Estimate Est.Error       Q2.5      Q97.5
bwt_Intercept     1.0000000 0.0000000  1.0000000  1.0000000
tarsus_Intercept -0.6413329 0.1968102 -0.9745925 -0.2367393


, , tarsus_Intercept
```

```
                   Estimate Est.Error       Q2.5      Q97.5
bwt_Intercept    -0.6413329 0.1968102 -0.9745925 -0.2367393
tarsus_Intercept  1.0000000 0.0000000  1.0000000  1.0000000



$mother$cov
, , bwt_Intercept


                  Estimate Est.Error       Q2.5      Q97.5
bwt_Intercept     1.307139 0.2669748  0.8043132  1.8443762
tarsus_Intercept -1.467511 0.3650113 -2.1491979 -0.6718737

, , tarsus_Intercept


                  Estimate Est.Error      Q2.5      Q97.5
bwt_Intercept    -1.467511 0.3650113 -2.149198 -0.6718737
tarsus_Intercept  4.444274 1.2018090  2.379517  7.1491575




$residual__
$residual__$sd
       Estimate Est.Error     Q2.5    Q97.5
bwt    1.396815 0.1597393 1.052042 1.684810
tarsus 3.733614 0.3170549 3.140204 4.319446

$residual__$cor
, , bwt


        Estimate Est.Error      Q2.5     Q97.5
bwt    1.0000000 0.0000000 1.0000000 1.0000000
tarsus 0.8925119 0.0672286 0.7167862 0.9774545
```

```
, , tarsus

        Estimate Est.Error      Q2.5     Q97.5
bwt    0.8925119 0.0672286 0.7167862 0.9774545
tarsus 1.0000000 0.0000000 1.0000000 1.0000000



$residual__$cov
, , bwt

       Estimate Est.Error     Q2.5    Q97.5
bwt    1.976584 0.4347085 1.106793 2.838585
tarsus 4.683451 0.9103808 2.846560 6.440550

, , tarsus

        Estimate Est.Error     Q2.5    Q97.5
bwt     4.683451 0.9103808 2.846560  6.44055
tarsus 14.040300 2.3674563 9.860883 18.65761
```

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

```
cor_g <- as.mcmc((VarCorr(brms_m2.2, summary = FALSE)$animal$cor[, 1, 2]))
cor_res <- as.mcmc((VarCorr(brms_m2.2, summary = FALSE)$residual$cor[, 1, 2]))
cor_mother <- as.mcmc((VarCorr(brms_m2.2, summary = FALSE)$mother$cor[, 1, 2]))
cor_byear <- as.mcmc((VarCorr(brms_m2.2, summary = FALSE)$byear$cor[, 1, 2]))

summary(cor_g)
```

```
Iterations = 1:1000
Thinning interval = 1
```

```
Number of chains = 1

Sample size per chain = 1000


1. Empirical mean and standard deviation for each variable,

   plus standard error of the mean:


          Mean             SD       Naive SE Time-series SE

      0.596151       0.172794       0.005464       0.028178


2. Quantiles for each variable:


  2.5%    25%    50%    75%  97.5%

0.1850 0.5065 0.6117 0.7064 0.8930
```

```r
summary(cor_mother)
```

```
Iterations = 1:1000

Thinning interval = 1

Number of chains = 1

Sample size per chain = 1000


1. Empirical mean and standard deviation for each variable,

   plus standard error of the mean:


          Mean             SD       Naive SE Time-series SE

     -0.641333       0.196810       0.006224       0.021355


2. Quantiles for each variable:


   2.5%     25%     50%     75%   97.5%

-0.9746 -0.7933 -0.6507 -0.5027 -0.2367
```

```r
summary(cor_byear)
```

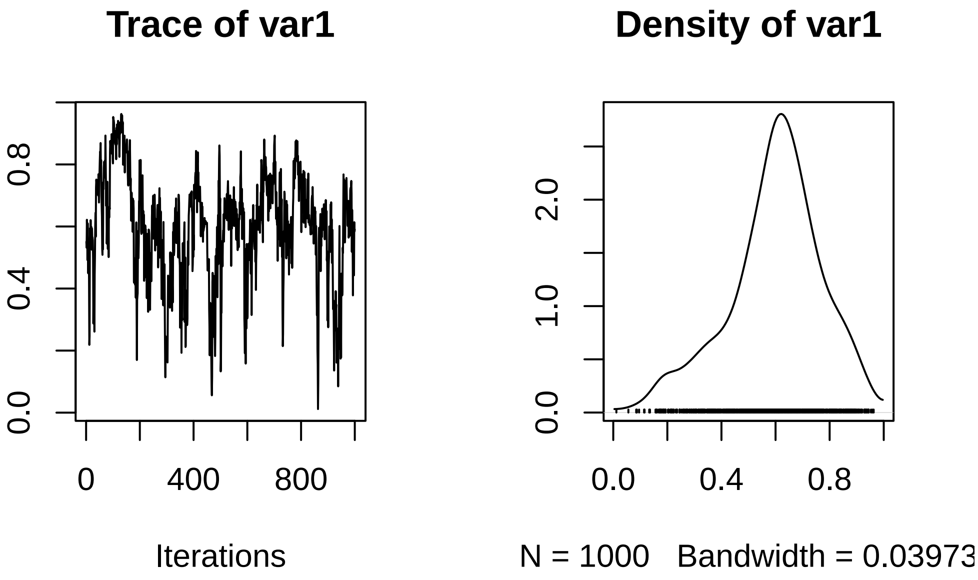
```

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

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

          Mean             SD       Naive SE Time-series SE 
      0.013514       0.220619       0.006977       0.009633 

2. Quantiles for each variable:

    2.5%      25%      50%      75%    97.5% 
-0.43678 -0.13505  0.02408  0.16947  0.44123 
```

```r
summary(cor_res)
```

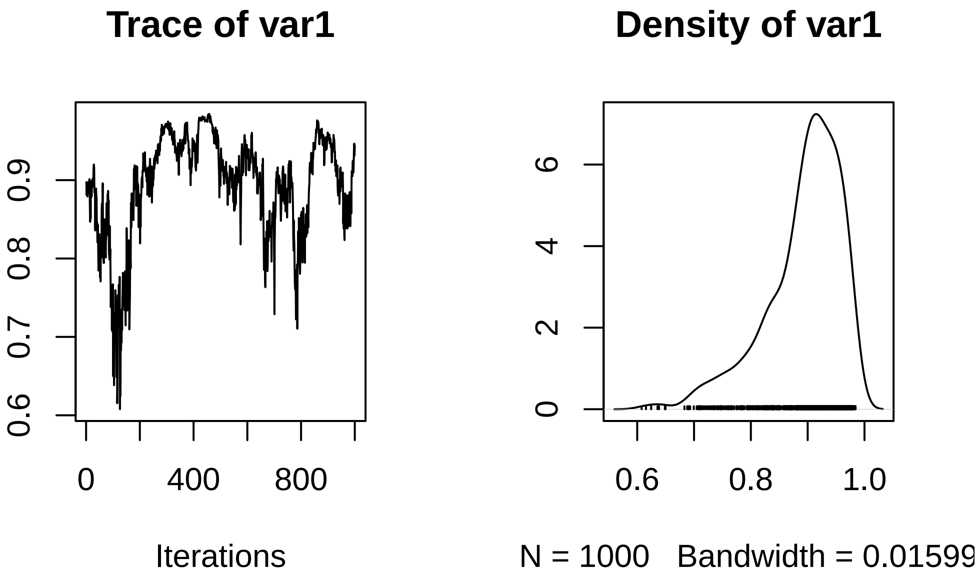
```

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

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

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

```
2. Quantiles for each variable:


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

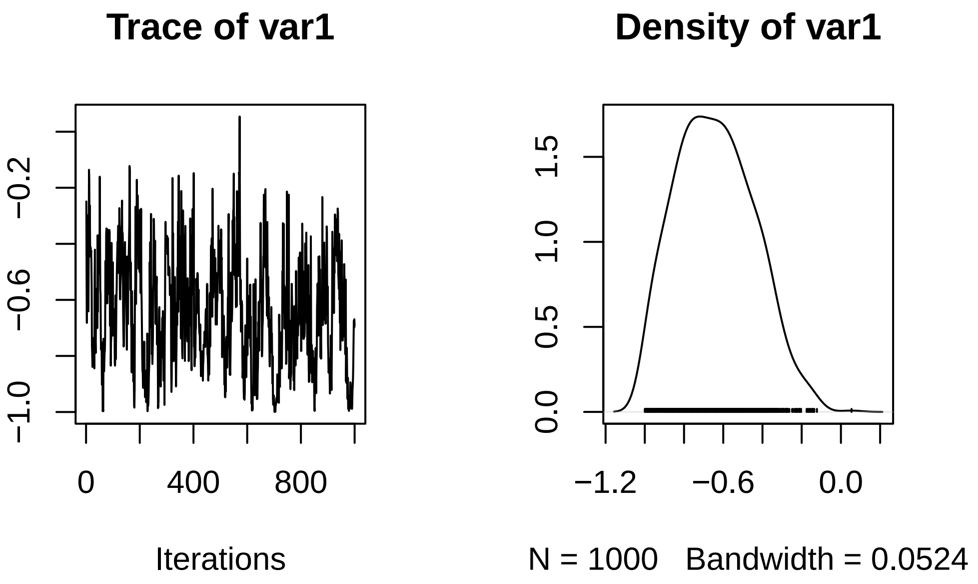
```r
plot(cor_g)
```



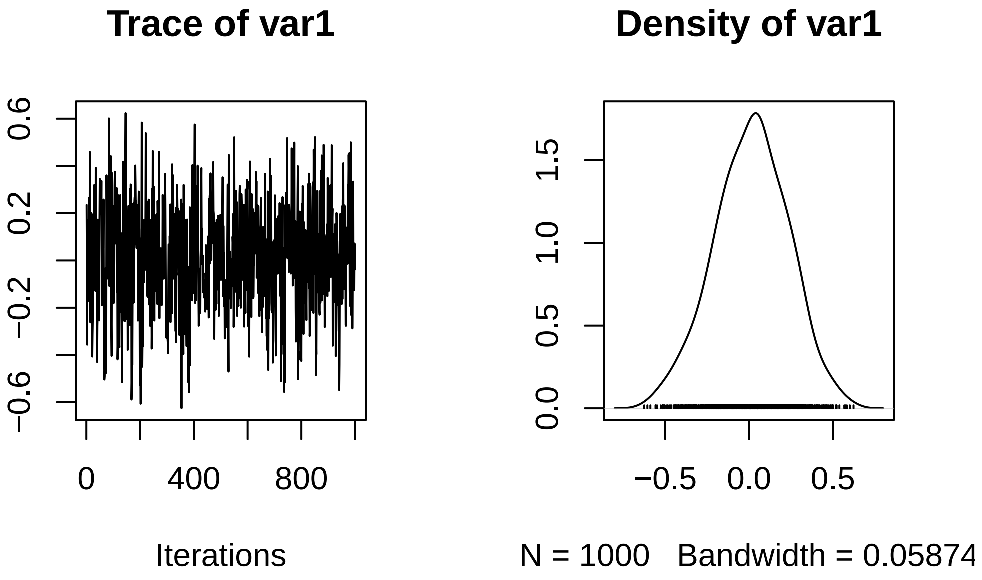
```r
plot(cor_res)
```



```r
plot(cor_mother)
```



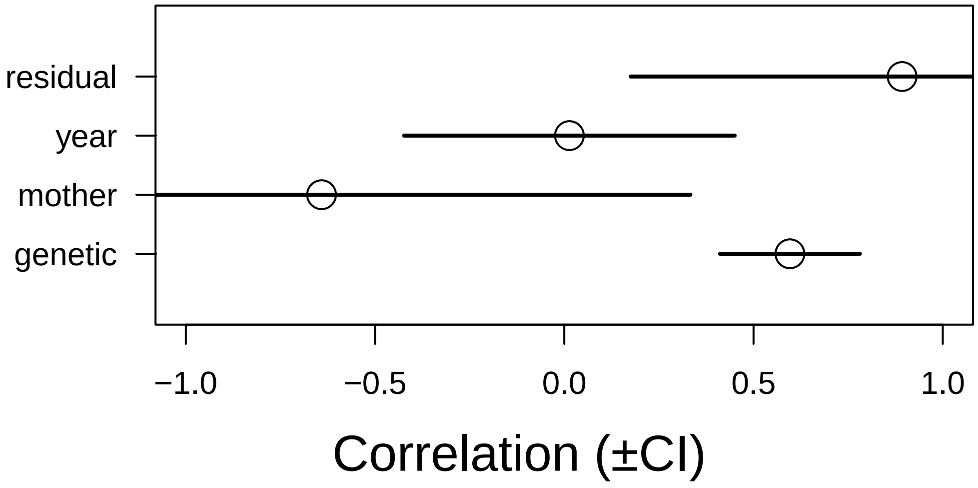
```r
plot(cor_byear)
```



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

```r
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)$quantiles[1], summary(cor_mother)$
  cbind(summary(cor_byear)$statistics[1], summary(cor_byear)$quantiles[1], summary(cor_byear)$qua
  cbind(summary(cor_res)$statistics[1], summary(cor_res)$quantiles[1], summary(cor_res)$quantiles
)
```

```
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 (±CI)", side = 1, las = 1, adj = 0.4, line = 3, cex = 1.6)
axis(2, at = 1, labels = c("genetic"), las = 2, cex.axis = 1)
axis(2, at = 2, labels = c("mother"), las = 2, cex.axis = 1)
axis(2, at = 3, labels = c("year"), las = 2, cex.axis = 1)
axis(2, at = 4, labels = c("residual"), las = 2, cex.axis = 1)
```



Note, brms estimates the correlation and also the covariance. We can also recalculate the correlation directly from the covariance.To facilitate the extraction of the different parameter, we can the fucntion `as_draws_df`

```
cov_g <- (VarCorr(brms_m2.2, summary = FALSE)$animal$cov)[, 1, 2]
cov_res <- (VarCorr(brms_m2.2, summary = FALSE)$residual$cov)[, 1, 2]
cov_mother <- (VarCorr(brms_m2.2, summary = FALSE)$mother$cov)[, 1, 2]
cov_byear <- (VarCorr(brms_m2.2, summary = FALSE)$byear$cov)[, 1, 2]

var.est <- as_draws_df(brms_m2.2, variable = c("sd", "sigma"), regex = TRUE)
var.est <- var.est^2

cor_g_2 <- as.mcmc(cov_g / sqrt(var.est[1] * var.est[2]))
cor_byear_2 <- as.mcmc(cov_byear / sqrt(var.est[3] * var.est[4]))
```

```r
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
```

```r
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
```

```r
summary(cor_mother_2)
```

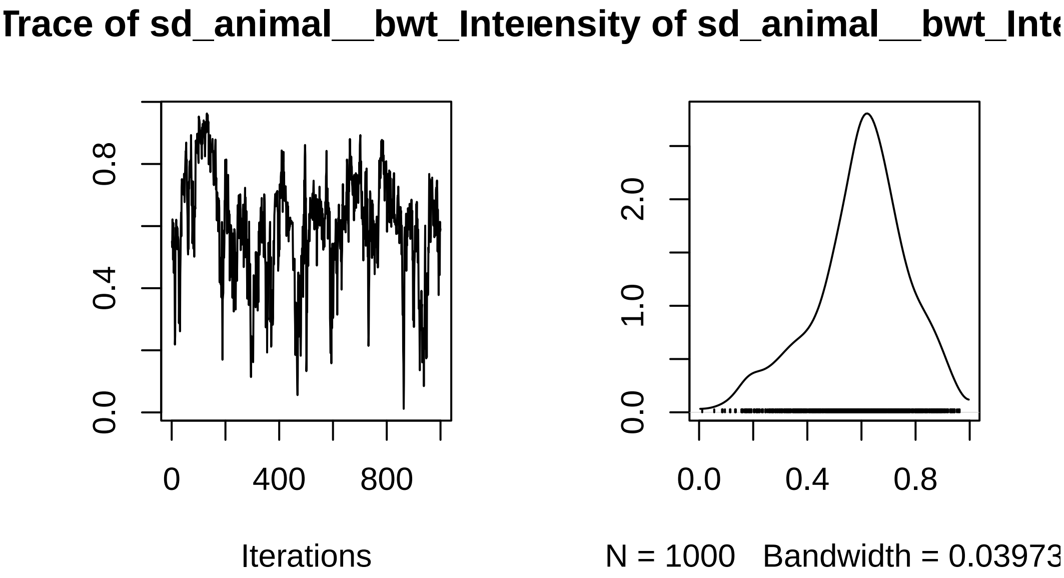
```


Iterations = 1:1000

Thinning interval = 1

Number of chains = 1

Sample size per chain = 1000


1. Empirical mean and standard deviation for each variable,

   plus standard error of the mean:


          Mean             SD       Naive SE Time-series SE

       1.01862        0.46337        0.01465        0.06126


2. Quantiles for each variable:


  2.5%    25%    50%    75%  97.5%

0.1514 0.6969 1.0310 1.3241 2.0032
```

```r
summary(cor_res_2)
```

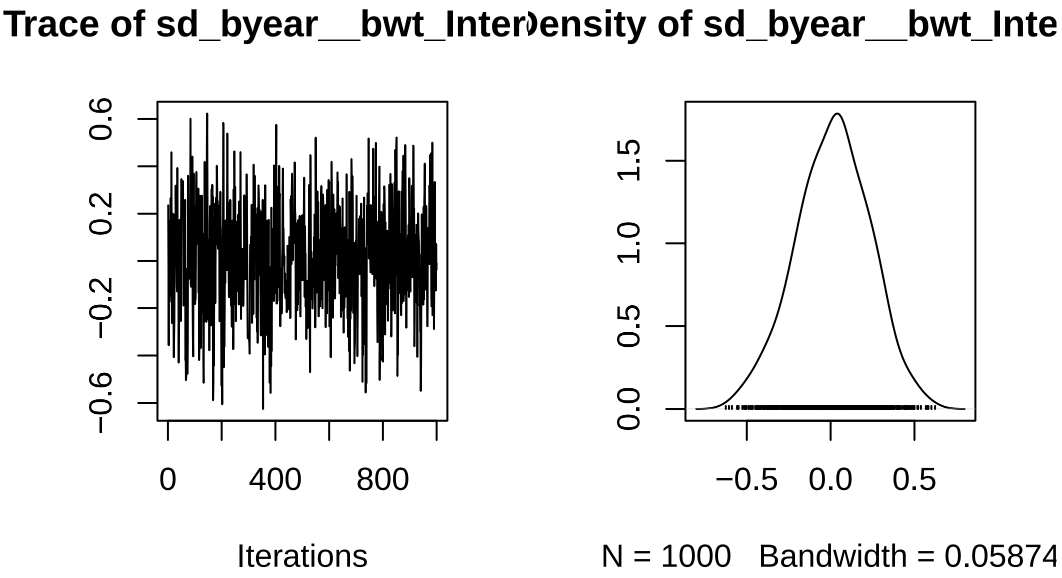
```


Iterations = 1:1000

Thinning interval = 1

Number of chains = 1

Sample size per chain = 1000
```

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

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

2. Quantiles for each variable:

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

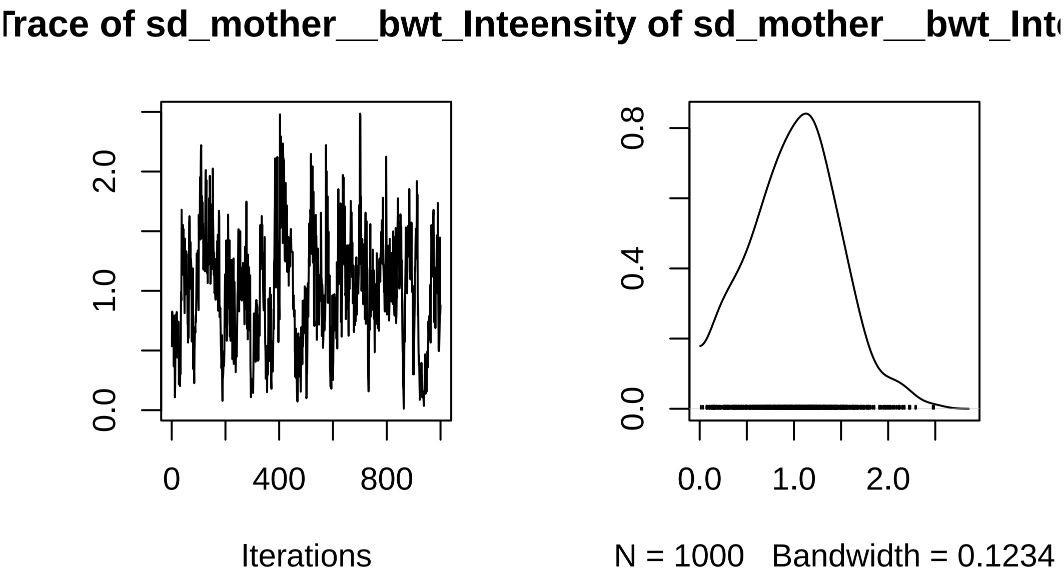
```r
plot(cor_g_2)
```



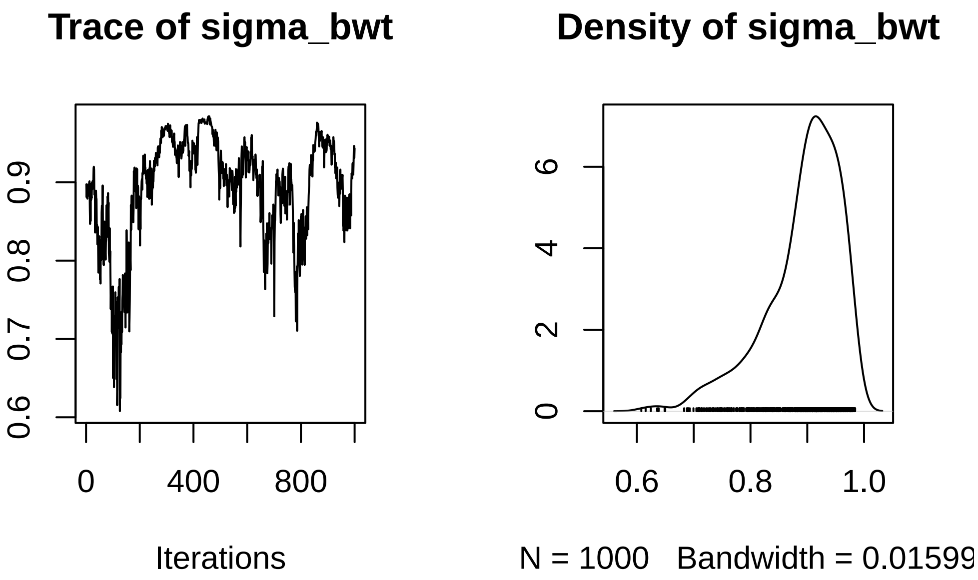
```r
plot(cor_byear_2)
```



```r
plot(cor_mother_2)
```



```r
plot(cor_res_2)
```



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 = "r-obj/brms_m2_3.rda")
```

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

```
load("r-obj/brms_m2_3.rda")
summary(brms_m2.3)
```

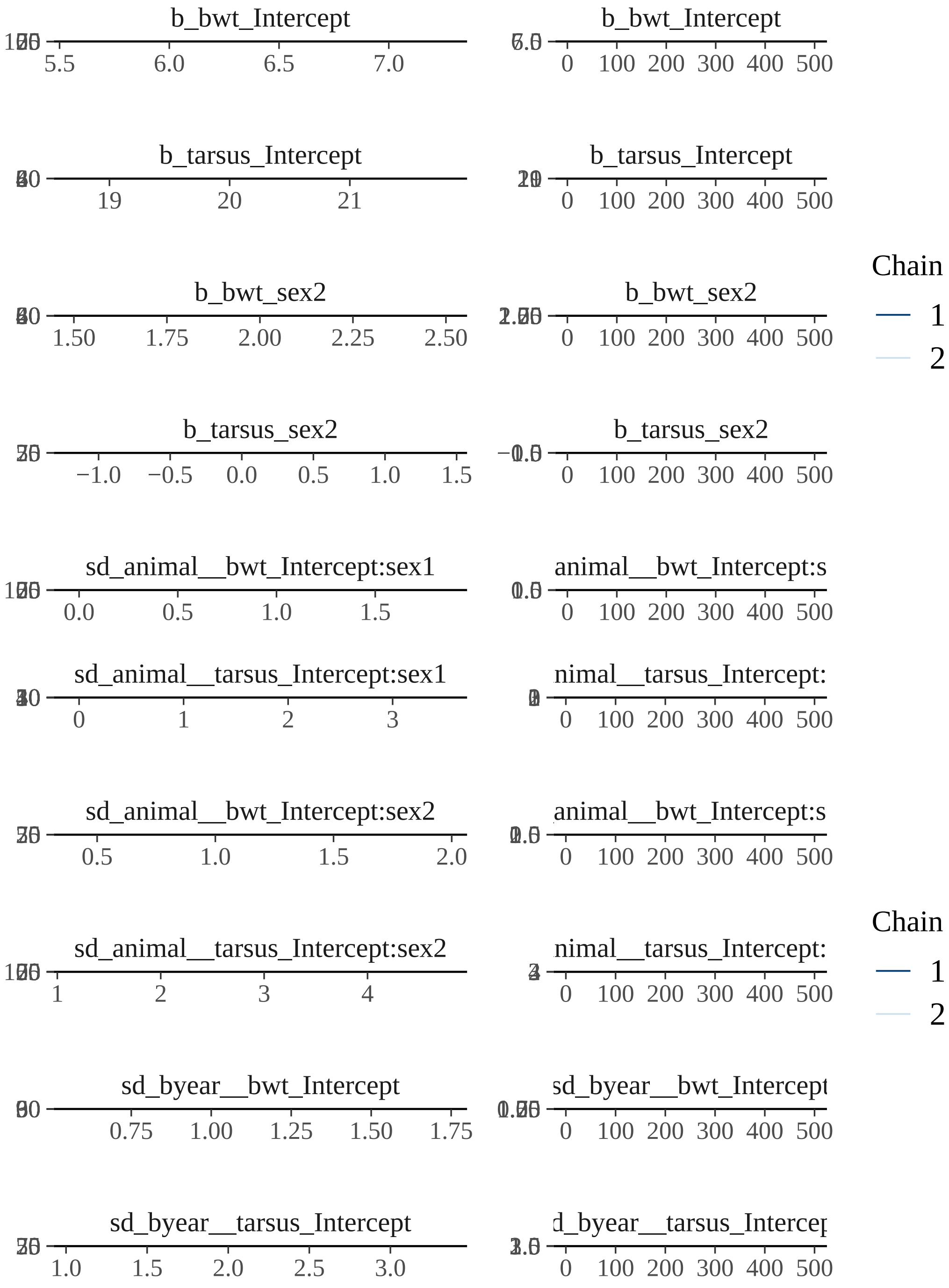
```
Warning: Parts of the model have not converged (some Rhats are > 1.05). Be
```

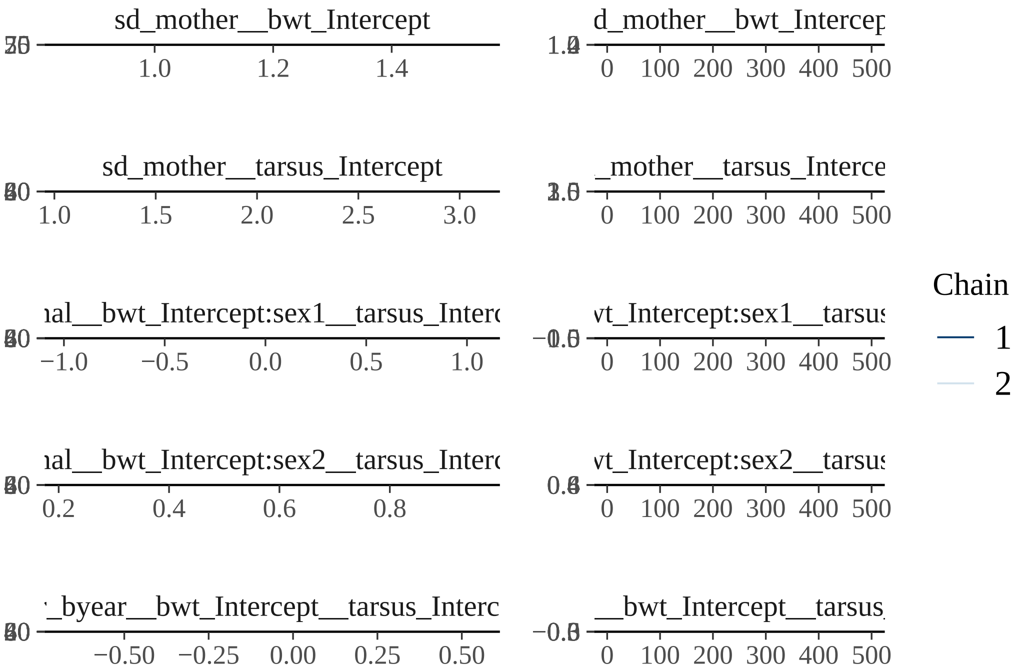
```
careful when analysing the results! We recommend running more iterations and/or
setting stronger priors.

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)
```

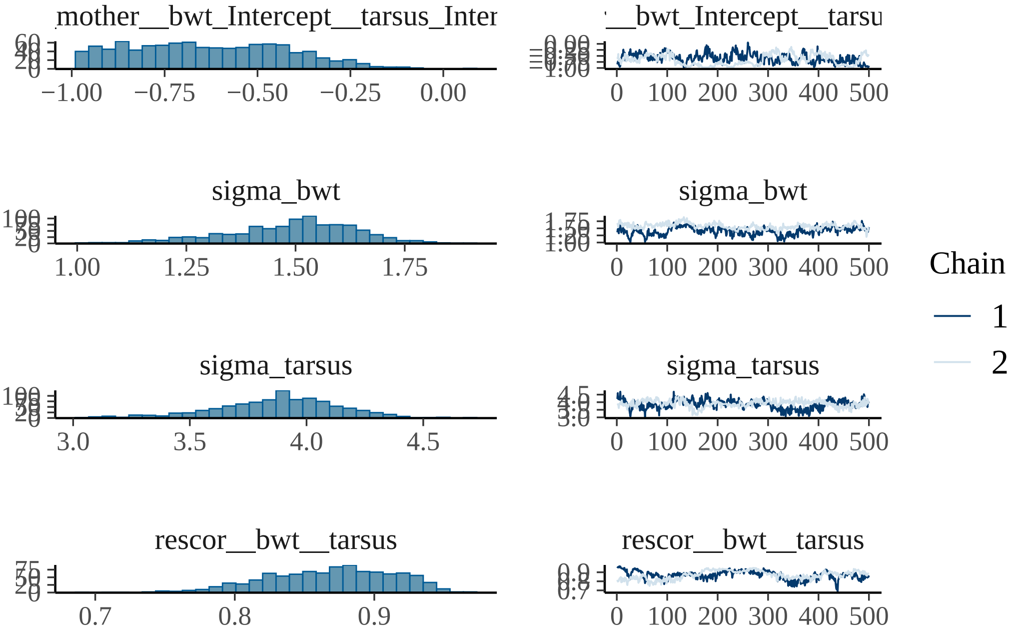
```
                                    Estimate Est.Error l-95% CI u-95% CI Rhat
sd(bwt_Intercept)                       0.97      0.14     0.70     1.26 1.01
sd(tarsus_Intercept)                    2.03      0.34     1.47     2.80 1.00
cor(bwt_Intercept,tarsus_Intercept)     0.01      0.21    -0.41     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).
```

```r
plot(brms_m2.3, ask = FALSE)
```







```r
VarCorr(brms_m2.3)
```

```
$animal
$animal$sd
                      Estimate Est.Error      Q2.5    Q97.5
bwt_Intercept:sex1    1.051791 0.2757021 0.4836926 1.575837
tarsus_Intercept:sex1 1.573820 0.7777373 0.1389929 3.025426
bwt_Intercept:sex2    1.232722 0.2436415 0.7075357 1.650628
```

```
tarsus_Intercept:sex2 3.237363 0.4773725 2.1667846 4.126560


$animal$cor
, , bwt_Intercept:sex1

                       Estimate Est.Error       Q2.5     Q97.5
bwt_Intercept:sex1    1.0000000 0.0000000  1.0000000 1.0000000
tarsus_Intercept:sex1 0.3232502 0.4324034 -0.7811983 0.9007145
bwt_Intercept:sex2    0.0000000 0.0000000  0.0000000 0.0000000
tarsus_Intercept:sex2 0.0000000 0.0000000  0.0000000 0.0000000

, , tarsus_Intercept:sex1

                       Estimate Est.Error       Q2.5     Q97.5
bwt_Intercept:sex1    0.3232502 0.4324034 -0.7811983 0.9007145
tarsus_Intercept:sex1 1.0000000 0.0000000  1.0000000 1.0000000
bwt_Intercept:sex2    0.0000000 0.0000000  0.0000000 0.0000000
tarsus_Intercept:sex2 0.0000000 0.0000000  0.0000000 0.0000000

, , bwt_Intercept:sex2

                       Estimate Est.Error      Q2.5     Q97.5
bwt_Intercept:sex1    0.0000000 0.0000000 0.0000000 0.0000000
tarsus_Intercept:sex1 0.0000000 0.0000000 0.0000000 0.0000000
bwt_Intercept:sex2    1.0000000 0.0000000 1.0000000 1.0000000
tarsus_Intercept:sex2 0.6975925 0.1213692 0.4474181 0.9047623

, , tarsus_Intercept:sex2

                       Estimate Est.Error      Q2.5     Q97.5
bwt_Intercept:sex1    0.0000000 0.0000000 0.0000000 0.0000000
tarsus_Intercept:sex1 0.0000000 0.0000000 0.0000000 0.0000000
bwt_Intercept:sex2    0.6975925 0.1213692 0.4474181 0.9047623
```

```
tarsus_Intercept:sex2 1.0000000 0.0000000 1.0000000 1.0000000



$animal$cov
, , bwt_Intercept:sex1

                       Estimate Est.Error       Q2.5    Q97.5
bwt_Intercept:sex1    1.1821990 0.5768155  0.2339592 2.483263
tarsus_Intercept:sex1 0.7957577 0.9482719 -0.4879668 3.035395
bwt_Intercept:sex2    0.0000000 0.0000000  0.0000000 0.000000
tarsus_Intercept:sex2 0.0000000 0.0000000  0.0000000 0.000000

, , tarsus_Intercept:sex1

                       Estimate Est.Error        Q2.5    Q97.5
bwt_Intercept:sex1    0.7957577 0.9482719 -0.48796685 3.035395
tarsus_Intercept:sex1 3.0811806 2.5183190  0.01931907 9.153208
bwt_Intercept:sex2    0.0000000 0.0000000  0.00000000 0.000000
tarsus_Intercept:sex2 0.0000000 0.0000000  0.00000000 0.000000

, , bwt_Intercept:sex2

                      Estimate Est.Error      Q2.5    Q97.5
bwt_Intercept:sex1    0.000000 0.0000000 0.0000000 0.000000
tarsus_Intercept:sex1 0.000000 0.0000000 0.0000000 0.000000
bwt_Intercept:sex2    1.578907 0.5865683 0.5006069 2.724572
tarsus_Intercept:sex2 2.842372 1.0153859 1.1593760 5.086448

, , tarsus_Intercept:sex2

                       Estimate Est.Error     Q2.5     Q97.5
bwt_Intercept:sex1     0.000000  0.000000 0.000000  0.000000
tarsus_Intercept:sex1  0.000000  0.000000 0.000000  0.000000
```

```
bwt_Intercept:sex2     2.842372  1.015386 1.159376  5.086448
tarsus_Intercept:sex2 10.708178  3.017245 4.694964 17.028497



$byear
$byear$sd
                  Estimate Est.Error      Q2.5    Q97.5
bwt_Intercept    0.9676965 0.1434955 0.7018779 1.258518
tarsus_Intercept 2.0290144 0.3382466 1.4650518 2.801932

$byear$cor
, , bwt_Intercept

                    Estimate Est.Error       Q2.5    Q97.5
bwt_Intercept    1.000000000 0.0000000  1.0000000 1.000000
tarsus_Intercept 0.009103073 0.2077977 -0.4096021 0.410902

, , tarsus_Intercept

                    Estimate Est.Error       Q2.5    Q97.5
bwt_Intercept    0.009103073 0.2077977 -0.4096021 0.410902
tarsus_Intercept 1.000000000 0.0000000  1.0000000 1.000000


$byear$cov
, , bwt_Intercept

                   Estimate Est.Error       Q2.5    Q97.5
bwt_Intercept    0.95700691 0.2875804  0.4926327 1.583869
tarsus_Intercept 0.04233908 0.4457863 -0.8475401 1.014920

, , tarsus_Intercept
```

```
                  Estimate Est.Error       Q2.5    Q97.5
bwt_Intercept    0.04233908 0.4457863 -0.8475401 1.014920
tarsus_Intercept 4.23119588 1.4453420  2.1463767 7.850826



$mother
$mother$sd
                 Estimate Est.Error     Q2.5    Q97.5
bwt_Intercept    1.175168 0.1083817 0.958963 1.388926
tarsus_Intercept 2.038471 0.3445355 1.327549 2.648997

$mother$cor
, , bwt_Intercept

                  Estimate Est.Error       Q2.5      Q97.5
bwt_Intercept     1.0000000 0.0000000  1.0000000  1.0000000
tarsus_Intercept -0.6301934 0.2113836 -0.9652044 -0.2283133

, , tarsus_Intercept

                  Estimate Est.Error       Q2.5      Q97.5
bwt_Intercept    -0.6301934 0.2113836 -0.9652044 -0.2283133
tarsus_Intercept  1.0000000 0.0000000  1.0000000  1.0000000



$mother$cov
, , bwt_Intercept

                  Estimate Est.Error       Q2.5     Q97.5
bwt_Intercept     1.392755 0.2562907  0.9196105  1.929117
tarsus_Intercept -1.434727 0.3664843 -2.0769067 -0.674943
```

```
, , tarsus_Intercept

                  Estimate Est.Error      Q2.5     Q97.5
bwt_Intercept    -1.434727 0.3664843 -2.076907 -0.674943
tarsus_Intercept  4.273951 1.3914013  1.762387  7.017188



$residual__
$residual__$sd
       Estimate Est.Error     Q2.5    Q97.5
bwt    1.489342 0.1489641 1.162192 1.741559
tarsus 3.875633 0.2650604 3.268802 4.345400

$residual__$cor
, , bwt

        Estimate  Est.Error      Q2.5     Q97.5
bwt    1.0000000 0.00000000 1.0000000 1.0000000
tarsus 0.8685184 0.04534008 0.7772864 0.9414488

, , tarsus

        Estimate  Est.Error      Q2.5     Q97.5
bwt    0.8685184 0.04534008 0.7772864 0.9414488
tarsus 1.0000000 0.00000000 1.0000000 1.0000000



$residual__$cov
, , bwt

       Estimate Est.Error     Q2.5    Q97.5
```

```
bwt    2.240307 0.4341334 1.350691 3.033029
tarsus 5.034739 0.7852137 3.272088 6.400539

, , tarsus

        Estimate Est.Error      Q2.5     Q97.5
bwt     5.034739 0.7852137  3.272088  6.400539
tarsus 15.090721 2.0309529 10.685067 18.882505
```

However, this model is lacking an important and essentiel group-specific partitionning (we do with the asreml-R and MCMCglmm). We need to partition the residual variance (or sigma) as well. Doing so, we will use the argument ‘sigma“ to parititon the model by sex. To avoid an estimation of the difference between sexes, we need to remove the estimate of the intercept at the sigma level.

```r
bf_bwt_4 <- bf(bwt ~ 1 + sex + ((1 | a | gr(animal, cov = Amat, by = sex))) + (1 | b | 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 = "r-obj/brms_m2_4.rda")
```

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

```r
load("r-obj/brms_m2_4.rda")
summary(brms_m2.4)
```

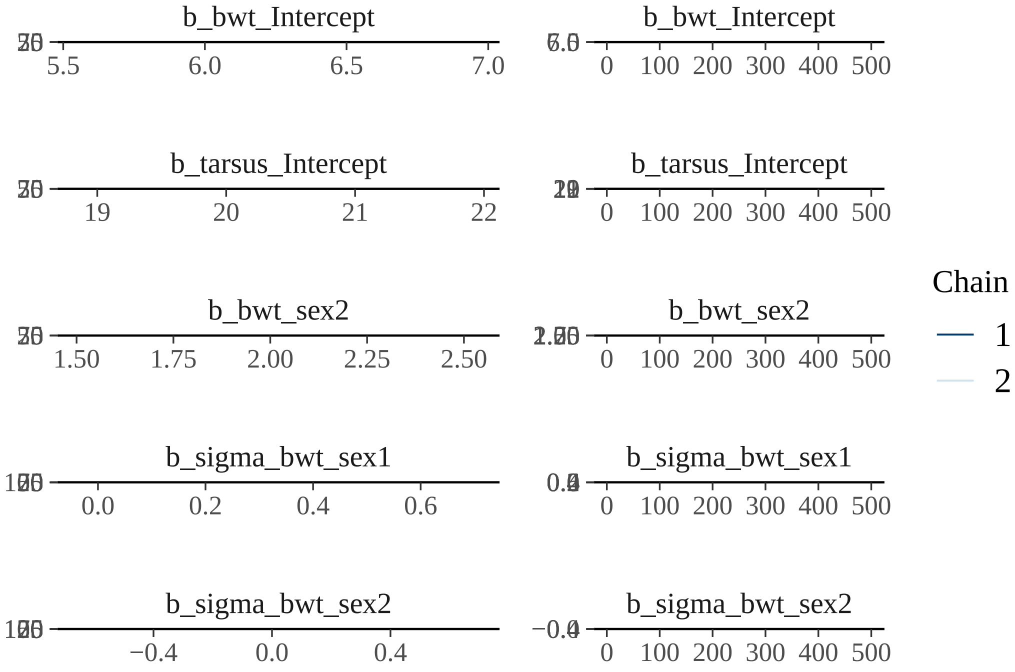
```
Warning: Parts of the model have not converged (some Rhats are > 1.05). Be
careful when analysing the results! We recommend running more iterations and/or
setting stronger priors.
```

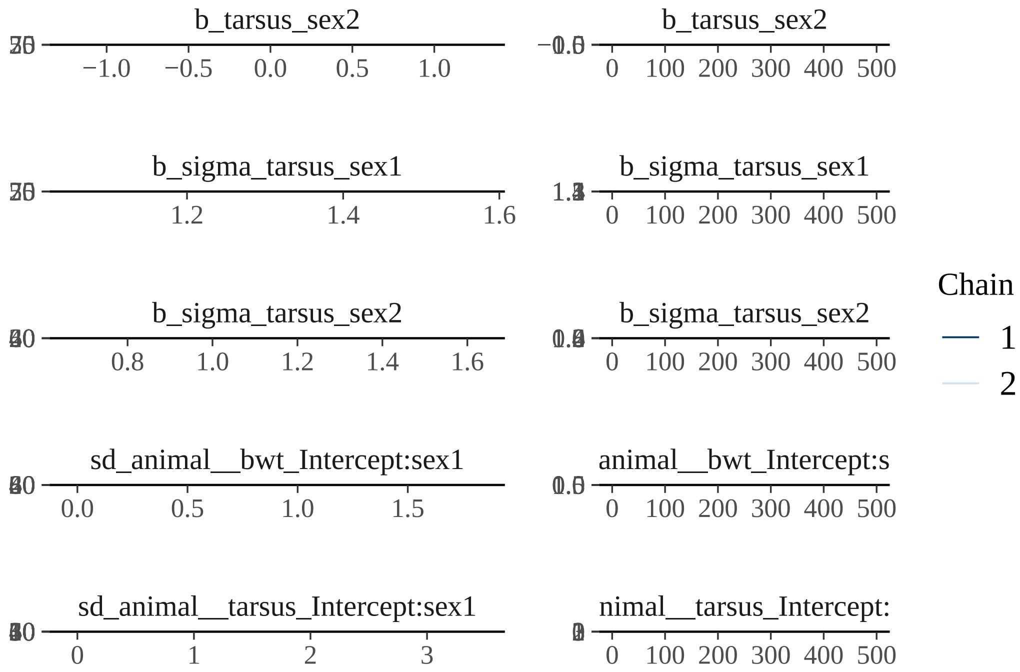
```
Warning: There were 6 divergent transitions after warmup. Increasing
adapt_delta above 0.8 may help. See
http://mc-stan.org/misc/warnings.html#divergent-transitions-after-warmup

 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
sd(bwt_Intercept:sex1)                            0.86      0.35     0.14
sd(tarsus_Intercept:sex1)                         1.40      0.82     0.10
sd(bwt_Intercept:sex2)                            1.40      0.23     0.94
sd(tarsus_Intercept:sex2)                         3.49      0.72     1.96
cor(bwt_Intercept:sex1,tarsus_Intercept:sex1)     0.28      0.51    -0.85
cor(bwt_Intercept:sex2,tarsus_Intercept:sex2)     0.78      0.10     0.56
                                              u-95% CI Rhat Bulk_ESS Tail_ESS
sd(bwt_Intercept:sex1)                            1.48 1.00       59      101
sd(tarsus_Intercept:sex1)                         3.00 1.07       45      111
sd(bwt_Intercept:sex2)                            1.83 1.04       42       40
sd(tarsus_Intercept:sex2)                         4.62 1.22        8       50
cor(bwt_Intercept:sex1,tarsus_Intercept:sex1)     0.94 1.05       60      287
cor(bwt_Intercept:sex2,tarsus_Intercept:sex2)     0.97 1.09       30       94

~byear (Number of levels: 34)
                                    Estimate Est.Error l-95% CI u-95% CI Rhat
```

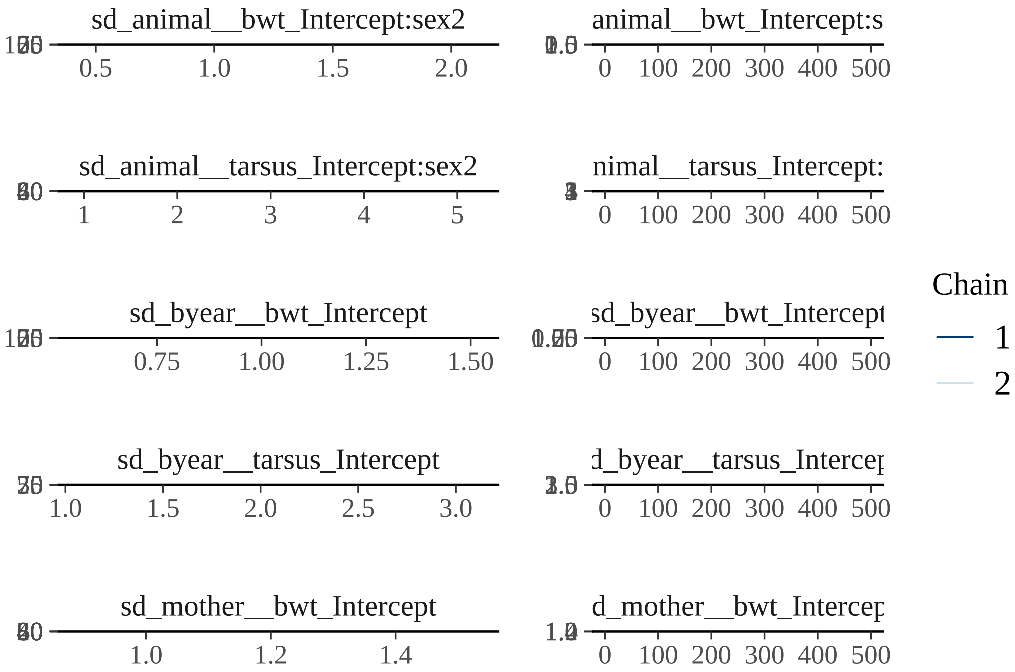
```
sd(bwt_Intercept)                    0.97      0.15     0.73     1.30 1.01
sd(tarsus_Intercept)                 2.01      0.33     1.41     2.70 1.00
cor(bwt_Intercept,tarsus_Intercept)  -0.00      0.22    -0.42     0.45 1.02
                                    Bulk_ESS Tail_ESS
sd(bwt_Intercept)                        283      412
sd(tarsus_Intercept)                     349      554
cor(bwt_Intercept,tarsus_Intercept)      225      256

~mother (Number of levels: 352)
                                    Estimate Est.Error l-95% CI u-95% CI Rhat
sd(bwt_Intercept)                        1.19      0.11     0.98     1.42 1.00
sd(tarsus_Intercept)                     2.14      0.30     1.57     2.71 1.05
cor(bwt_Intercept,tarsus_Intercept)     -0.55      0.21    -0.96    -0.16 1.04
                                    Bulk_ESS Tail_ESS
sd(bwt_Intercept)                        279      434
sd(tarsus_Intercept)                      46      227
cor(bwt_Intercept,tarsus_Intercept)       46      122

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
```

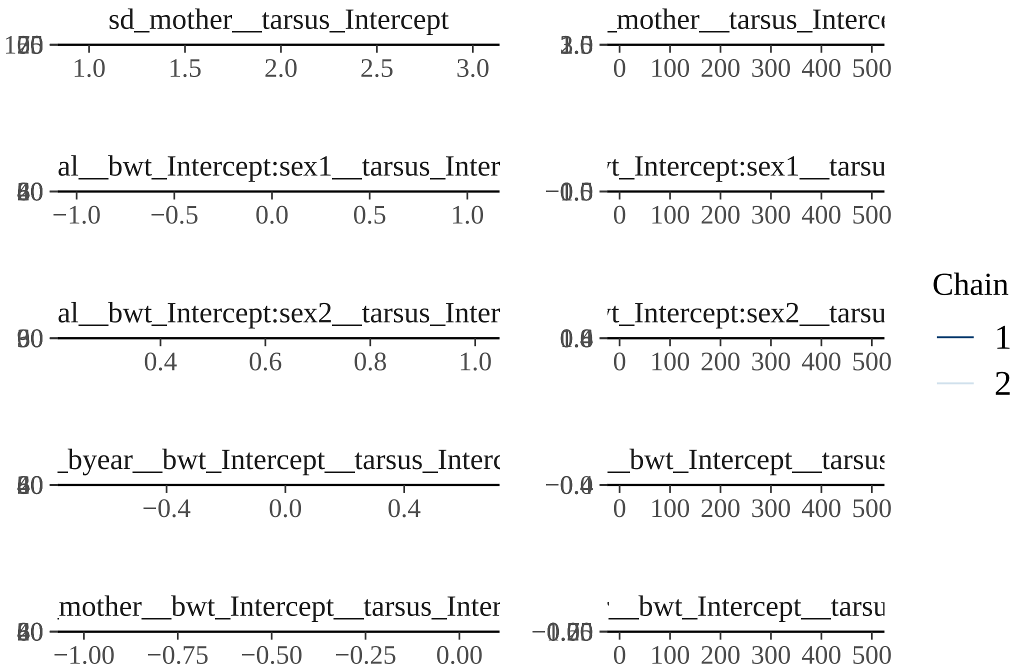
```
Draws were sampled using sampling(NUTS). For each parameter, Bulk_ESS
and Tail_ESS are effective sample size measures, and Rhat is the potential
scale reduction factor on split chains (at convergence, Rhat = 1).
```

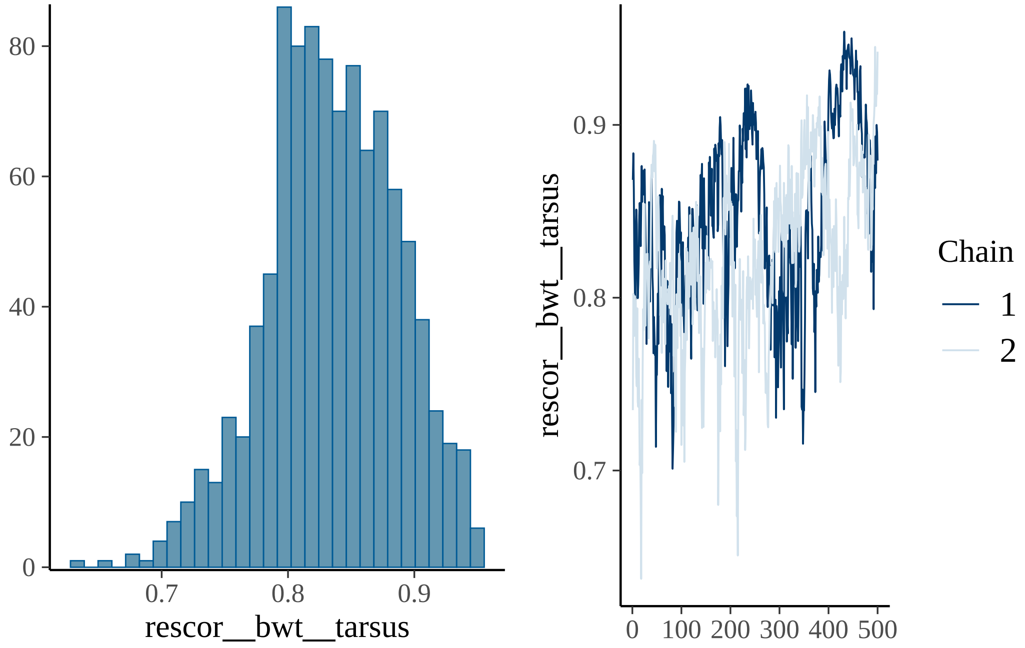
```r
plot(brms_m2.4, ask = FALSE)
```






sd_animal__bwt_Intercept:sex2
0.5
1.0
1.5
2.0
animal__bwt_Intercept:s
0 100 200 300 400 500
sd_animal__tarsus_Intercept:sex2
1 2 3 4 5
nimal__tarsus_Intercept:
0 100 200 300 400 500
sd_byear__bwt_Intercept
0.75 1.00 1.25 1.50
sd_byear__bwt_Intercept
0 100 200 300 400 500
sd_byear__tarsus_Intercept
1.0 1.5 2.0 2.5 3.0
d_byear__tarsus_Intercep
0 100 200 300 400 500
sd_mother__bwt_Intercept
1.0 1.2 1.4
d_mother__bwt_Intercep
0 100 200 300 400 500
Chain
1
2


sd_mother__tarsus_Intercept
1.0 1.5 2.0 2.5 3.0
_mother__tarsus_Interc
0 100 200 300 400 500
al__bwt_Intercept:sex1__tarsus_Inter
−1.0 −0.5 0.0 0.5 1.0
t_Intercept:sex1__tarsu
0 100 200 300 400 500
al__bwt_Intercept:sex2__tarsus_Inter
0.4 0.6 0.8 1.0
t_Intercept:sex2__tarsu
0 100 200 300 400 500
_byear__bwt_Intercept__tarsus_Interc
−0.4 0.0 0.4
__bwt_Intercept__tarsus
0 100 200 300 400 500
mother__bwt_Intercept__tarsus_Inter
−1.00 −0.75 −0.50 −0.25 0.00
__bwt_Intercept__tarsu
0 100 200 300 400 500
Chain
1
2



```r
VarCorr(brms_m2.4)
```

```
$animal
$animal$sd
                      Estimate Est.Error       Q2.5    Q97.5
bwt_Intercept:sex1    0.8628389 0.3531696 0.14360929 1.481121
tarsus_Intercept:sex1 1.3985239 0.8163731 0.09977045 3.002609
bwt_Intercept:sex2    1.4023202 0.2325863 0.93896619 1.833688
tarsus_Intercept:sex2 3.4858243 0.7167230 1.96177030 4.620105

$animal$cor
, , bwt_Intercept:sex1

                      Estimate Est.Error       Q2.5     Q97.5
bwt_Intercept:sex1    1.000000 0.0000000  1.0000000 1.0000000
tarsus_Intercept:sex1 0.277338 0.5119501 -0.8479996 0.9398158
bwt_Intercept:sex2    0.000000 0.0000000  0.0000000 0.0000000
tarsus_Intercept:sex2 0.000000 0.0000000  0.0000000 0.0000000

, , tarsus_Intercept:sex1
```

```
                      Estimate Est.Error       Q2.5     Q97.5
bwt_Intercept:sex1    0.277338 0.5119501 -0.8479996 0.9398158
tarsus_Intercept:sex1 1.000000 0.0000000  1.0000000 1.0000000
bwt_Intercept:sex2    0.000000 0.0000000  0.0000000 0.0000000
tarsus_Intercept:sex2 0.000000 0.0000000  0.0000000 0.0000000

, , bwt_Intercept:sex2

                       Estimate  Est.Error     Q2.5     Q97.5
bwt_Intercept:sex1    0.0000000 0.00000000 0.000000 0.0000000
tarsus_Intercept:sex1 0.0000000 0.00000000 0.000000 0.0000000
bwt_Intercept:sex2    1.0000000 0.00000000 1.000000 1.0000000
tarsus_Intercept:sex2 0.7781659 0.09850178 0.564036 0.9699765

, , tarsus_Intercept:sex2

                       Estimate  Est.Error     Q2.5     Q97.5
bwt_Intercept:sex1    0.0000000 0.00000000 0.000000 0.0000000
tarsus_Intercept:sex1 0.0000000 0.00000000 0.000000 0.0000000
bwt_Intercept:sex2    0.7781659 0.09850178 0.564036 0.9699765
tarsus_Intercept:sex2 1.0000000 0.00000000 1.000000 1.0000000



$animal$cov
, , bwt_Intercept:sex1

                       Estimate Est.Error       Q2.5    Q97.5
bwt_Intercept:sex1    0.8690949 0.6002446  0.0206250 2.193721
tarsus_Intercept:sex1 0.6483841 0.9143700 -0.4481203 2.989048
bwt_Intercept:sex2    0.0000000 0.0000000  0.0000000 0.000000
tarsus_Intercept:sex2 0.0000000 0.0000000  0.0000000 0.000000

, , tarsus_Intercept:sex1
```

```
                       Estimate Est.Error         Q2.5    Q97.5
bwt_Intercept:sex1    0.6483841  0.914370 -0.448120294 2.989048
tarsus_Intercept:sex1 2.6216677  2.500989  0.009954235 9.015666
bwt_Intercept:sex2    0.0000000  0.000000  0.000000000 0.000000
tarsus_Intercept:sex2 0.0000000  0.000000  0.000000000 0.000000

, , bwt_Intercept:sex2

                      Estimate Est.Error      Q2.5    Q97.5
bwt_Intercept:sex1    0.000000  0.000000 0.0000000 0.000000
tarsus_Intercept:sex1 0.000000  0.000000 0.0000000 0.000000
bwt_Intercept:sex2    2.020544  0.639550 0.8816577 3.362416
tarsus_Intercept:sex2 3.875299  1.298562 1.4247624 6.415724

, , tarsus_Intercept:sex2

                       Estimate Est.Error     Q2.5     Q97.5
bwt_Intercept:sex1     0.000000  0.000000 0.000000  0.000000
tarsus_Intercept:sex1  0.000000  0.000000 0.000000  0.000000
bwt_Intercept:sex2     3.875299  1.298562 1.424762  6.415724
tarsus_Intercept:sex2 12.664149  4.814957 3.848544 21.345370




$byear
$byear$sd
                  Estimate Est.Error      Q2.5    Q97.5
bwt_Intercept    0.9707654 0.1478361 0.7256973 1.298668
tarsus_Intercept 2.0073203 0.3290043 1.4102530 2.699770

$byear$cor
, , bwt_Intercept
```

```
                     Estimate Est.Error       Q2.5     Q97.5
bwt_Intercept     1.000000000 0.0000000  1.0000000 1.0000000
tarsus_Intercept -0.001551923 0.2236193 -0.4237849 0.4526618

, , tarsus_Intercept

                     Estimate Est.Error       Q2.5     Q97.5
bwt_Intercept    -0.001551923 0.2236193 -0.4237849 0.4526618
tarsus_Intercept  1.000000000 0.0000000  1.0000000 1.0000000


$byear$cov
, , bwt_Intercept

                  Estimate Est.Error       Q2.5    Q97.5
bwt_Intercept    0.9642191 0.3021042  0.5266366 1.686538
tarsus_Intercept 0.0252866 0.4713288 -0.8080314 1.069567

, , tarsus_Intercept

                  Estimate Est.Error       Q2.5    Q97.5
bwt_Intercept    0.0252866 0.4713288 -0.8080314 1.069567
tarsus_Intercept 4.1374703 1.3676889  1.9888135 7.288761



$mother
$mother$sd
                 Estimate Est.Error      Q2.5    Q97.5
bwt_Intercept    1.189902 0.1113270 0.9791374 1.423333
tarsus_Intercept 2.139290 0.2985875 1.5714814 2.708199
```

```
$mother$cor
, , bwt_Intercept

                   Estimate Est.Error       Q2.5      Q97.5
bwt_Intercept     1.0000000 0.0000000  1.0000000  1.0000000
tarsus_Intercept -0.5501934 0.2066985 -0.9589938 -0.1591737

, , tarsus_Intercept

                   Estimate Est.Error       Q2.5      Q97.5
bwt_Intercept    -0.5501934 0.2066985 -0.9589938 -0.1591737
tarsus_Intercept  1.0000000 0.0000000  1.0000000  1.0000000



$mother$cov
, , bwt_Intercept

                  Estimate Est.Error      Q2.5      Q97.5
bwt_Intercept     1.428247 0.2672833  0.958710  2.0258758
tarsus_Intercept -1.335450 0.3932707 -2.051866 -0.5146954

, , tarsus_Intercept

                  Estimate Est.Error      Q2.5      Q97.5
bwt_Intercept    -1.335450 0.3932707 -2.051866 -0.5146954
tarsus_Intercept  4.665626 1.2688941  2.469554  7.3343400
```

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

```r
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)
```

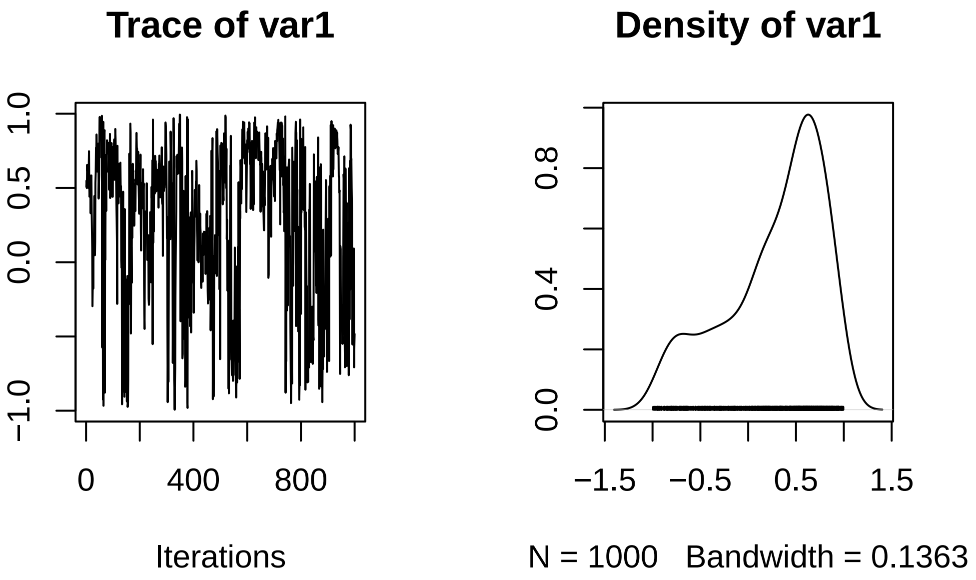
```


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)
```

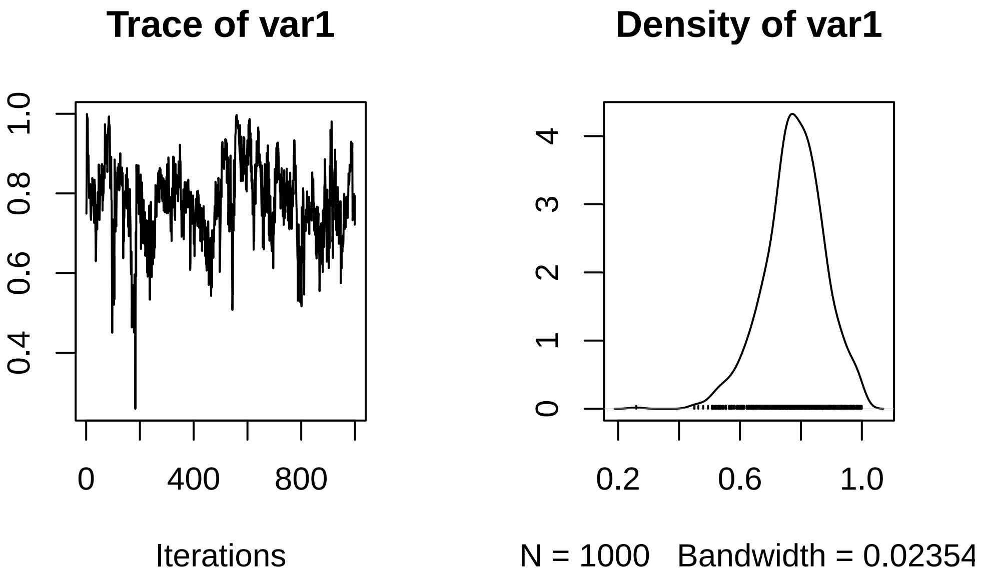
```


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)
```

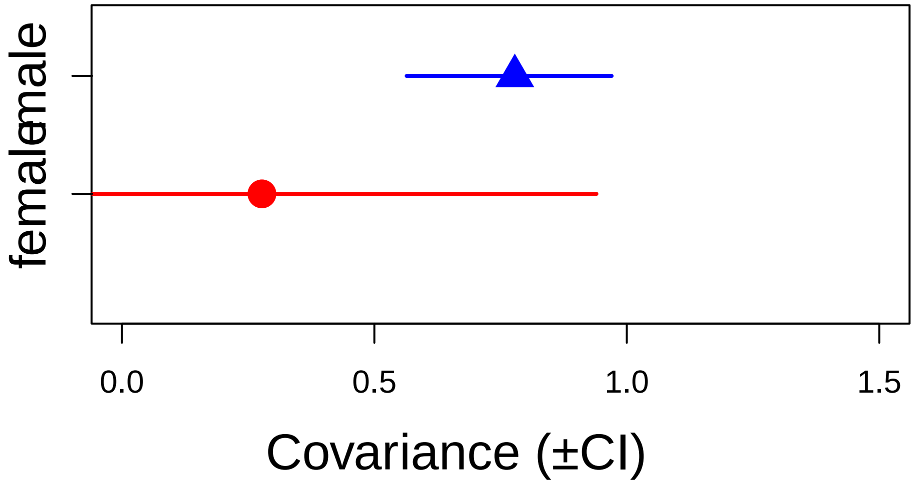


```
plot(cor_g_M)
```



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)$quantiles
  cbind(summary(cor_g_M)$statistics[1], summary(cor_g_M)$quantiles[1], summary(cor_g_M)$quantiles
)



plot(c(1, 2) ~ cor.est[, 1], xlim = c(0, 1.5), ylim = c(0, 2.5), xlab = "", ylab = "", col = c("r
segments(y0 = 1, x0 = cor.est[1, 2], y1 = 1, x1 = cor.est[1, 3], col = c("red"), lwd = 2)
segments(y0 = 2, x0 = cor.est[2, 2], y1 = 2, x1 = cor.est[2, 3], col = c("blue"), lwd = 2)
mtext("Covariance (±CI)", side = 1, las = 1, adj = 0.4, line = 3, cex = 1.6)
axis(2, at = 1, labels = c("female"), las = 3, cex.axis = 1.6)
axis(2, at = 2, labels = c("male"), las = 3, cex.axis = 1.6)
```

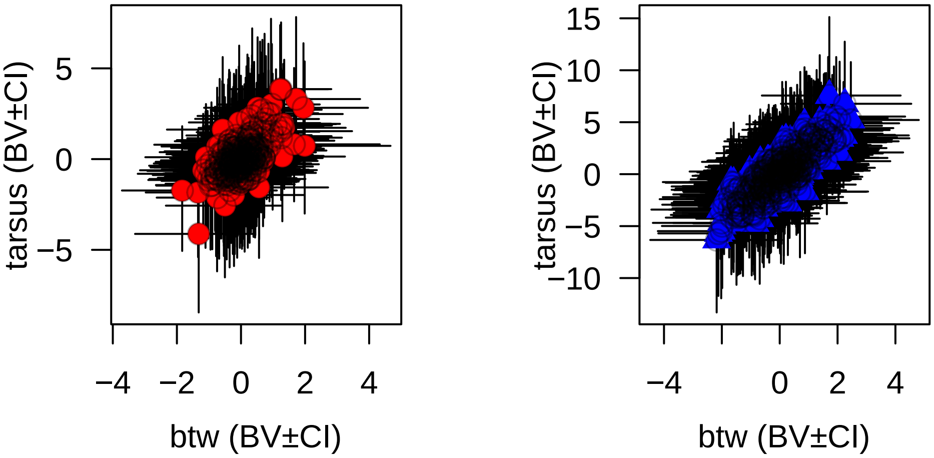


Here a simple plot of the sex-specific genetic correlation using the BLUPs

```
bls_m2.4 <- ranef(brms_m2.4)$animal
bl_m2.4 <- as.data.frame(abind::abind(lapply(1:dim(bls_m2.4)[3], function(x) bls_m2.4[, c(1, 3, 4
colnames(bl_m2.4) <- paste0(rep(dimnames(bls_m2.4)[[3]], each = 3), c("", "_lo", "_up"))
bl_m2.4$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 ontogenic or sexual conflict, which can constraint or enhanced response to evolution. As an example, we estimate the cross-sex genetic correlation `r_{fm}`

It is important to keep in mind the covariance matrix at the residual level is zero and it is important to avoid estimating the cross-sex residual covariance because no individual switched sex during the experiment.

Note: the way of partitionning variance per sex is a bit different then the previous code ",by=sex".
This code is faster and also easier to understand. Note, it is possible to play with the `|` or `||` to estimate or not covariance between sexes.

```
bf_bwt_5 <- bf(
  bwt ~ 1 + sex + (0 + sex | a | gr(animal, cov = Amat)) + (0 + sex | b | mother) + (0 + 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 = "r-obj/brms_m2_5.rda")
```

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

```
load("r-obj/brms_m2_5.rda")
summary(brms_m2.5)
```

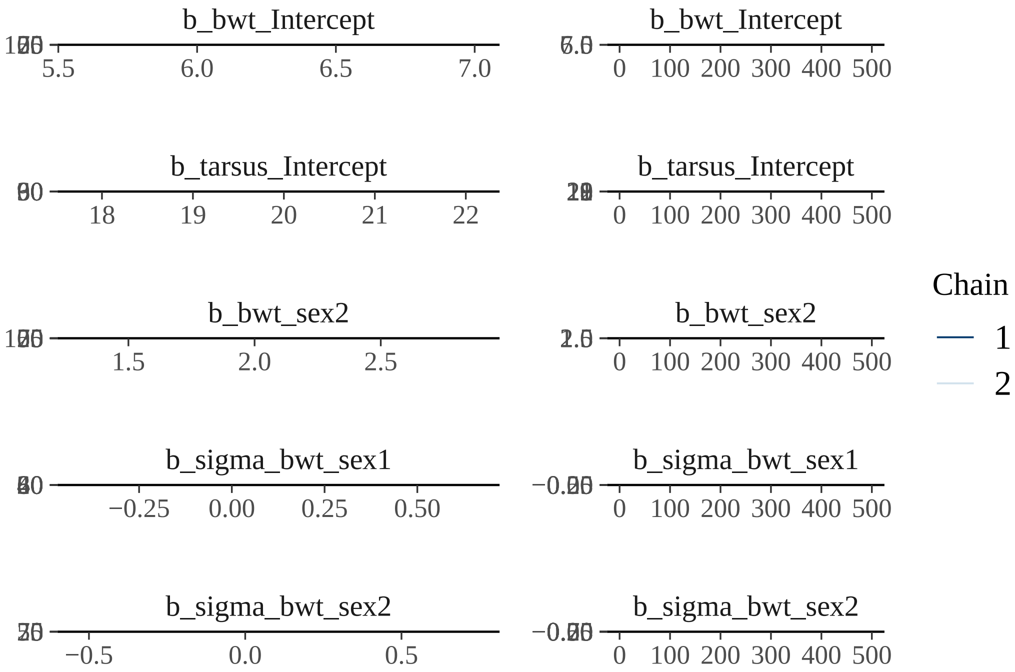
```
Warning: Parts of the model have not converged (some Rhats are > 1.05). Be
careful when analysing the results! We recommend running more iterations and/or
setting stronger priors.

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

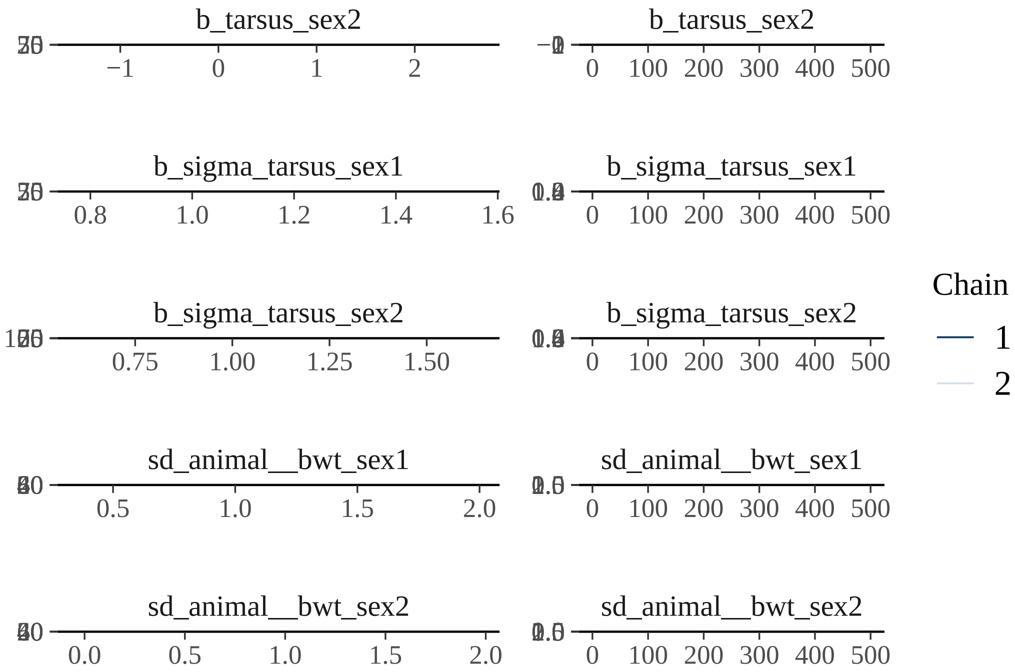
```
   Data: gryphon (Number of observations: 683)
  Draws: 2 chains, each with iter = 1000; warmup = 500; thin = 1;
         total post-warmup draws = 1000

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
```

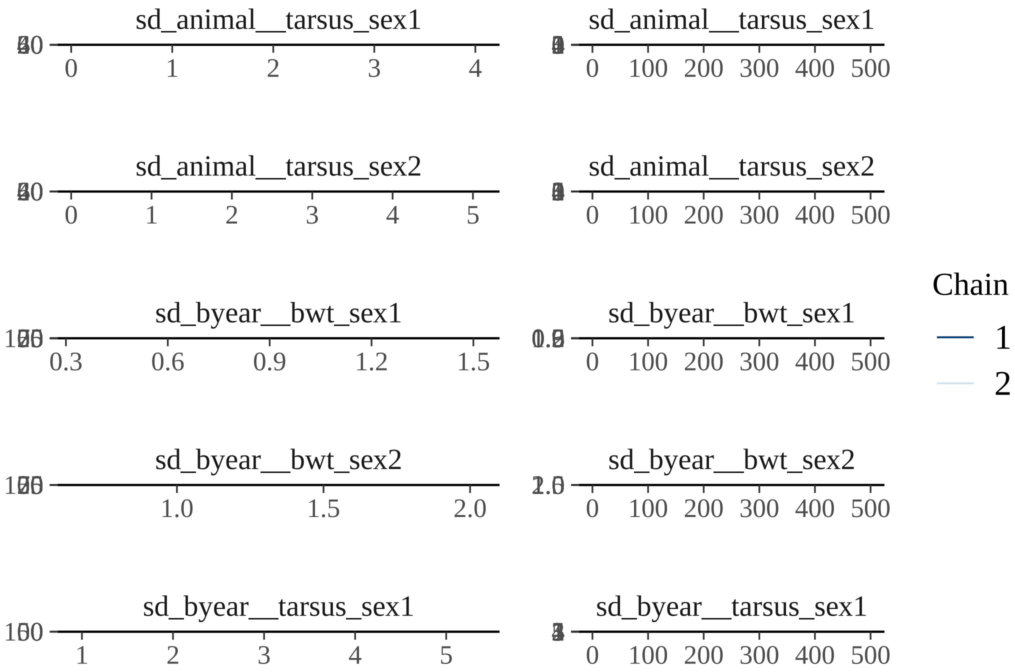
```
sd(tarsus_sex1)                  2.23      0.46     1.50     3.18 1.01      297
sd(tarsus_sex2)                  2.34      0.49     1.56     3.41 1.01      229
cor(bwt_sex1,bwt_sex2)           0.74      0.15     0.35     0.96 1.01      266
cor(bwt_sex1,tarsus_sex1)       -0.11      0.24    -0.55     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 l-95% CI u-95% CI Rhat Bulk_ESS
sd(bwt_sex1)                     1.08      0.15     0.79     1.39 1.01      281
sd(bwt_sex2)                     1.33      0.15     1.03     1.62 1.00      233
sd(tarsus_sex1)                  2.21      0.40     1.36     2.95 1.01       72
sd(tarsus_sex2)                  2.31      0.49     1.38     3.34 1.05       50
cor(bwt_sex1,bwt_sex2)           0.83      0.11     0.57     0.98 1.01       68
cor(bwt_sex1,tarsus_sex1)       -0.50      0.24    -0.91    -0.07 1.01       57
cor(bwt_sex2,tarsus_sex1)       -0.64      0.17    -0.93    -0.28 1.06       50
cor(bwt_sex1,tarsus_sex2)       -0.51      0.22    -0.88    -0.08 1.05       67
cor(bwt_sex2,tarsus_sex2)       -0.36      0.26    -0.84     0.11 1.05       54
cor(tarsus_sex1,tarsus_sex2)     0.72      0.16     0.37     0.95 1.01      249
                             Tail_ESS
```

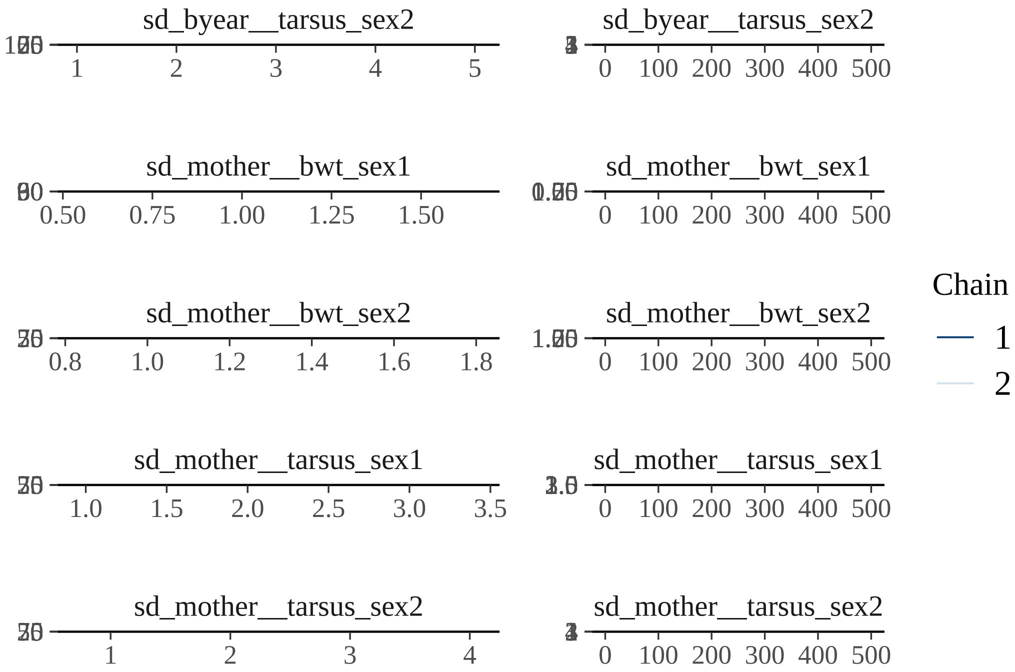
```
sd(bwt_sex1)                  518
sd(bwt_sex2)                  585
sd(tarsus_sex1)               224
sd(tarsus_sex2)               191
cor(bwt_sex1,bwt_sex2)        296
cor(bwt_sex1,tarsus_sex1)     156
cor(bwt_sex2,tarsus_sex1)     268
cor(bwt_sex1,tarsus_sex2)     124
cor(bwt_sex2,tarsus_sex2)     297
cor(tarsus_sex1,tarsus_sex2)  596

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).
```

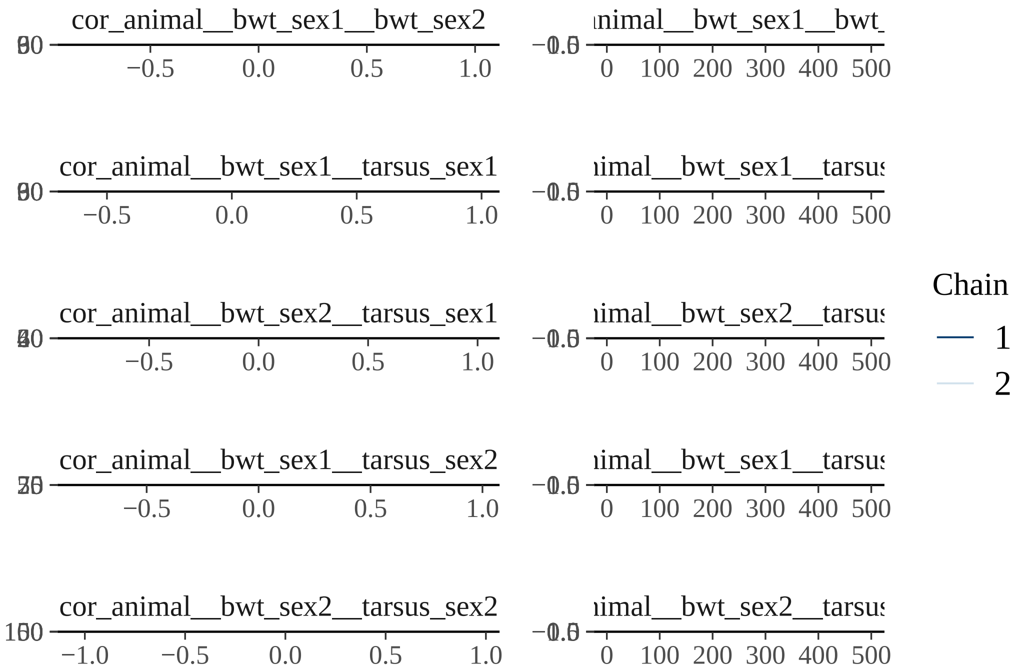
```r
plot(brms_m2.5, ask = FALSE)
```

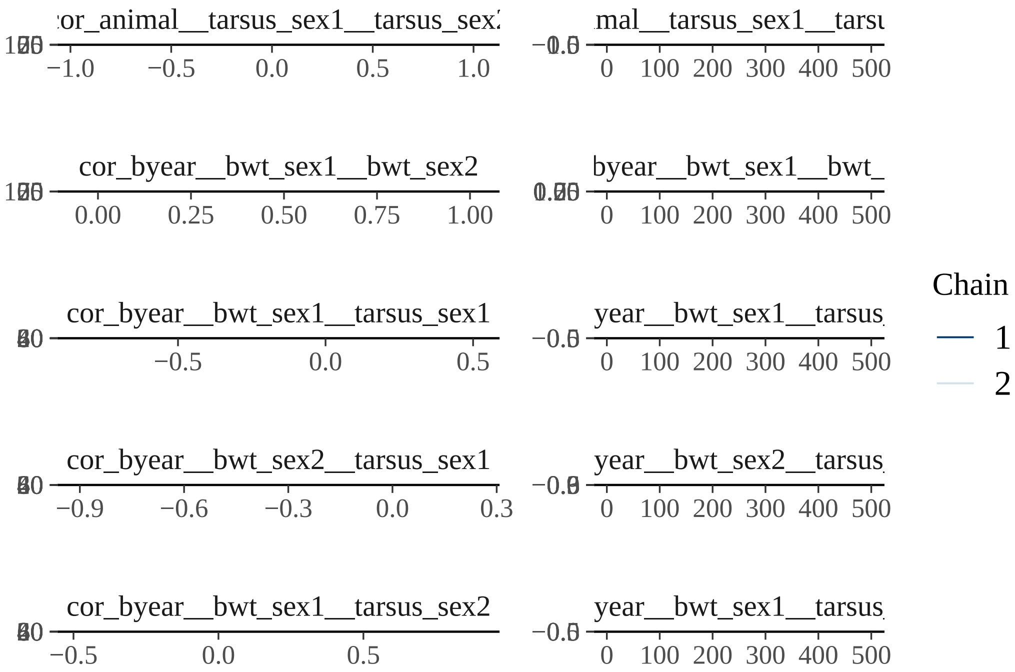

b_bwt_Intercept
5.5
6.0
6.5
7.0
b_bwt_Intercept
0
100
200
300
400
500
b_tarsus_Intercept
18
19
20
21
22
b_tarsus_Intercept
0
100
200
300
400
500
Chain
1
2
b_bwt_sex2
1.5
2.0
2.5
b_bwt_sex2
0
100
200
300
400
500
b_sigma_bwt_sex1
−0.25
0.00
0.25
0.50
b_sigma_bwt_sex1
0
100
200
300
400
500
b_sigma_bwt_sex2
−0.5
0.0
0.5
b_sigma_bwt_sex2
0
100
200
300
400
500

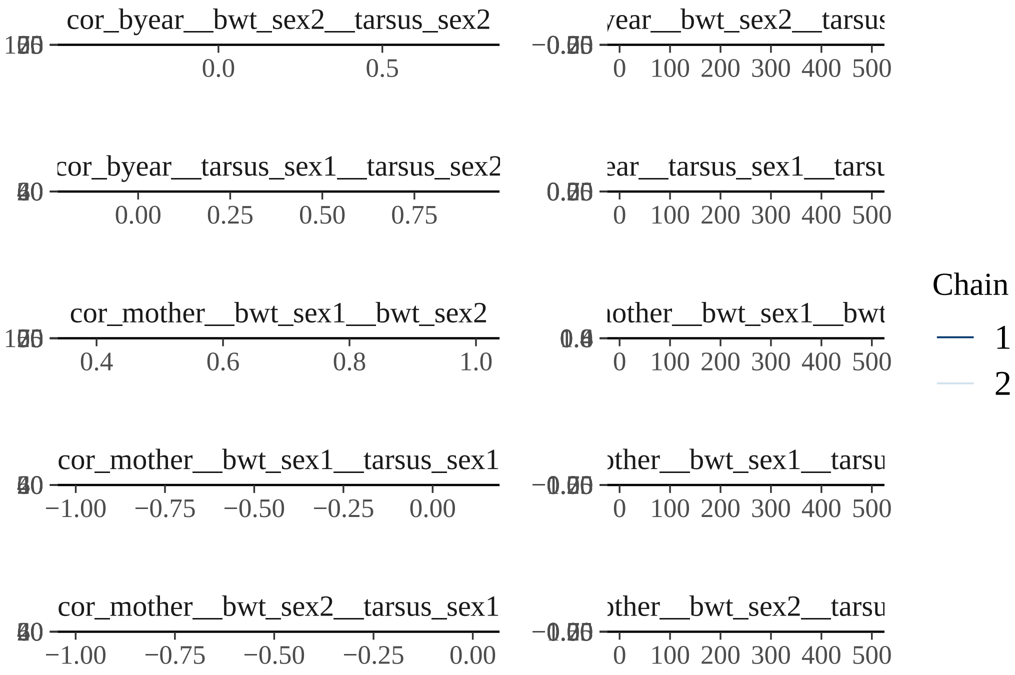

b_tarsus_sex2
−1
0
1
2
b_tarsus_sex2
0
100
200
300
400
500
b_sigma_tarsus_sex1
0.8
1.0
1.2
1.4
1.6
b_sigma_tarsus_sex1
0
100
200
300
400
500
Chain
1
2
b_sigma_tarsus_sex2
0.75
1.00
1.25
1.50
b_sigma_tarsus_sex2
0
100
200
300
400
500
sd_animal__bwt_sex1
0.5
1.0
1.5
2.0
sd_animal__bwt_sex1
0
100
200
300
400
500
sd_animal__bwt_sex2
0.0
0.5
1.0
1.5
2.0
sd_animal__bwt_sex2
0
100
200
300
400
500

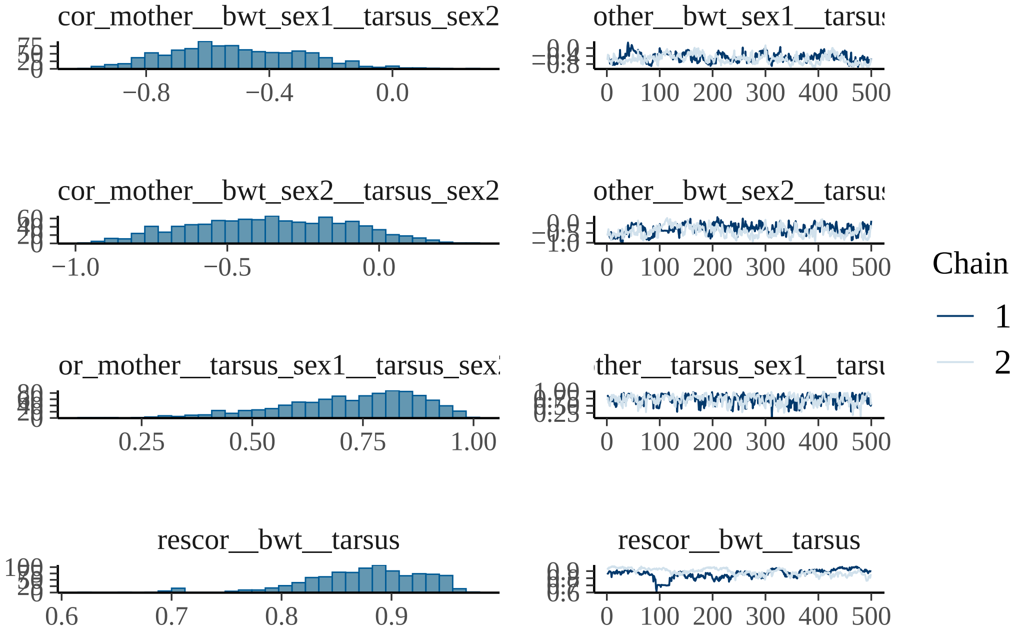

sd_animal__tarsus_sex1
0
1
2
3
4
sd_animal__tarsus_sex1
0
100
200
300
400
500
sd_animal__tarsus_sex2
0
1
2
3
4
5
sd_animal__tarsus_sex2
0
100
200
300
400
500
Chain
1
2
sd_byear__bwt_sex1
0.3
0.6
0.9
1.2
1.5
sd_byear__bwt_sex1
0
100
200
300
400
500
sd_byear__bwt_sex2
1.0
1.5
2.0
sd_byear__bwt_sex2
0
100
200
300
400
500
sd_byear__tarsus_sex1
1
2
3
4
5
sd_byear__tarsus_sex1
0
100
200
300
400
500


sd_byear__tarsus_sex2
1
2
3
4
5
sd_byear__tarsus_sex2
0
100
200
300
400
500
sd_mother__bwt_sex1
0.50
0.75
1.00
1.25
1.50
sd_mother__bwt_sex1
0
100
200
300
400
500
Chain
1
2
sd_mother__bwt_sex2
0.8
1.0
1.2
1.4
1.6
1.8
sd_mother__bwt_sex2
0
100
200
300
400
500
sd_mother__tarsus_sex1
1.0
1.5
2.0
2.5
3.0
3.5
sd_mother__tarsus_sex1
0
100
200
300
400
500
sd_mother__tarsus_sex2
1
2
3
4
sd_mother__tarsus_sex2
0
100
200
300
400
500


cor_animal__bwt_sex1__bwt_sex2
−0.5 0.0 0.5 1.0
nimal__bwt_sex1__bwt_
0 100 200 300 400 500
cor_animal__bwt_sex1__tarsus_sex1
−0.5 0.0 0.5 1.0
iimal__bwt_sex1__tarsus
0 100 200 300 400 500
cor_animal__bwt_sex2__tarsus_sex1
−0.5 0.0 0.5 1.0
iimal__bwt_sex2__tarsus
0 100 200 300 400 500
cor_animal__bwt_sex1__tarsus_sex2
−0.5 0.0 0.5 1.0
iimal__bwt_sex1__tarsus
0 100 200 300 400 500
cor_animal__bwt_sex2__tarsus_sex2
−1.0 −0.5 0.0 0.5 1.0
iimal__bwt_sex2__tarsus
0 100 200 300 400 500
Chain
1
2


cor_animal__tarsus_sex1__tarsus_sex2
−1.0 −0.5 0.0 0.5 1.0
mal__tarsus_sex1__tarsu
0 100 200 300 400 500
cor_byear__bwt_sex1__bwt_sex2
0.00 0.25 0.50 0.75 1.00
byear__bwt_sex1__bwt_
0 100 200 300 400 500
cor_byear__bwt_sex1__tarsus_sex1
−0.5 0.0 0.5
year__bwt_sex1__tarsus
0 100 200 300 400 500
cor_byear__bwt_sex2__tarsus_sex1
−0.9 −0.6 −0.3 0.0 0.3
year__bwt_sex2__tarsus
0 100 200 300 400 500
cor_byear__bwt_sex1__tarsus_sex2
−0.5 0.0 0.5
year__bwt_sex1__tarsus
0 100 200 300 400 500
Chain
1
2





```r
VarCorr(brms_m2.5)
```

```
$animal
$animal$sd
            Estimate Est.Error      Q2.5    Q97.5
bwt_sex1    1.256797 0.3027123 0.6293789 1.733715
bwt_sex2    1.077842 0.4168427 0.1958640 1.767136
tarsus_sex1 2.259727 0.7239967 0.6135135 3.567762
```

```
tarsus_sex2 2.744785 1.0537686 0.6051135 4.468542


$animal$cor
, , bwt_sex1

             Estimate Est.Error        Q2.5     Q97.5
bwt_sex1    1.0000000 0.0000000  1.00000000 1.0000000
bwt_sex2    0.4823461 0.2872049 -0.23539931 0.8699222
tarsus_sex1 0.5711397 0.2473353 -0.06616842 0.8936581
tarsus_sex2 0.1685774 0.3102320 -0.48914110 0.7539686

, , bwt_sex2

             Estimate Est.Error       Q2.5     Q97.5
bwt_sex1    0.4823461 0.2872049 -0.2353993 0.8699222
bwt_sex2    1.0000000 0.0000000  1.0000000 1.0000000
tarsus_sex1 0.3772862 0.3765302 -0.5312556 0.9085651
tarsus_sex2 0.5246223 0.3336679 -0.3678213 0.8692250

, , tarsus_sex1

             Estimate Est.Error        Q2.5     Q97.5
bwt_sex1    0.5711397 0.2473353 -0.06616842 0.8936581
bwt_sex2    0.3772862 0.3765302 -0.53125561 0.9085651
tarsus_sex1 1.0000000 0.0000000  1.00000000 1.0000000
tarsus_sex2 0.4401433 0.2929178 -0.29616405 0.8720453

, , tarsus_sex2

             Estimate Est.Error       Q2.5     Q97.5
bwt_sex1    0.1685774 0.3102320 -0.4891411 0.7539686
bwt_sex2    0.5246223 0.3336679 -0.3678213 0.8692250
tarsus_sex1 0.4401433 0.2929178 -0.2961641 0.8720453
```

```
tarsus_sex2 1.0000000 0.0000000  1.0000000 1.0000000



$animal$cov
, , bwt_sex1

             Estimate Est.Error        Q2.5    Q97.5
bwt_sex1    1.6710810 0.7317405  0.39611874 3.005768
bwt_sex2    0.7428820 0.5579922 -0.10600955 2.049110
tarsus_sex1 1.8733421 1.2159805 -0.05815667 4.340959
tarsus_sex2 0.6471034 1.0646022 -1.25297349 2.930019

, , bwt_sex2

            Estimate Est.Error        Q2.5    Q97.5
bwt_sex1    0.742882 0.5579922 -0.10600955 2.049110
bwt_sex2    1.335327 0.8557561  0.03836336 3.122771
tarsus_sex1 1.105102 1.0991534 -0.68104784 3.388813
tarsus_sex2 2.171388 1.8198507 -0.18718074 5.946047

, , tarsus_sex1

            Estimate Est.Error        Q2.5     Q97.5
bwt_sex1    1.873342  1.215980 -0.05815667  4.340959
bwt_sex2    1.105102  1.099153 -0.68104784  3.388813
tarsus_sex1 5.630014  3.143741  0.37639882 12.728924
tarsus_sex2 3.150235  2.476892 -0.67170548  8.755673

, , tarsus_sex2

             Estimate Est.Error       Q2.5     Q97.5
bwt_sex1    0.6471034  1.064602 -1.2529735  2.930019
bwt_sex2    2.1713876  1.819851 -0.1871807  5.946047
```

```
tarsus_sex1 3.1502347  2.476892 -0.6717055  8.755673
tarsus_sex2 8.6431609  5.649764  0.3661935 19.967865



$byear
$byear$sd
             Estimate Est.Error      Q2.5    Q97.5
bwt_sex1    0.7989572 0.1620838 0.5318383 1.156162
bwt_sex2    1.1420876 0.1912205 0.8090083 1.549360
tarsus_sex1 2.2286834 0.4609182 1.4995560 3.183107
tarsus_sex2 2.3428101 0.4941316 1.5596304 3.405106

$byear$cor
, , bwt_sex1

              Estimate Est.Error       Q2.5     Q97.5
bwt_sex1     1.0000000 0.0000000  1.0000000 1.0000000
bwt_sex2     0.7404024 0.1542690  0.3534945 0.9558481
tarsus_sex1 -0.1137836 0.2357386 -0.5534464 0.3543949
tarsus_sex2  0.2922708 0.2345550 -0.1749420 0.7113421

, , bwt_sex2

              Estimate Est.Error       Q2.5       Q97.5
bwt_sex1     0.7404024 0.1542690  0.3534945 0.955848060
bwt_sex2     1.0000000 0.0000000  1.0000000 1.000000000
tarsus_sex1 -0.3874250 0.1987378 -0.7323699 0.004258363
tarsus_sex2  0.2937354 0.2059346 -0.1577533 0.659531338

, , tarsus_sex1

              Estimate Est.Error       Q2.5       Q97.5
```

```
bwt_sex1    -0.1137836 0.2357386 -0.5534464 0.354394929
bwt_sex2    -0.3874250 0.1987378 -0.7323699 0.004258363
tarsus_sex1  1.0000000 0.0000000  1.0000000 1.000000000
tarsus_sex2  0.5226217 0.1897518  0.1183176 0.839911077

, , tarsus_sex2

             Estimate Est.Error      Q2.5     Q97.5
bwt_sex1    0.2922708 0.2345550 -0.1749420 0.7113421
bwt_sex2    0.2937354 0.2059346 -0.1577533 0.6595313
tarsus_sex1 0.5226217 0.1897518  0.1183176 0.8399111
tarsus_sex2 1.0000000 0.0000000  1.0000000 1.0000000



$byear$cov
, , bwt_sex1

              Estimate Est.Error       Q2.5     Q97.5
bwt_sex1     0.6645776 0.2761781  0.2828520 1.3367115
bwt_sex2     0.6843681 0.2597687  0.2749460 1.2955568
tarsus_sex1 -0.1581409 0.4589758 -1.0281983 0.8339776
tarsus_sex2  0.5456796 0.5013040 -0.3608892 1.5951028

, , bwt_sex2

              Estimate Est.Error       Q2.5       Q97.5
bwt_sex1     0.6843681 0.2597687  0.2749460 1.295556807
bwt_sex2     1.3408929 0.4593417  0.6544951 2.400516888
tarsus_sex1 -1.0167438 0.6693667 -2.4775184 0.009371017
tarsus_sex2  0.8646682 0.7242669 -0.3384814 2.623722863

, , tarsus_sex1
```

```
              Estimate Est.Error       Q2.5        Q97.5
bwt_sex1    -0.1581409 0.4589758 -1.0281983  0.833977585
bwt_sex2    -1.0167438 0.6693667 -2.4775184  0.009371017
tarsus_sex1  5.1792626 2.3047474  2.2486683 10.132170288
tarsus_sex2  2.7818157 1.5318128  0.5297591  5.970346660

, , tarsus_sex2

             Estimate Est.Error       Q2.5     Q97.5
bwt_sex1    0.5456796 0.5013040 -0.3608892  1.595103
bwt_sex2    0.8646682 0.7242669 -0.3384814  2.623723
tarsus_sex1 2.7818157 1.5318128  0.5297591  5.970347
tarsus_sex2 5.7326811 2.5639312  2.4324504 11.594758



$mother
$mother$sd
            Estimate Est.Error      Q2.5    Q97.5
bwt_sex1    1.076447 0.1526711 0.7866154 1.390273
bwt_sex2    1.325206 0.1540539 1.0256350 1.621175
tarsus_sex1 2.214033 0.3976449 1.3647309 2.946910
tarsus_sex2 2.310902 0.4940802 1.3795156 3.339175

$mother$cor
, , bwt_sex1

              Estimate Est.Error       Q2.5       Q97.5
bwt_sex1     1.0000000 0.0000000  1.0000000  1.00000000
bwt_sex2     0.8260360 0.1110784  0.5676601  0.97826511
tarsus_sex1 -0.5024557 0.2385053 -0.9137423 -0.06798800
tarsus_sex2 -0.5073494 0.2162931 -0.8806394 -0.07677131
```

```
, , bwt_sex2

              Estimate Est.Error      Q2.5      Q97.5
bwt_sex1     0.8260360 0.1110784  0.5676601  0.9782651
bwt_sex2     1.0000000 0.0000000  1.0000000  1.0000000
tarsus_sex1 -0.6373889 0.1744852 -0.9272366 -0.2775698
tarsus_sex2 -0.3593672 0.2577845 -0.8364419  0.1135921

, , tarsus_sex1

              Estimate Est.Error      Q2.5      Q97.5
bwt_sex1    -0.5024557 0.2385053 -0.9137423 -0.0679880
bwt_sex2    -0.6373889 0.1744852 -0.9272366 -0.2775698
tarsus_sex1  1.0000000 0.0000000  1.0000000  1.0000000
tarsus_sex2  0.7206209 0.1561300  0.3688228  0.9518425

, , tarsus_sex2

              Estimate Est.Error      Q2.5       Q97.5
bwt_sex1    -0.5073494 0.2162931 -0.8806394 -0.07677131
bwt_sex2    -0.3593672 0.2577845 -0.8364419  0.11359208
tarsus_sex1  0.7206209 0.1561300  0.3688228  0.95184250
tarsus_sex2  1.0000000 0.0000000  1.0000000  1.00000000



$mother$cov
, , bwt_sex1

             Estimate Est.Error      Q2.5      Q97.5
bwt_sex1     1.182023 0.3330334  0.6187659  1.9328578
bwt_sex2     1.179468 0.2744898  0.6821359  1.7479435
tarsus_sex1 -1.110068 0.4557029 -1.9379754 -0.2103052
tarsus_sex2 -1.223308 0.5582766 -2.3558658 -0.1900476
```

```
, , bwt_sex2

              Estimate Est.Error      Q2.5      Q97.5
bwt_sex1     1.1794683 0.2744898  0.6821359  1.7479435
bwt_sex2     1.7798788 0.4088241  1.0519272  2.6282093
tarsus_sex1 -1.8437371 0.5678929 -2.9129058 -0.7723013
tarsus_sex2 -0.9438083 0.6393327 -2.0044262  0.4581811

, , tarsus_sex1

             Estimate Est.Error      Q2.5      Q97.5
bwt_sex1    -1.110068 0.4557029 -1.937975 -0.2103052
bwt_sex2    -1.843737 0.5678929 -2.912906 -0.7723013
tarsus_sex1  5.059904 1.7495725  1.862491  8.6842757
tarsus_sex2  3.692391 1.3309441  1.432767  6.5202798

, , tarsus_sex2

              Estimate Est.Error      Q2.5      Q97.5
bwt_sex1    -1.2233079 0.5582766 -2.355866 -0.1900476
bwt_sex2    -0.9438083 0.6393327 -2.004426  0.4581811
tarsus_sex1  3.6923914 1.3309441  1.432767  6.5202798
tarsus_sex2  5.5841373 2.3245515  1.903063 11.1500916
```

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

```r
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)
```

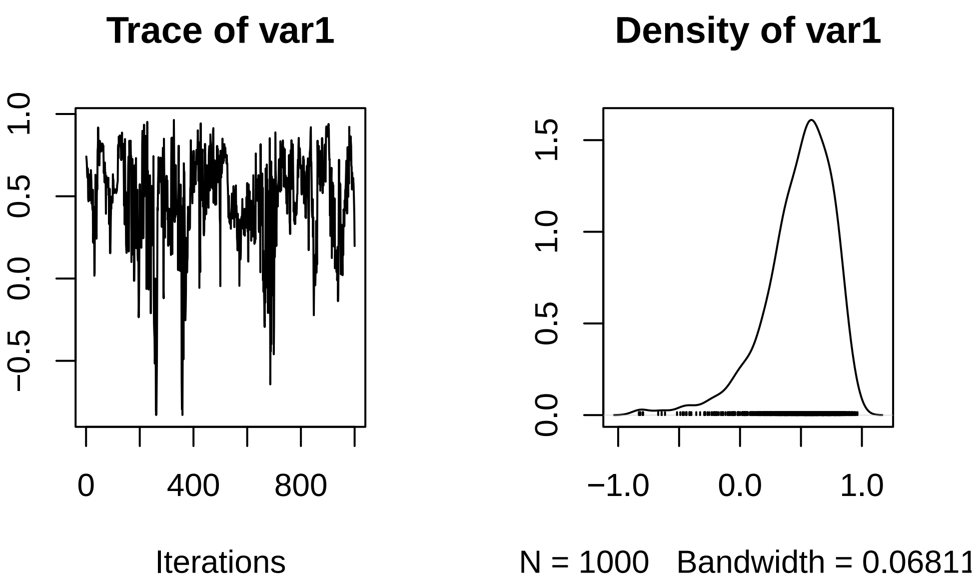
```
Iterations = 1:1000
Thinning interval = 1
Number of chains = 1
Sample size per chain = 1000

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
```

```r
summary(cross_sex.cor.tarsus)
```

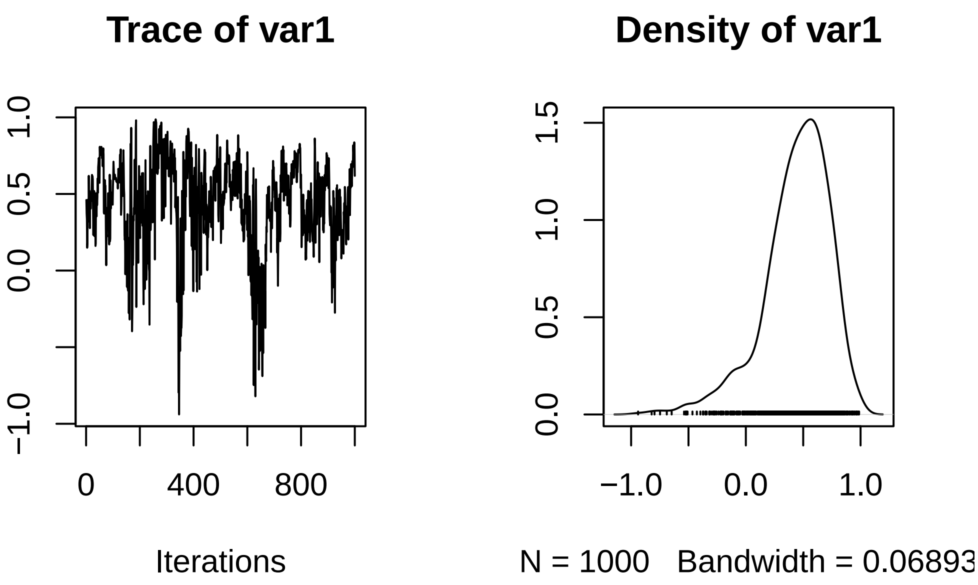
```
Iterations = 1:1000
Thinning interval = 1
Number of chains = 1
Sample size per chain = 1000

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

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

2. Quantiles for each variable:

   2.5%     25%     50%     75%   97.5%
```

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

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



```r
plot(cross_sex.cor.tarsus)
```

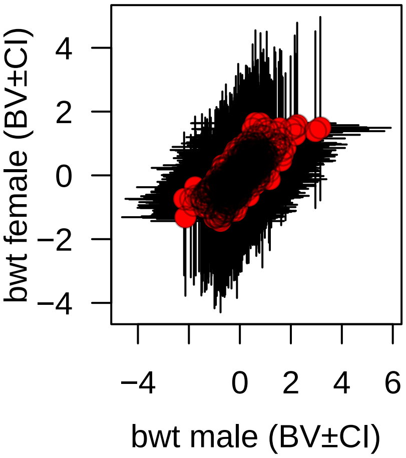


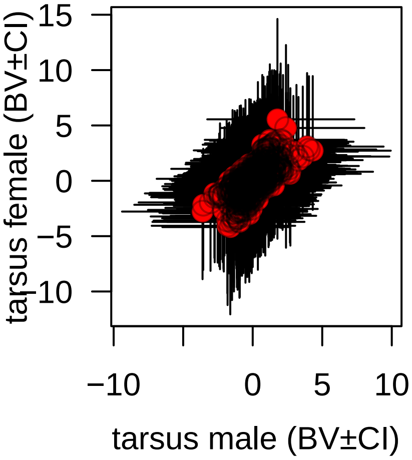
Here, some simple code to extract the BLUP.

```r
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 = "b
with(bl_m2.5, segments(x0 = bwt_sex1_lo, y0 = bwt_sex2, x1 = bwt_sex1_up, y1 = bwt_sex2, col = "b
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_
with(bl_m2.5, segments(x0 = tarsus_sex1_lo, y0 = tarsus_sex2, x1 = tarsus_sex1_up, y1 = tarsus_se
points(tarsus_sex2 ~ tarsus_sex1, bl_m2.5, pch = 16, col = "red", cex = 1.5)
points(tarsus_sex2 ~ tarsus_sex1, bl_m2.5, pch = 1, col = rgb(0, 0, 0, 0.3), cex = c(1.5))
mtext("tarsus male (BV±CI)", side = 1, line = 2.4)
mtext("tarsus female (BV±CI)", side = 2, line = 2, las = 3)
```





Within this model, we also have acces to the rest of the B-matrix. Note, the cross-sex genetic correlation is just the diagonal of the B matrix. For now on, you can explore this matrix and estimate the cross-sex-cross-trait genetic correlation.

partie 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.

```r
str(gryphonRM)
```

```
'data.frame':	1607 obs. of  5 variables:
 $ animal : Factor w/ 469 levels "1","2","3","8",..: 1 1 1 1 1 2 2 2 3 3 ...
 $ byear  : Factor w/ 34 levels "968","970","971",..: 22 22 22 22 22 22 22 22 22 22 ...
 $ age    : Factor w/ 5 levels "2","3","4","5",..: 1 2 3 4 5 1 2 3 1 2 ...
 $ year   : Factor w/ 39 levels "970","971","972",..: 23 24 25 26 27 23 24 25 23 24 ...
 $ laydate: num  19 23 24 23 29 21 17 21 20 20 ...
```

```r
summary(gryphonRM)
```

```
    animal          byear        age           year          laydate     
 1       :   5   1000    : 109   2:308   1004    :  79   Min.   : 0.00  
 3       :   5   1001    :  98   3:322   1005    :  78   1st Qu.:20.00  
 9       :   5   999     :  86   4:339   1003    :  69   Median :24.00  
 17      :   5   1002    :  85   5:315   1006    :  64   Mean   :23.54  
 42      :   5   987     :  70   6:323   1002    :  60   3rd Qu.:27.00  
 50      :   5   989     :  66           988     :  54   Max.   :41.00  
 (Other):1577   (Other):1093           (Other):1203
```

```
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

Chapitre 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
```

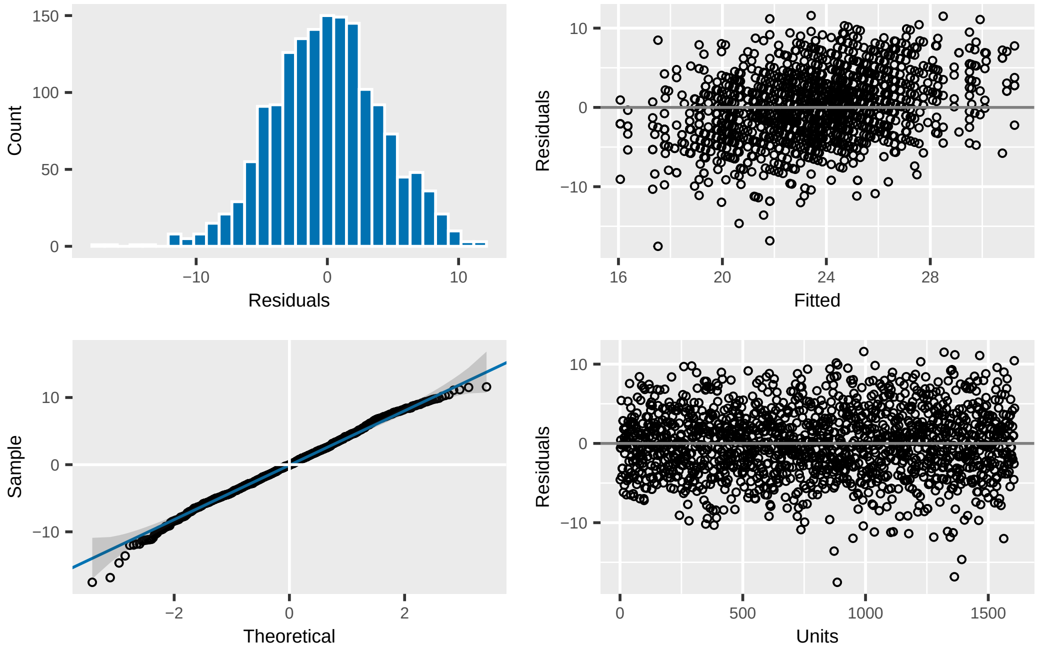
8.0.1. Estimating repeatability

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")
)
```

```
ASReml Version 4.2 08/10/2024 11:38:12
          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
```

```r
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")
)
```

```
ASReml Version 4.2 08/10/2024 11:38:13
          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
```

```r
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
```

```
ASReml Version 4.2 08/10/2024 11:38:14
          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")
)
```

```
ASReml Version 4.2 08/10/2024 11:38:14
          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")
)
```

```
ASReml Version 4.2 08/10/2024 11:38:14
```

```
        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")
)
```

```
ASReml Version 4.2 08/10/2024 11:38:14
          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")
)
```

```
ASReml Version 4.2 08/10/2024 11:38:15
          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")
)
```

```
ASReml Version 4.2 08/10/2024 11:38:15
          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
```

```r
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


ASReml Version 4.2 08/10/2024 11:38:15

          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

Chapitre 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 unformative prior with one estimate for the G matrix and one estimate for the Residual matrix, in addition

```
# p.var <- var(gryphonRM$laydate, na.rm = TRUE)
prior3.1 <- list(G = list(G1 = list(V = 1, nu = 0.002)), R = list(
  V = 1,
  nu = 0.002
))
model3.1 <- MCMCglmm(laydate ~ 1,
  random = ~animal, data = gryphonRM,
  prior = prior3.1, verbose = FALSE
)
posterior.mode(model3.1$VCV)
```

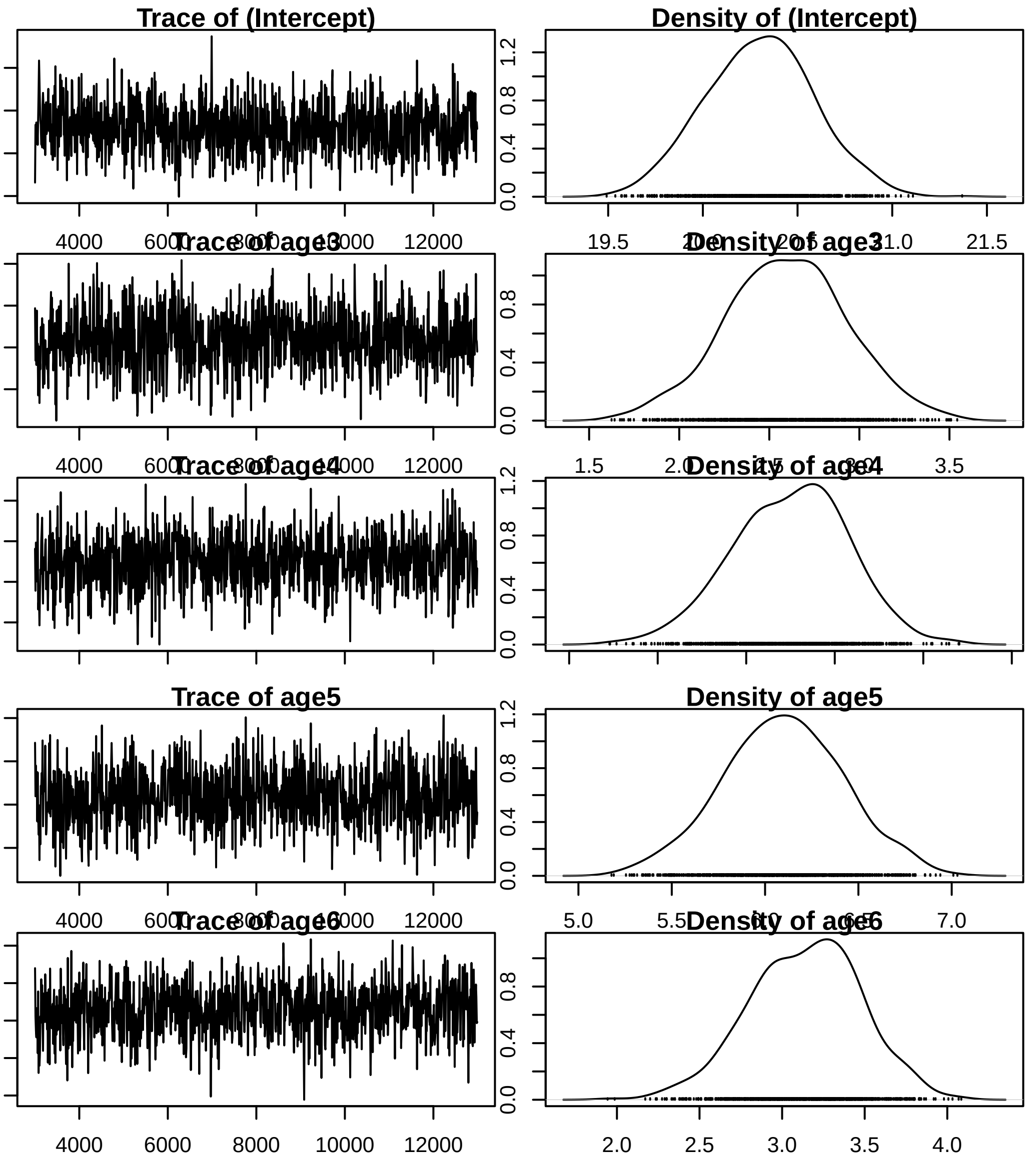
```
  animal    units
10.67985 21.28520
```

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`.

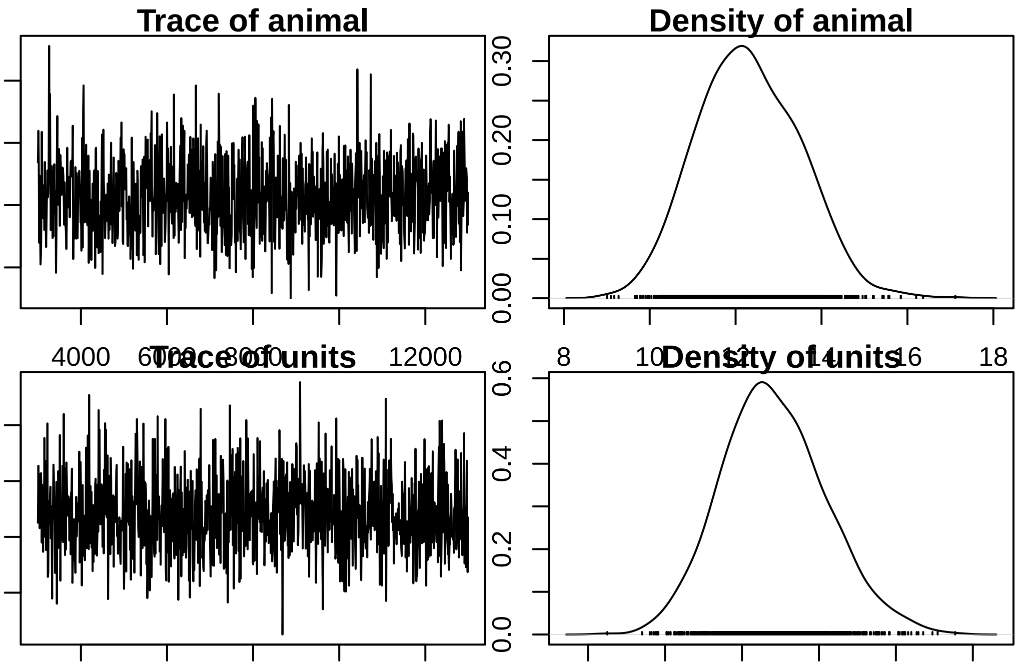
Here then the repeatability of the `laydate` can be determined as: 22.29 (*i.e.*, as 10.68/(10.68 + 21.285)). Just a friendly remember, we work with Monte Carlo chain with model iteration, so the point estimate can be different (but very similar) each time you run the model.

Mean lay date might change with age, so we could ask what the repeatability of lay date is after conditioning on age. This would be done by adding `age` into the model as a fixed effect.

```
model3.2 <- MCMCglmm(laydate ~ age,
  random = ~animal, data = gryphonRM,
  prior = prior3.1, verbose = FALSE
)
par(mar = c(1, 1, 1, 1))
plot(model3.2$Sol)
```



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



```r
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.

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

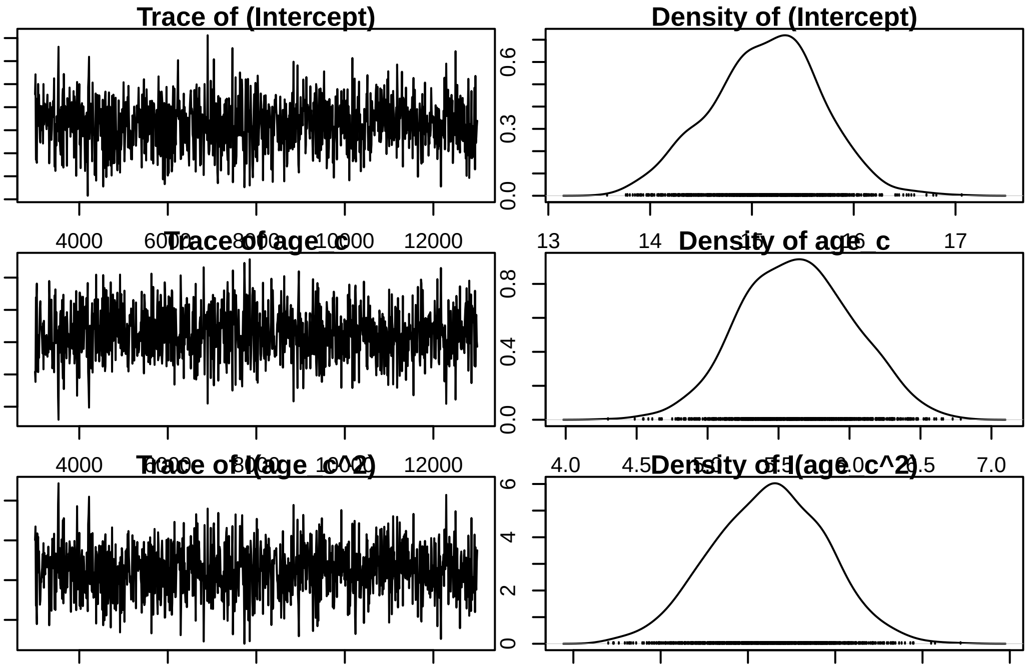
```
(Intercept)        age3        age4        age5        age6
  20.361160    2.743338    4.419162    6.038813    3.290132
```

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

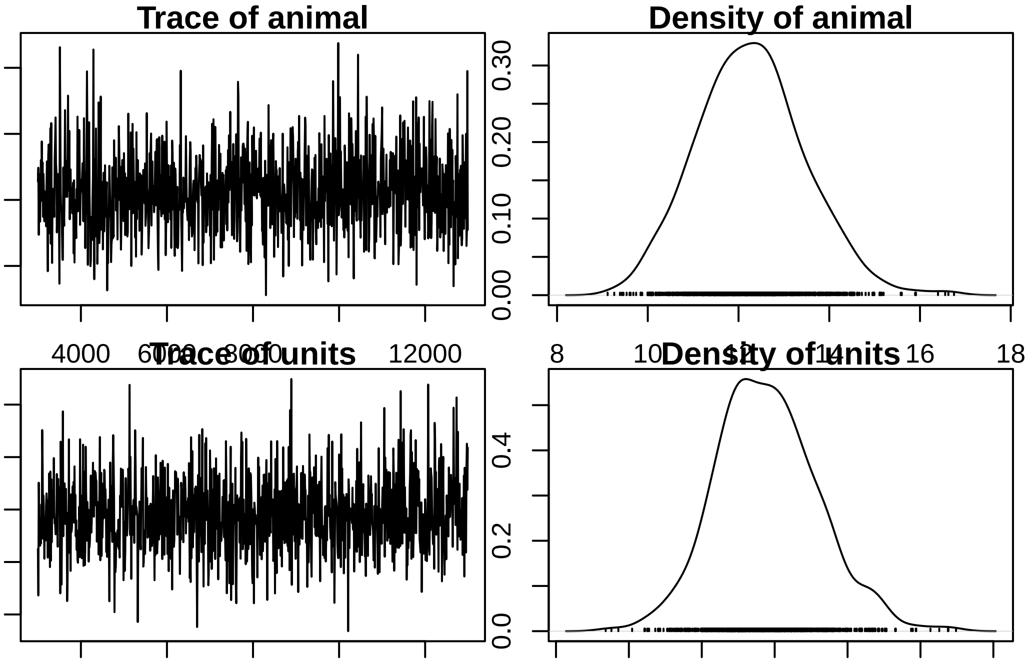
```
                lower     upper
(Intercept) 19.775827 20.887996
age3         1.863914  3.209940
age4         3.657741  4.913932
age5         5.480571  6.753545
age6         2.509874  3.803416
attr(,"Probability")
[1] 0.95
```

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.

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

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



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



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

```
  animal    units
12.77266 16.51431
```

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

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

```
HPDinterval(model3.2_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 o obtain an unbiased estimate of V_A, we need to fit the individual identity twice in the model: once linked to the pedigree (genetic effect) and once not linked to the pedigree (permanent environment effect).To do so, we need to duplicate the variable containing the individual identity `animal` and give it a new name. In addition, the prior need to be modified to integrate a seconf random effect.An more appropriate estimate of V_A is given by the model:

```
gryphonRM$animal_pe <- gryphonRM$animal
# p.var <- var(gryphonRM$laydate, na.rm = TRUE)
prior3.4 <- list(G = list(G1 = list(V = 1, nu = 0.002), G2 = list(
  V = 1,
  nu = 0.002
)), R = list(V = 1, nu = 0.002))
model3.4 <- MCMCglmm(laydate ~ 1 + age,
  random = ~ animal + animal_pe,
  ginv = list(animal = Ainv), data = gryphonRM, prior = prior3.4, verbose = FALSE
)
posterior.mode(model3.4$VCV)
```

```
   animal  animal_pe     units
 5.000774   6.931818 16.712970
```

The estimate ofV_A is now much lower (reduced from 13.6735 to 5.1238) due to a proper separation in the additive and permanent environment effects. We can estimate h^2 and the repeatability from this model:

```
model3.4.VP <- model3.4$VCV[, "animal"] + model3.4$VCV[, "animal_pe"] + model3.4$VCV[, "units"]
model3.4.PE_VA <- model3.4$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.

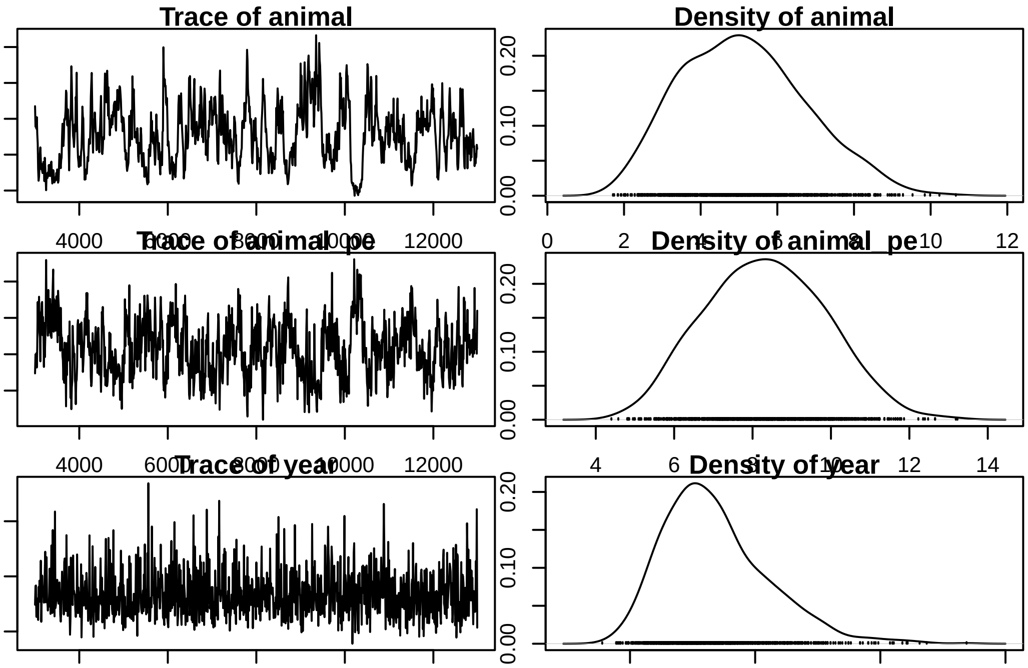
```
# p.var <- var(gryphonRM$laydate, na.rm = TRUE)
prior3.5 <- list(G = list(G1 = list(V = 1, nu = 0.002), G2 = list(
  V = 1,
  nu = 0.002
), G3 = list(V = 1, nu = 0.002), G4 = list(
  V = 1,
  nu = 0.002
)), R = list(V = 1, nu = 0.002))

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)
```

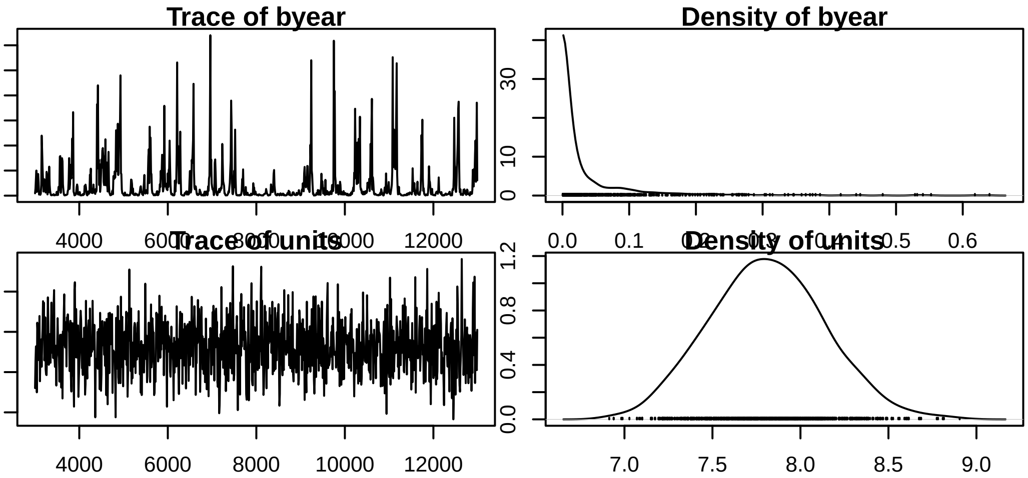
```
     animal    animal_pe         year        byear        units
4.955518461 8.396521169 7.673492341 0.002060264 7.747678616
```

```r
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
```

```r
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.

Chapitre 10

brms

```r
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)
```

Chapitre 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 et 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 et Burchett (2017)

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Annexe A

Données et objet R utilisés dans le livre

A.1. Zip tout en un

Tous les fichiers de données et de code dans un **fichier zip**

A.2. Données

- gryphon.csv
- gryphonped.csv
- gryphonRM.csv
- gryphonRM.txt

A.3. Objets R

- brms_m1_1.rda
- brms_m1_2.rda
- brms_m1_3.rda
- brms_m1_4.rda
- brms_m1_5.rda
- brms_m2_1.rda
- brms_m2_2.rda
- brms_m2_3.rda

- brms_m2_4.rda
- brms_m2_5.rda
- MCMCglmm_model_BivSex_LongRun.rda
- MCMCglmm_model_MultivSex_LongRun.rda
- MCMCglmm_model2_1_LongRun.rda
- MCMCglmm_model2_2_LongRun.rda
- MCMCglmm_model2_3_LongRun.rda
- MCMCglmm_model2_4_LongRun.rda
- MCMCglmm_model2_5_LongRun.rda

A.4. Code et fonctions R