

Structured Random Effects

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A Cross-fostering Experiment in Blue Tits

```
> head(dat)
```

	bird_id	year	nest	sex	tarsus_mm	surv
1	X551797	2010	10_11	F	16.9	0
2	L970891	2013	13_2	F	16.7	0
3	L298884	2011	11_154	M	16.2	1
4	L298943	2011	11_A7	F	17.0	0
5	L969109	2011	11_A21	M	17.0	0
6	L970180	2012	12_A35	F	16.7	0

Nest effects assumed to be i.i.d:

$$\mathbf{u}_n \sim N(\mathbf{0}, \sigma_n^2 \mathbf{I})$$

Nest effects assumed to be i.i.d:

$$\mathbf{u}_n \sim N(\mathbf{0}, \sigma_n^2 \mathbf{I})$$

Breeding values assumed to be correlated:

$$\mathbf{u}_a \sim N(\mathbf{0}, \sigma_a^2 \mathbf{A})$$

Structured Random Effects: A

```
> head(ped[c(169,197,249,672,2728),])
```

	[,1]	[,2]	[,3]
[1,]	"X552101"	NA	NA
[2,]	"L002118"	NA	NA
[3,]	"L002174"	NA	NA
[4,]	"X551614"	"L002118"	"X552101"
[5,]	"D517001"	"L002174"	"X551614"

Structured Random Effects: **A**

```
> head(ped[c(169,197,249,672,2728),])
```

```
      [,1]      [,2]      [,3]
[1,] "X552101" NA        NA
[2,] "L002118" NA        NA
[3,] "L002174" NA        NA
[4,] "X551614" "L002118" "X552101"
[5,] "D517001" "L002174" "X551614"
```

$$\mathbf{A} = \begin{bmatrix} 1.00 & 0.00 & 0.00 & 0.50 & 0.25 \\ 0.00 & 1.00 & 0.00 & 0.50 & 0.25 \\ 0.00 & 0.00 & 1.00 & 0.00 & 0.50 \\ 0.50 & 0.50 & 0.00 & 1.00 & 0.50 \\ 0.25 & 0.25 & 0.50 & 0.50 & 1.00 \end{bmatrix}$$

Structured Random Effects: \mathbf{A}^{-1}

```
> library(MasterBayes)
> ped<-orderPed(ped)
> ped<-insertPed(ped)
```

```
> library(MasterBayes)
> ped<-orderPed(ped)
> ped<-insertPed(ped)

> ped<-prunePed(ped, keep=dat$bird_id, make.base=TRUE)
```



```
> library(MasterBayes)
> ped<-orderPed(ped)
> ped<-insertPed(ped)

> ped<-prunePed(ped, keep=dat$bird_id, make.base=TRUE)

> Ainv<-inverseA(ped)$A
```

A simple animal model

```
> m1<-MCMCglmm(tarsus_mm~year+sex, random=~nest+bird_id, data=dat,  
+ ginverse=list(bird_id=Ainv))
```

A simple animal model

```
> m1<-MCMCglmm(tarsus_mm~year+sex, random=~nest+bird_id, data=dat,
+ ginverse=list(bird_id=Ainv))
> summary(m1)

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

DIC: 1636.448

G-structure: ~nest

      post.mean l-95% CI u-95% CI eff.samp
nest    0.1265   0.1014   0.1521     1285

      ~bird_id

      post.mean l-95% CI u-95% CI eff.samp
bird_id  0.1616   0.1248   0.1964     626.4

R-structure: ~units

      post.mean l-95% CI u-95% CI eff.samp
units    0.06093  0.04062  0.08125     636
```

A simple animal model

```
> h2<-m1$VCV[,"bird_id"]/rowSums(m1$VCV)
```

A simple animal model

```
> h2<-m1$VCV[,"bird_id"]/rowSums(m1$VCV)
> plot(h2)
```

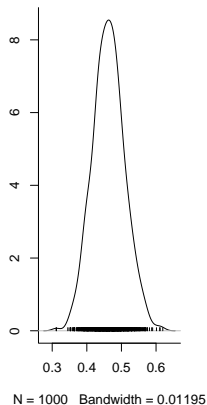
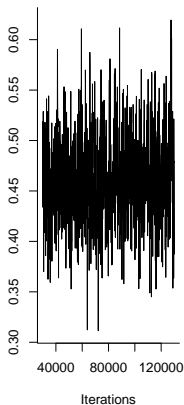


Figure: Time-series of MCMC output (left) and smoothed posterior distribution (right) for the heritability.

A simple animal model

```
> h2<-m1$VCV[,"bird_id"]/rowSums(m1$VCV)
> plot(h2)
```

```
> HPDinterval(h2)
           lower      upper
var1 0.3761899 0.5567254
attr(,"Probability")
[1] 0.95
```

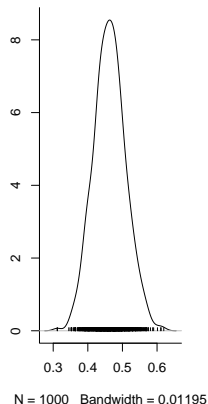
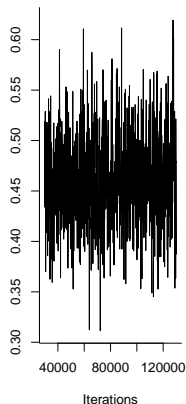


Figure: Time-series of MCMC output (left) and smoothed posterior distribution (right) for the heritability.

Variance Functions: why do we have (1|...) in lmer?

(1|nest)

- Think of the left hand side as a model formula:

Variance Functions: why do we have (1|...) in lmer?

(1|nest)

- Think of the left hand side as a model formula:

```
> head(model.matrix(~1, data=dat))
```

```
(Intercept)
```

```
1      1
2      1
3      1
4      1
5      1
6      1
```


Variance Functions: why do we have (1|...) in lmer?

(1|nest)

- Think of the left hand side as a model formula:

```
> head(model.matrix(~1, data=dat))
```

```
(Intercept)
```

```
1      1
2      1
3      1
4      1
5      1
6      1
```

	13_59	10_A15	11_142	12_156	...
(Int)	(Int).13_59	(Int).10_A15	(Int).11_142	(Int).12_156	...

Variance Functions: MCMCglmm

```
vf(sex):nest
```

- Think of the term in brackets as a model formula (with the intercept removed):

```
vf(sex):nest
```

- Think of the term in brackets as a model formula (with the intercept removed):

```
> head(model.matrix(~sex-1, data=dat))
```

```
sexF sexM
1    1    0
2    1    0
3    0    1
4    1    0
5    0    1
6    1    0
```

Variance Functions: MCMCglmm

`vf(sex):nest`

- Think of the term in brackets as a model formula (with the intercept removed):

```
> head(model.matrix(~sex-1, data=dat))
```

```
sexF sexM
1    1    0
2    1    0
3    0    1
4    1    0
5    0    1
6    1    0
```

	13_59	10_A15	11_142	12_156	13_A3	...
F	F.13_59	F.10_A15	F.11_142	F.12_156	F.13_A3	...
M	M.13_59	M.10_A15	M.11_142	M.12_156	M.13_A3	...

Variance Functions: MCMCglmm

	13_59	10_A15	11_142	12_156	13_A3	...
F	F.13_59	F.10_A15	F.11_142	F.12_156	F.13_A3	...
M	M.13_59	M.10_A15	M.11_142	M.12_156	M.13_A3	...

Variance Functions: MCMCglmm

	13_59	10_A15	11_142	12_156	13_A3	...
F	F.13_59	F.10_A15	F.11_142	F.12_156	F.13_A3	...
M	M.13_59	M.10_A15	M.11_142	M.12_156	M.13_A3	...

us(sex):nest

$$\mathbf{V}_{\text{nest}} = \begin{bmatrix} \sigma_F^2 & \sigma_{F,M} \\ \sigma_{F,M} & \sigma_M^2 \end{bmatrix}$$

Variance Functions: MCMCglmm

	13_59	10_A15	11_142	12_156	13_A3	...
F	F.13_59	F.10_A15	F.11_142	F.12_156	F.13_A3	...
M	M.13_59	M.10_A15	M.11_142	M.12_156	M.13_A3	...

us(sex):nest

$$\mathbf{V}_{\text{nest}} = \begin{bmatrix} \sigma_F^2 & \sigma_{F,M} \\ \sigma_{F,M} & \sigma_M^2 \end{bmatrix}$$

idh(sex):nest

$$\mathbf{V}_{\text{nest}} = \begin{bmatrix} \sigma_F^2 & 0 \\ 0 & \sigma_M^2 \end{bmatrix}$$

Variance Functions: MCMCglmm

	13_59	10_A15	11_142	12_156	13_A3	...
F	F.13_59	F.10_A15	F.11_142	F.12_156	F.13_A3	...
M	M.13_59	M.10_A15	M.11_142	M.12_156	M.13_A3	...

us(sex):nest

$$\mathbf{V}_{\text{nest}} = \begin{bmatrix} \sigma_F^2 & \sigma_{F,M} \\ \sigma_{F,M} & \sigma_M^2 \end{bmatrix}$$

idh(sex):nest

$$\mathbf{V}_{\text{nest}} = \begin{bmatrix} \sigma_F^2 & 0 \\ 0 & \sigma_M^2 \end{bmatrix}$$

idv(sex):nest

$$\mathbf{V}_{\text{nest}} = \begin{bmatrix} \sigma^2 & 0 \\ 0 & \sigma^2 \end{bmatrix}$$

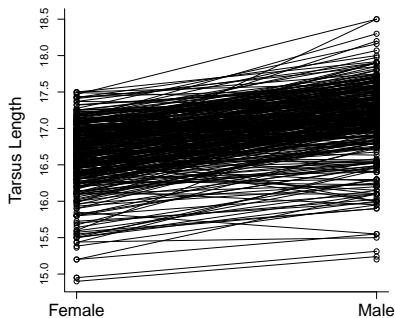


Figure: Tarsus lengths for males and females averaged within nests. The lines join (foster) sisters and their (foster) brothers.

A G \times Sex animal model

```
> m2<-MCMCglmm(tarsus_mm~year+sex,  
+             random=~us(sex):nest+us(sex):bird_id,  
+             rcov=~idh(sex):units,  
+             data=dat, ginverse=list(bird_id=Ainv), prior=prior)
```

A $G \times$ Sex animal model

```
> prior<-list(  
+ R=list(V=diag(2), nu=0.002),  
+ G=list(  
+ G1=list(V=diag(2), nu=2, alpha.mu=c(0,0), alpha.V=diag(2)*1000),  
+ G2=list(V=diag(2), nu=2, alpha.mu=c(0,0), alpha.V=diag(2)*1000)  
+ )  
+ )  
  
> m2<-MCMCglmm(tarsus_mm~year+sex,  
+ random=~us(sex):nest+us(sex):bird_id,  
+ rcov=~idh(sex):units,  
+ data=dat, ginverse=list(bird_id=Ainv), prior=prior)
```

A G \times Sex animal model

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

DIC: 1340.186

G-structure: \sim us(sex):nest

	post.mean	l-95% CI	u-95% CI	eff.samp
F:F.nest	0.1142	0.08918	0.1460	1000
M:F.nest	0.1235	0.09777	0.1520	902
F:M.nest	0.1235	0.09777	0.1520	902
M:M.nest	0.1418	0.10968	0.1736	1000

\sim us(sex):bird_id

	post.mean	l-95% CI	u-95% CI	eff.samp
F:F.bird_id	0.1695	0.1321	0.2113	460.4
M:F.bird_id	0.1612	0.1219	0.1984	226.0
F:M.bird_id	0.1612	0.1219	0.1984	226.0
M:M.bird_id	0.1659	0.1217	0.2238	207.2

R-structure: \sim idh(sex):units

	post.mean	l-95% CI	u-95% CI	eff.samp
F.units	0.06147	0.03686	0.08510	415.3
M.units	0.05030	0.01788	0.07938	188.9

Location effects: tarsus_mm \sim year + sex

A G \times Sex animal model

```
> nest.cor<-m2$VCV[,"M:F.nest"]/sqrt(m2$VCV[,"M:M.nest"]*m2$VCV[,"F:F.nest"])
```

A $G \times$ Sex animal model

```
> nest.cor<-m2$VCV[,"M:F.nest"]/sqrt(m2$VCV[,"M:M.nest"*m2$VCV[,"F:F.nest"])  
> genetic.cor<-m2$VCV[,"M:F.bird_id"]/sqrt(m2$VCV[,"M:M.bird_id"*m2$VCV[,"F:F.bird_id"])  
> plot(mcmc(cbind(nest.cor, genetic.cor)))
```

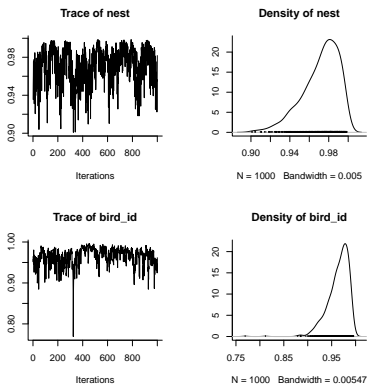


Figure: Time-series of MCMC output (left) and smoothed posterior distribution (right) for the inter-sex correlations at the nest (above) and genetic (below) levels.

A threshold animal model

```
> m3<-MCMCglmm(surv~year+sex, random=~nest+bird_id, data=dat,  
+   ginverse=list(bird_id=Ainv), family="threshold", prior=prior)
```

A threshold animal model

```
> prior<-list(  
+ R=list(V=1, fix=1),  
+ G=list(  
+ G1=list(V=1, nu=1, alpha.mu=0, alpha.V=1000),  
+ G2=list(V=1, nu=1, alpha.mu=0, alpha.V=1000)  
+ )  
+ )  
  
> m3<-MCMCglmm(surv~year+sex, random=~nest+bird_id, data=dat,  
+ ginverse=list(bird_id=Ainv), family="threshold", prior=prior)
```


A threshold animal model

```
> summary(m3)
```

```
Iterations = 30001:129901
```

```
Thinning interval = 100
```

```
Sample size = 1000
```

```
DIC: 846.5204
```

```
G-structure: ~nest
```

	post.mean	l-95% CI	u-95% CI	eff.samp
nest	0.3302	0.1136	0.5976	393.4

```
~bird_id
```

	post.mean	l-95% CI	u-95% CI	eff.samp
bird_id	0.106	1.074e-07	0.3873	282.8

```
R-structure: ~units
```

	post.mean	l-95% CI	u-95% CI	eff.samp
units	1	1	1	0

```
Location effects: surv ~ year + sex
```

A threshold animal model

```
> h2<-m3$VCV[,"bird_id"]/rowSums(m3$VCV)
```

A threshold animal model

```
> h2<-m3$VCV[,"bird_id"]/rowSums(m3$VCV)
> plot(h2)
```

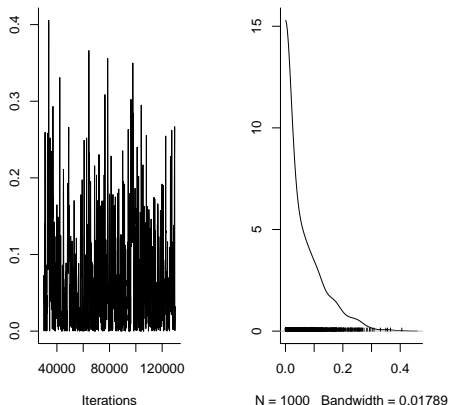


Figure: Time-series of MCMC output (left) and smoothed posterior distribution (right) for the heritability of survival (on the latent scale).

A threshold animal model

```
> h2<-m3$VCV[,"bird_id"]/rowSums(m3$VCV)
> plot(h2)
```

```
> HPDinterval(h2)
              lower      upper
var1 7.80482e-08 0.2104036
attr(,"Probability")
[1] 0.95
```

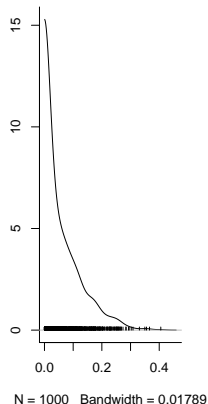
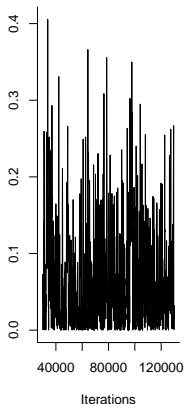


Figure: Time-series of MCMC output (left) and smoothed posterior distribution (right) for the heritability of survival (on the latent scale).

A multivariate animal model

```
m4 <- MCMCglmm(cbind(tarsus_mm, surv) ~ trait-1 + trait:sex .....
```

A multivariate animal model

```
m4<-MCMCglmm(cbind(tarsus_mm, surv)~trait-1+trait:sex .....
```

	tarsus	surv	sex
1	16.9	0	F
2	16.7	0	F
2	16.2	1	M
⋮	⋮	⋮	⋮
2448	17.3	0	F

A multivariate animal model

```
m4<-MCMCglmm(cbind(tarsus_mm, surv)~trait-1+trait:sex .....
```

					y	trait	units	sex
					16.9	tarsus	1	F
	tarsus	surv	sex		16.7	tarsus	2	F
1	16.9	0	F		16.2	tarsus	3	M
2	16.7	0	F		:	:	:	:
2	16.2	1	M	⇒	17.3	tarsus	2448	F
:	:	:	:		0	surv	1	F
2448	17.3	0	F		0	surv	2	F
					1	surv	3	M
					:	:	:	:
					0	surv	2448	F

A multivariate animal model

```
> m4<-MCMCglmm(cbind(tarsus_mm, surv)~trait-1+trait:year+trait:sex,  
+ random=~us(trait):nest+us(trait):bird_id,  
+ rcov=~us(trait):units,  
+ family=c("gaussian", "threshold"),  
+ data=dat, ginverse=list(bird_id=Ainv), prior=prior)
```


A multivariate animal model

```
> prior<-list(  
+ R=list(V=diag(2), nu=1.002, fix=2),  
+ G=list(  
+   G1=list(V=diag(2), nu=2, alpha.mu=c(0,0), alpha.V=diag(2)*1000),  
+   G2=list(V=diag(2), nu=2, alpha.mu=c(0,0), alpha.V=diag(2)*1000)  
+ )  
+ )  
  
> m4<-MCMCglmm(cbind(tarsus_mm, surv)~trait-1+trait:year+trait:sex,  
+ random=~us(trait):nest+us(trait):bird_id,  
+ rcov=~us(trait):units,  
+ family=c("gaussian", "threshold"),  
+ data=dat, ginverse=list(bird_id=Ainv), prior=prior)
```

A multivariate animal model

```
> summary(m4)
```

```
Iterations = 30001:129901
```

```
Thinning interval = 100
```

```
Sample size = 1000
```

```
DIC: 2681.098
```

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

	post.mean	l-95% CI	u-95% CI	eff.samp
tarsus_mm:tarsus_mm.nest	0.12897	0.10195	0.1545	1000.0
surv:tarsus_mm.nest	0.06538	0.01193	0.1335	838.6
tarsus_mm:surv.nest	0.06538	0.01193	0.1335	838.6
surv:surv.nest	0.33634	0.11999	0.5885	593.9

```
~us(trait):bird_id
```

	post.mean	l-95% CI	u-95% CI	eff.samp
tarsus_mm:tarsus_mm.bird_id	0.150259	1.201e-01	0.17926	900.0
surv:tarsus_mm.bird_id	-0.001779	-5.255e-02	0.04903	584.2
tarsus_mm:surv.bird_id	-0.001779	-5.255e-02	0.04903	584.2
surv:surv.bird_id	0.064083	5.736e-08	0.25784	286.1

```
R-structure: ~us(trait):units
```

Multivariate versus Univariate

- A univariate model of survival with tarsus fitted as a covariate estimates the regression β .

Multivariate versus Univariate

- A univariate model of survival with tarsus fitted as a covariate estimates the regression β .
- Assumes $\beta = \beta_n = \beta_b = \beta_u$

```
> beta.n<-m4$VCV[,"surv:tarsus_mm.nest"]/  
+   m4$VCV[,"tarsus_mm:tarsus_mm.nest"]
```

Multivariate versus Univariate

- A univariate model of survival with tarsus fitted as a covariate estimates the regression β .
- Assumes $\beta = \beta_n = \beta_b = \beta_u$

```
> beta.n<-m4$VCV[,"surv:tarsus_mm.nest"]/  
+   m4$VCV[,"tarsus_mm:tarsus_mm.nest"]
```

```
> beta.b<-m4$VCV[,"surv:tarsus_mm.bird_id"]/  
+   m4$VCV[,"tarsus_mm:tarsus_mm.bird_id"]
```

```
> beta.u<-m4$VCV[,"surv:tarsus_mm.units"]/  
+   m4$VCV[,"tarsus_mm:tarsus_mm.units"]
```

Multivariate versus Univariate

- A univariate model of survival with tarsus fitted as a covariate estimates the regression β .
- Assumes $\beta = \beta_n = \beta_b = \beta_u$

```
> beta.n<-m4$VCV[,"surv:tarsus_mm.nest"]/  
+   m4$VCV[,"tarsus_mm:tarsus_mm.nest"]
```

```
> beta.b<-m4$VCV[,"surv:tarsus_mm.bird_id"]/  
+   m4$VCV[,"tarsus_mm:tarsus_mm.bird_id"]
```

```
> beta.u<-m4$VCV[,"surv:tarsus_mm.units"]/  
+   m4$VCV[,"tarsus_mm:tarsus_mm.units"]
```

```
> plot(mcmc.list(beta.n, beta.b, beta.u), density=FALSE)
```

Multivariate versus Univariate

- A univariate model of survival with tarsus fitted as a covariate estimates the regression β .
- Assumes $\beta = \beta_n = \beta_b = \beta_u$

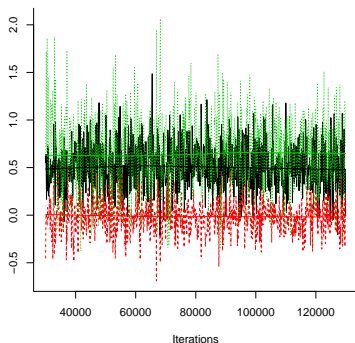


Figure: Regression of survival on tarsus length at different levels: nest (black), genetic (red) and residual (green)

Multivariate versus Univariate

- A univariate model of survival with tarsus fitted as a covariate estimates the regression β .
- Assumes $\beta = \beta_n = \beta_b = \beta_u$

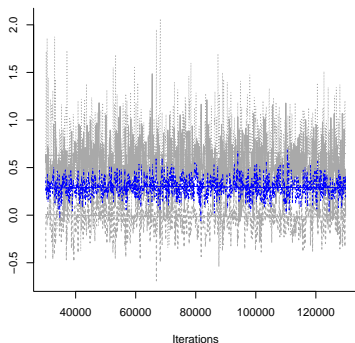


Figure: Regression of survival on tarsus length at different levels in grey and the regression coefficient of survival on tarsus from a univariate analysis in blue.