Quantifying Elephant Social Structure: Using a Bilinear Mixed Effects Model to Elicit Qualities of Elephant Behavior

Eric Vance

Institute of Statistics & Decision Sciences

BPCE, September 6, 2005

Elephant Social Structure

- Only females and juveniles form families. Adult males just run around looking to mate.
- The oldest female tends to be the leader since she's the largest and wisest.
- Elephants within a family are often related.

Scientific Questions

- What factors influence the development and evolution of social structure in elephants?
- What role does kinship play in the social structure?
- How does the social structure change in the Wet Season vs. the Dry Season?

Data Collection

- Biologists in Kenya ride into the National Park looking for herds of elephants.
- The adult female elephants are identified and recorded.
- The biologists either stay to observe the family or move on to find another herd.

Binomial Data Example

he total number of times data were recorded:

$$\text{Dry Season:} \quad N_{\text{Dry}} = 418$$

$$\text{Wet Season:} \quad N_{\text{Wet}} = 219$$

' Amy, Ang, and Aud are observed together, and the others are missing, then:

$$\boxed{\begin{aligned} y_{\text{AmyAng}} = y_{\text{AmyAud}} = y_{\text{AngAud}} = 1 \\ n_{\text{AmyAng}} = n_{\text{AmyAud}} = n_{\text{AngAud}} = 1 \end{aligned}}$$

While for one missing elephant: $\boxed{\begin{aligned} y_{\text{AmyAga}} = 0 \\ n_{\text{AmyAga}} = 1 \end{aligned}}$

Whereas for two missing elephants: $\boxed{\begin{aligned} y_{\text{AliAga}} = 0 \\ n_{\text{AliAga}} = 0 \end{aligned}}$

Binomial Data, Cont.

n this example of five elephants Amy, Angelina, Audrey, Alison, and Agatha at me $= t$, the $\mathbf{y}$ matrix of successful observations would be:

$_{\mathbf{t}} =$

	Amy	Ang	Aud	Ali	Aga
Amy	$\ddots$	1	1	0	0
Ang	1	$\ddots$	1	0	0
Aud	1	1	$\ddots$	0	0
Ali	0	0	0	$\ddots$	**0**
Aga	0	0	0	**0**	$\ddots$

he $\mathbf{n_t}$ matrix of potential observations =

	Amy	Ang	Aud	Ali	Aga
Amy	$\ddots$	1	1	1	1
Ang	1	$\ddots$	1	1	1
Aud	1	1	$\ddots$	1	1
Ali	1	1	1	$\ddots$	**0**
Aga	1	1	1	**0**	$\ddots$

The Model

- Data are binomial observations on pairs of elephants
  - $y_{ij} \sim \text{Bin}(n_{ij}, p_{ij})$
  - y_{ij} is the number of times elephants i and j observed together.
  - n_{ij} is the number of times either i or j observed.

- Use a Generalized Linear Model $\Longrightarrow$ Logistic regression
  - $E(y_{ij}|\,\theta_{\mathbf{ij}}) = g(\theta_{\mathbf{ij}})$.
  - g is the inverse logit link function.
  - The probability of elephants i and j being together is:

$$p_{ij} = \frac{\exp \theta_{\mathbf{ij}}}{1+\exp \theta_{\mathbf{ij}}}.$$

- θ_{ij} ***is the linear predictor.***

Linear Predictor θ_{ij}

How often are two elephants together?

- Common intercept β_0, a baseline probability.

- Intrinsic sociability a_i random effect.
  - Sociable elephants will more often be observed in large groups.

- Kinship relatedness $\beta_k\, k_{ij}$.

  1- DNA relatedness measure k_{1ij}: how closely elephants i and j are related

  2- Mother/Daughter pair indicator k_{2ij}

  3- Sisters pair indicator k_{3ij}

- Normal error γ_{ij} (unexplained error or white noise).

- **Pairwise effect** $z_i' z_j$ between elephants i and j.

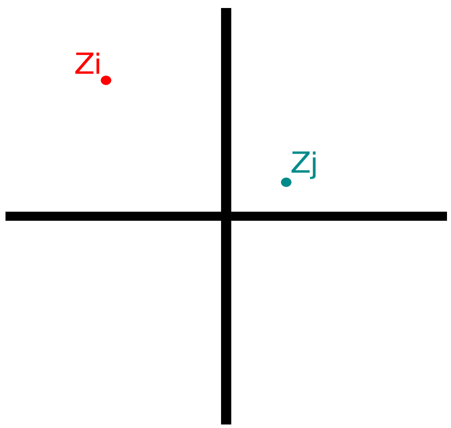
$$\boldsymbol{\theta_{ij} = \beta_0 + a_i + a_j + \beta_k\, k_{ij} + \gamma_{ij} + z_i' z_j}$$

Pairwise Effects

$z_i'z_j$ is the inner product of the positions of elephants i and j in latent (unobserved) Social Space.

- I choose the dimension of social space $k = 2$.

Elephants i and j have positions $\mathbf{z}_i$ and $\mathbf{z}_j$ in 2D social space.



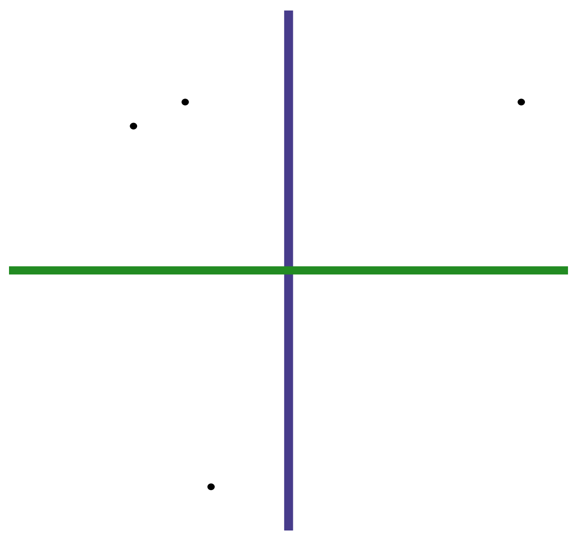
$$\mathbf{z}_i \sim N(\mathbf{0}, \sigma_z^2\,\mathrm{I})$$
$$\mathbf{z}_j \sim N(\mathbf{0}, \sigma_z^2\,\mathrm{I})$$

- If $\mathbf{z_i'z_j} = \mathbf{0}$ then elephants i and j interact as often as their sociabilities a_i, a_j and their kinships k_{ij} would predict.
- If $\mathbf{z_i'z_j} > \mathbf{0}$ then i and j like each other and are observed together more often than the model would otherwise predict.
- If $\mathbf{z_i'z_j} < \mathbf{0}$ then i and j dislike each other.

Social Space Example I Thought of Late Last Night

2 "most important" directions of compatibility

- Attitude towards money: Frugal ⟵ – – – – – – – – – ⟶ Extravagant
- Sleep schedule: Early bird ⟵ – – – – – – – ⟶ Night owl
- Combine both to create a Social Space



- The inner product of two vectors is the similarity of their directions, scaled by their lengths.

Vague Priors

$$\theta_{\mathbf{ij}} = \beta_{\mathbf{0}} + \mathbf{a_i} + \mathbf{a_j} + \beta_{\mathbf{k}}\,\mathbf{k_{ij}} + \gamma_{\mathbf{ij}} + \mathbf{z_i'z_j}$$

Intercept: $\beta_0 \sim N(0\,,\,100)$

Sociabilities: $a_i, a_j \sim N(0,\,\sigma^2_{\text{soc}}),$ $\sigma^2_{\text{soc}} \sim IG(\frac{1}{2}\,,\,\frac{1}{2})$

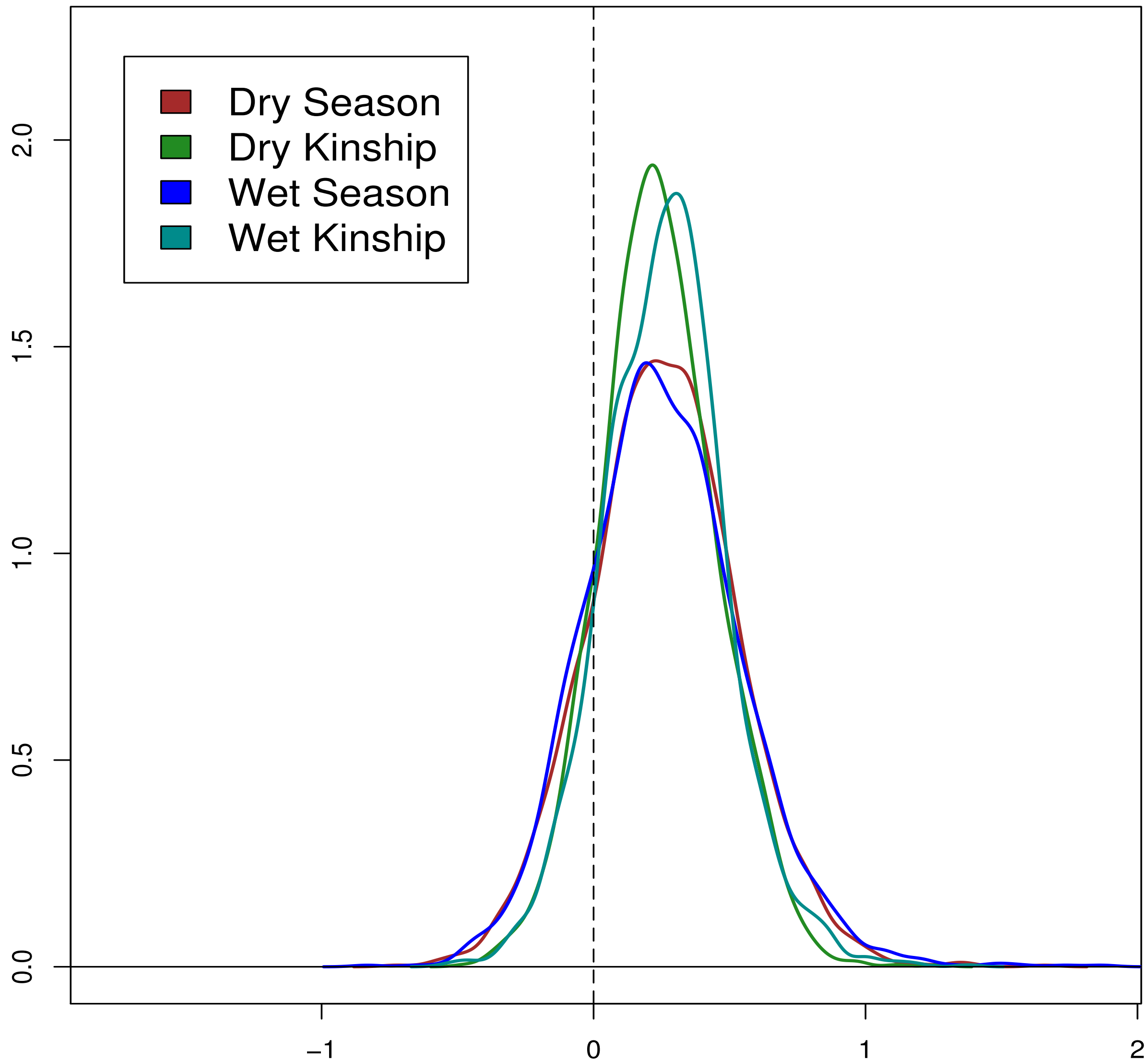
Kinship Coefficients: $\beta_k \sim N(\mathbf{0}, \begin{bmatrix} 100 & 0 & 0 \\ 0 & 100 & 0 \\ 0 & 0 & 100 \end{bmatrix})$

Pairwise error: $\gamma_{ij} \sim N(0,\,\sigma^2_\gamma),$ $\sigma^2_\gamma \sim IG(\frac{1}{2}\,,\,\frac{1}{2})$

Social space: $\mathbf{z}_i, \mathbf{z}_j \sim N(\mathbf{0}, \begin{bmatrix} \sigma^2_z & 0 \\ 0 & \sigma^2_z \end{bmatrix}),$ $\sigma^2_z \sim IG(\frac{1}{2}\,,\,\frac{1}{2})$

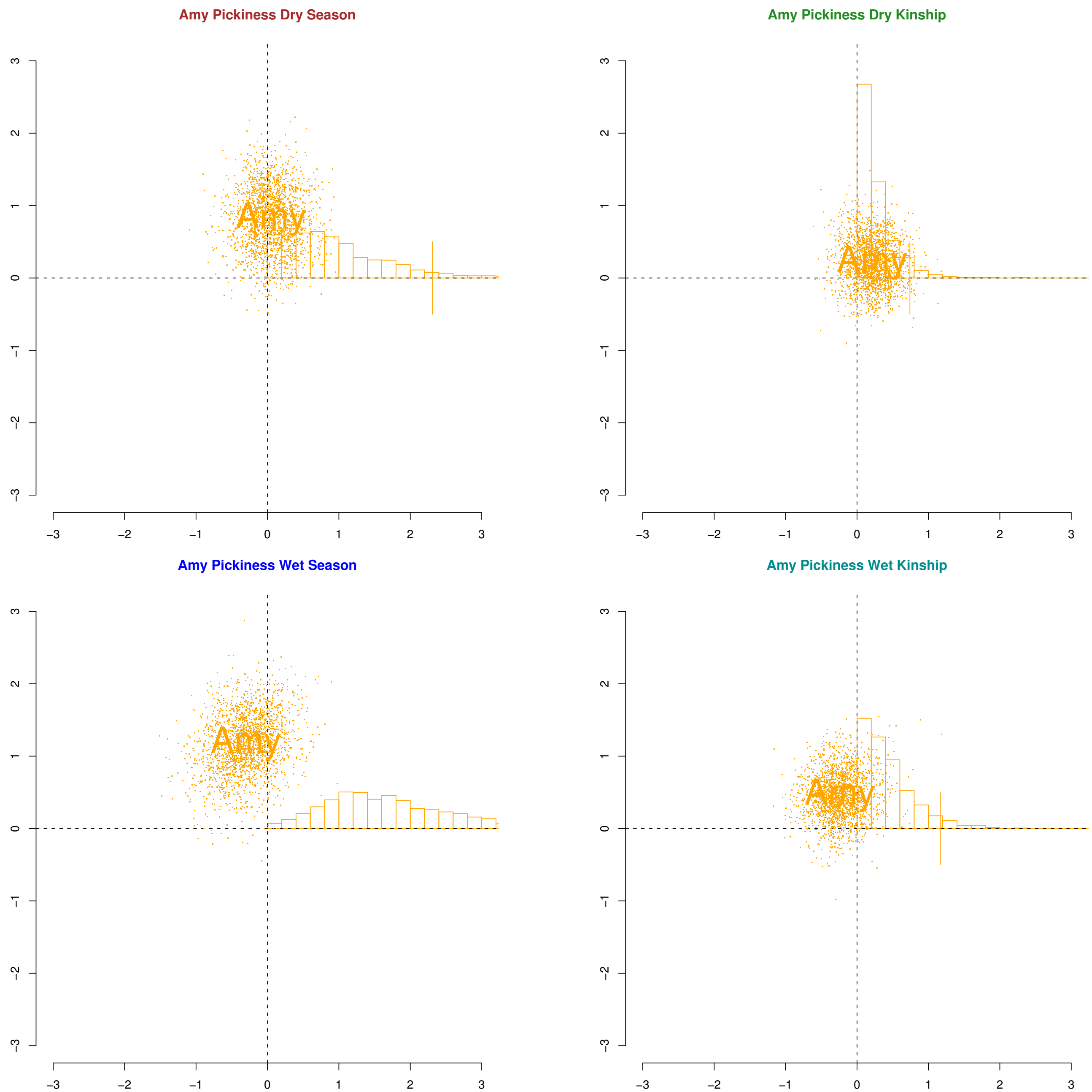
Results for Amy, Matriarch of Family AA

Amy Sociability Posterior Density $\mathbf{a}_{\mathbf{Amy}}$



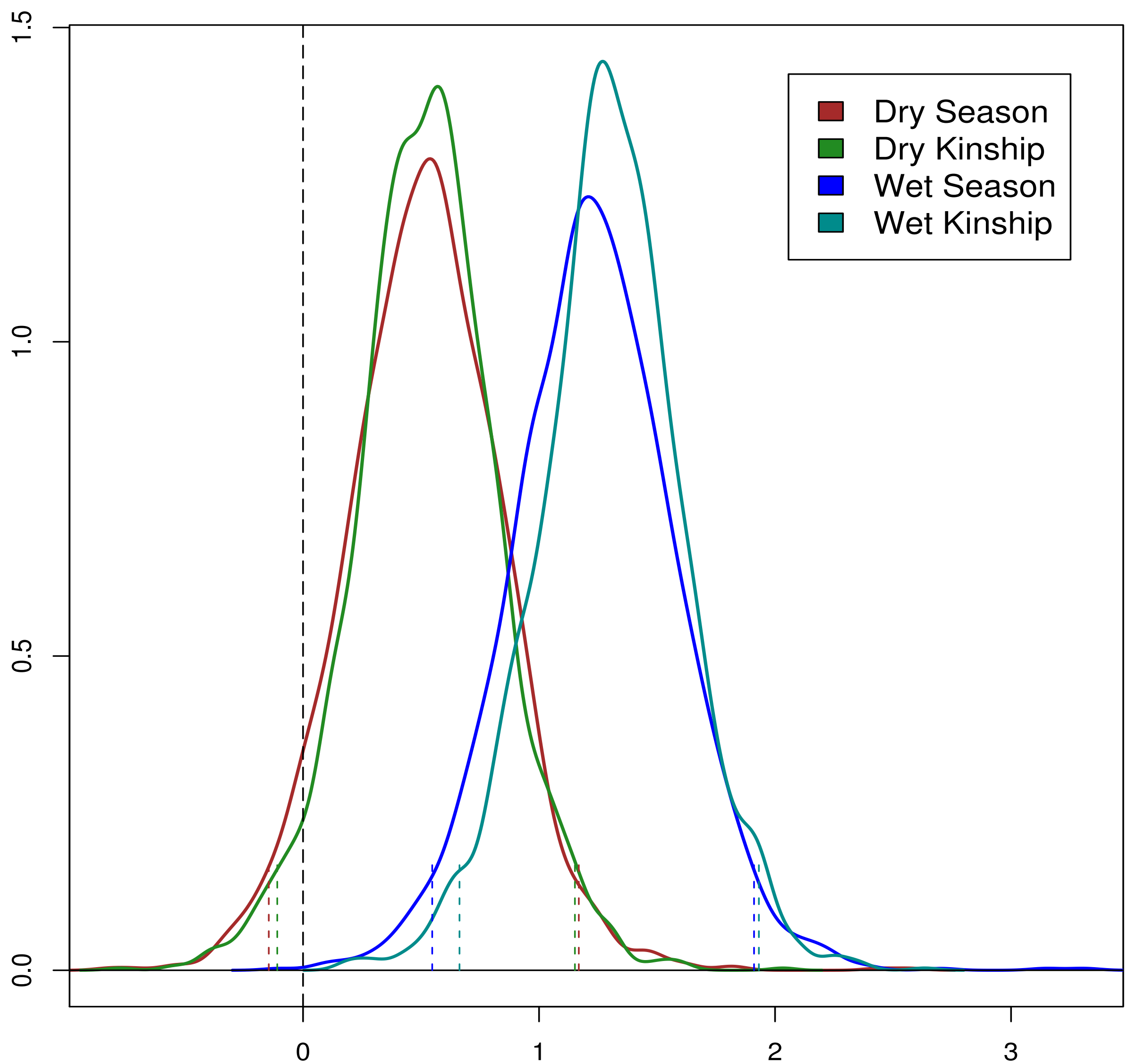
$$\theta_{\mathbf{ij}} = \beta_{\mathbf{0}} + \mathbf{a_i} + \mathbf{a_j} + \beta_{\mathbf{k}}\,\mathbf{k_{ij}} + \gamma_{\mathbf{ij}} + \mathbf{z}_{\mathbf{i}}'\mathbf{z}_{\mathbf{j}}$$

Amy's Posterior Pickiness



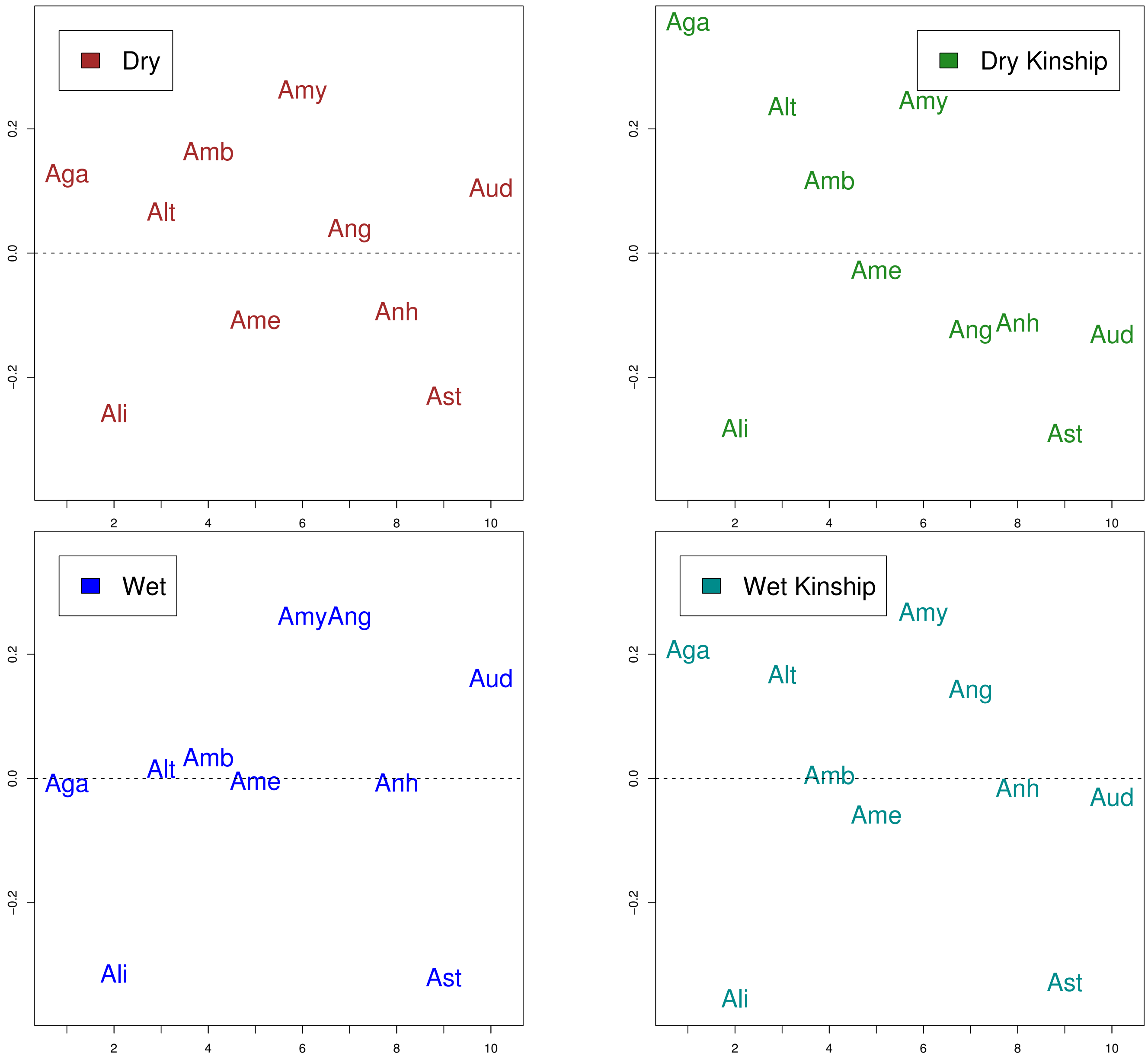
Elephant Family Results

Posterior Intercepts β_0



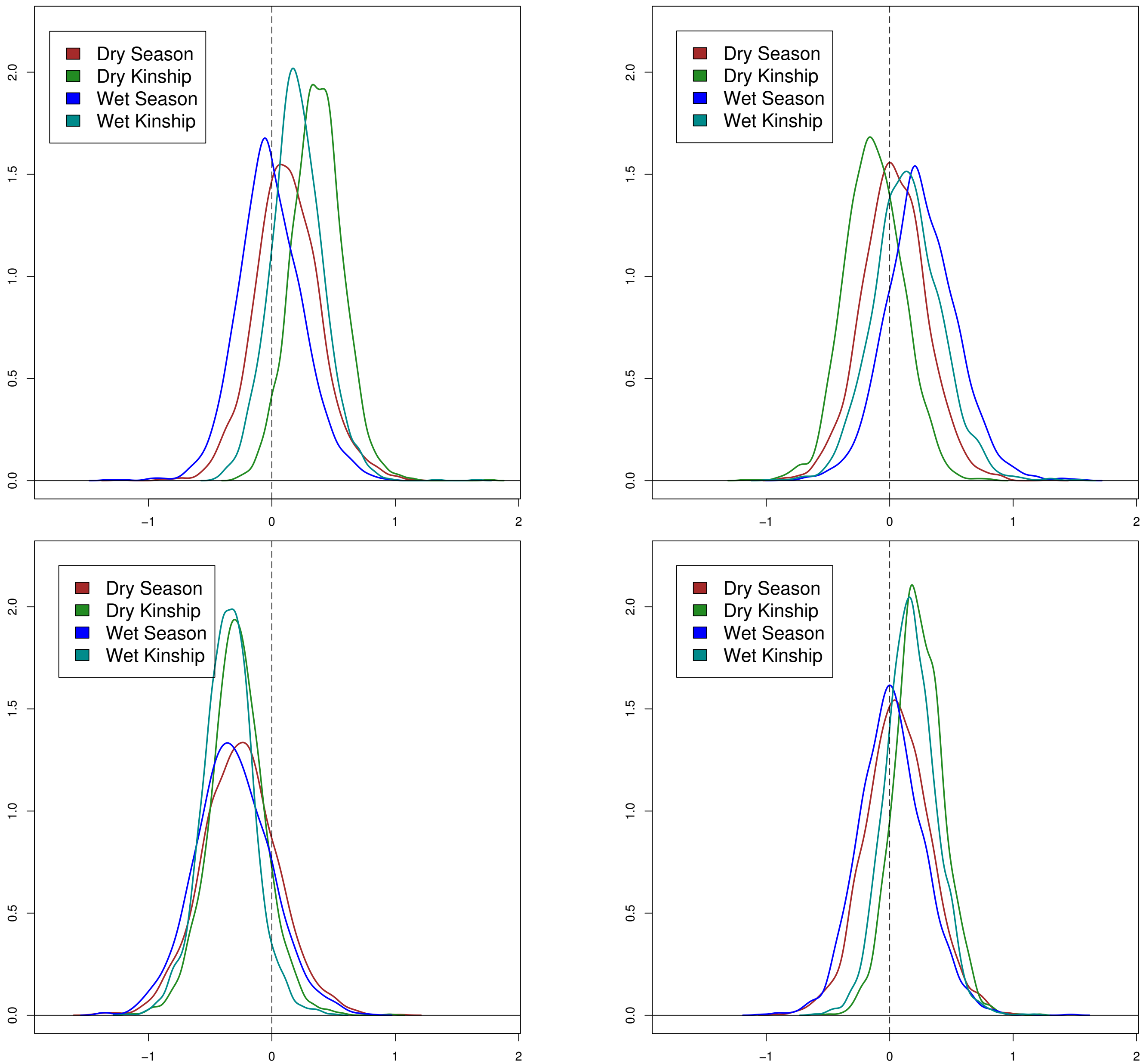
$$\theta_{ij} = \beta_0 + a_i + a_j + \beta_k k_{ij} + \gamma_{ij} + z_i' z_j$$

Posterior Sociabilities $\bar{a}$

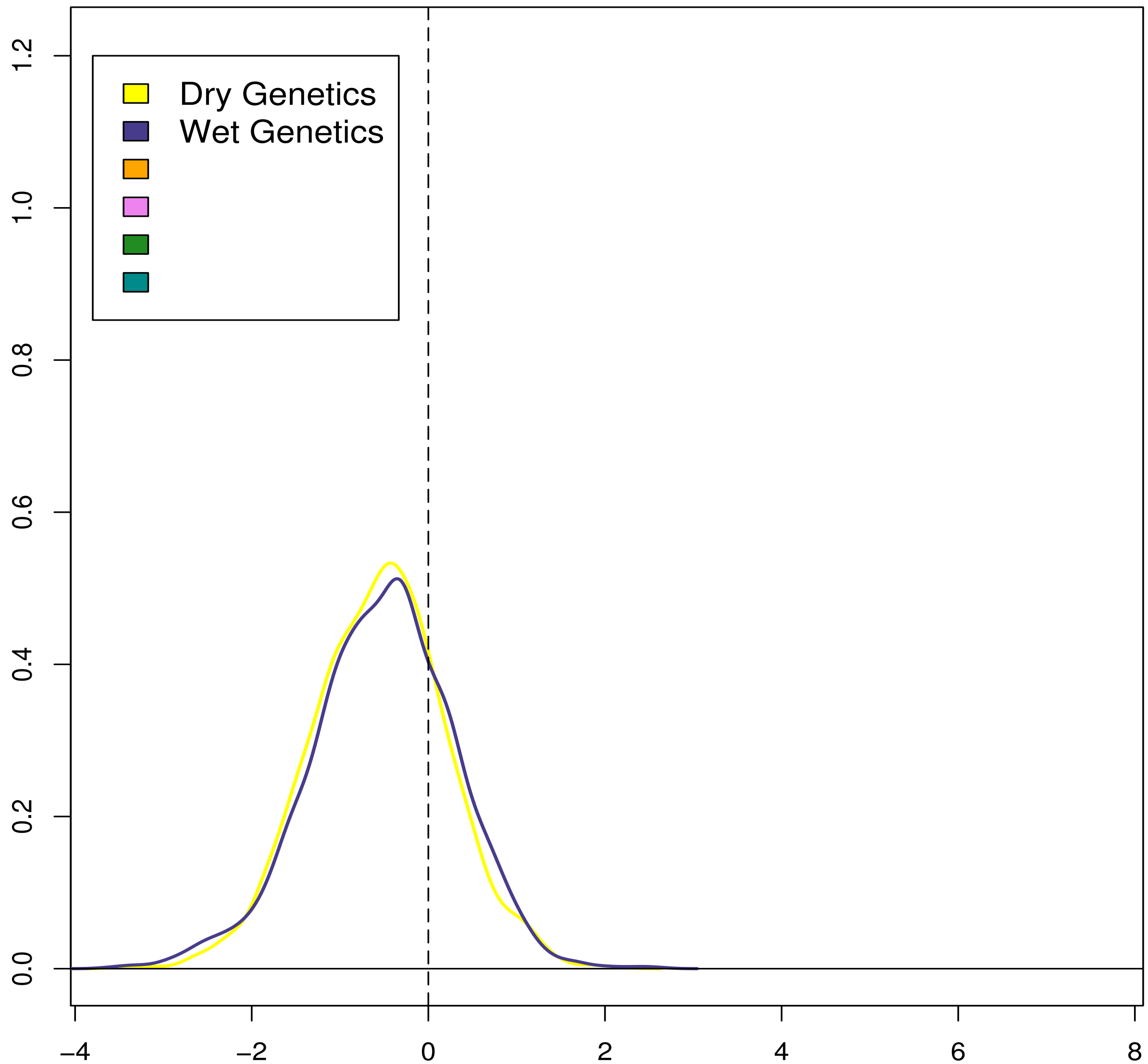


$$\theta_{\mathbf{ij}} = \beta_0 + \mathbf{a_i} + \mathbf{a_j} + \beta_{\mathbf{k}}\,\mathbf{k_{ij}} + \gamma_{\mathbf{ij}} + \mathbf{z_i'z_j}$$

Sociabilities for Aga, Ang, Ali, Alt

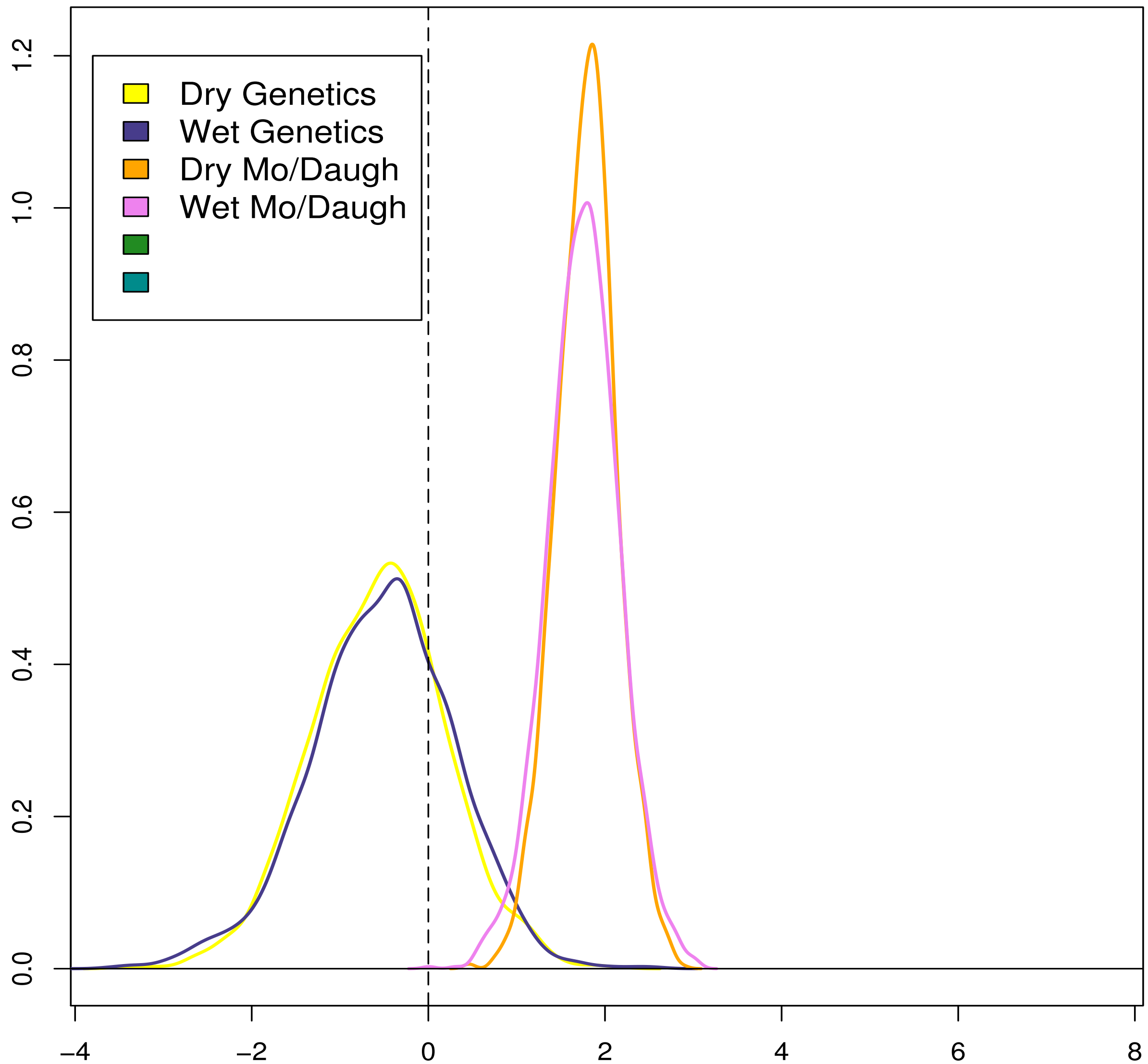


Posteriors for Kinship Coefficients $\beta_{\mathbf{k}}$



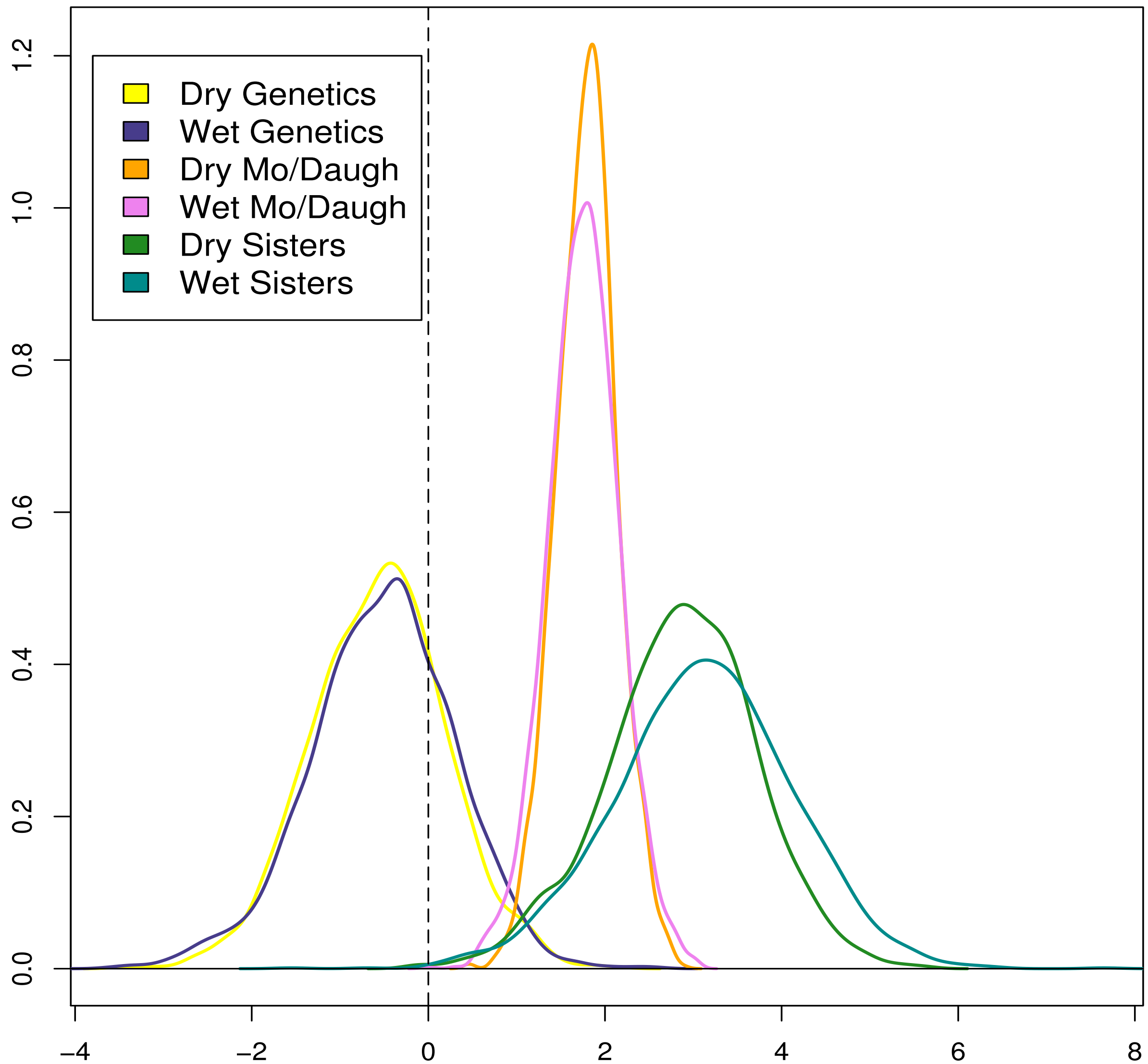
$$\theta_{\mathbf{ij}} = \beta_{\mathbf{0}} + \mathbf{a_i} + \mathbf{a_j} + \beta_{\mathbf{k1}}\,\mathbf{k_{1ij}} + \beta_{\mathbf{k2}}\,\mathbf{k_{2ij}} + \beta_{\mathbf{k3}}\,\mathbf{k_{3ij}} + \gamma_{\mathbf{ij}} + \mathbf{z_i'z_j}$$

Posteriors for Kinship Coefficients β_k



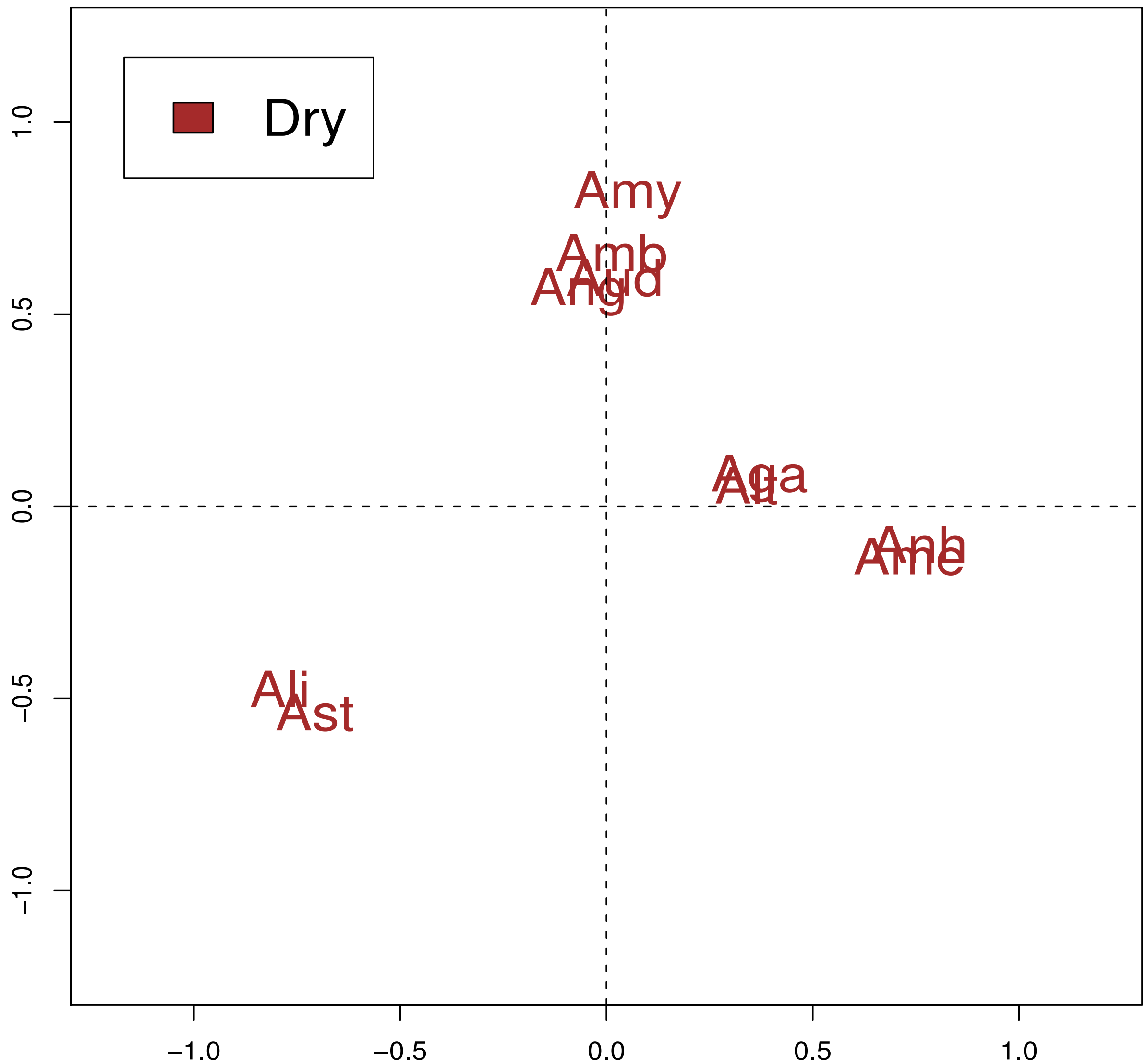
$$\theta_{ij} = \beta_0 + a_i + a_j + \beta_{k1} k_{1ij} + \beta_{k2} k_{2ij} + \beta_{k3} k_{3ij} + \gamma_{ij} + z_i' z_j$$

Posteriors for Kinship Coefficients β_k



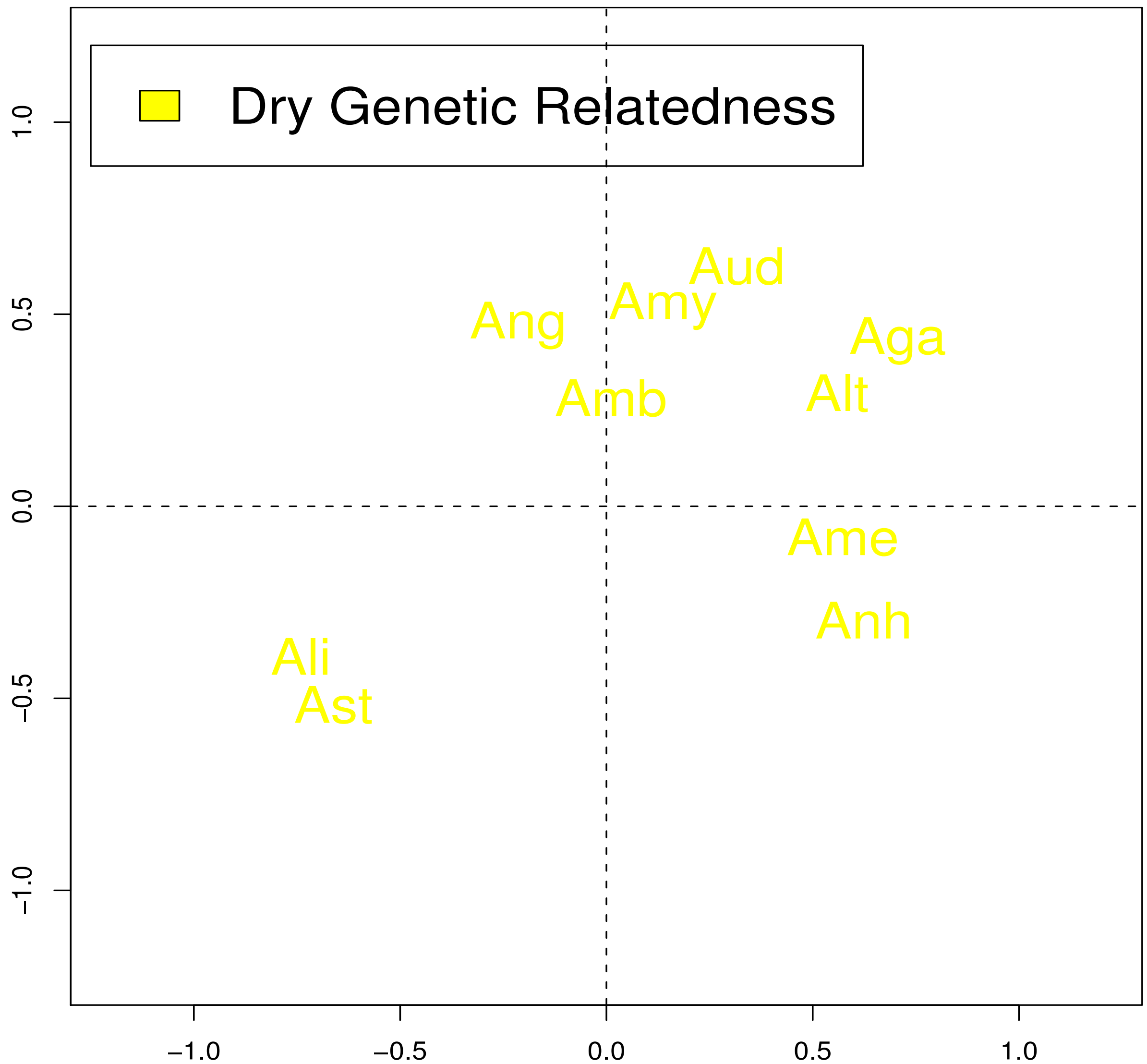
$$\theta_{ij} = \beta_0 + a_i + a_j + \beta_{k1} k_{1ij} + \beta_{k2} k_{2ij} + \beta_{k3} k_{3ij} + \gamma_{ij} + z_i' z_j$$

Dry Season Social Space $\bar{\mathbf{z}}_i$ Posteriors



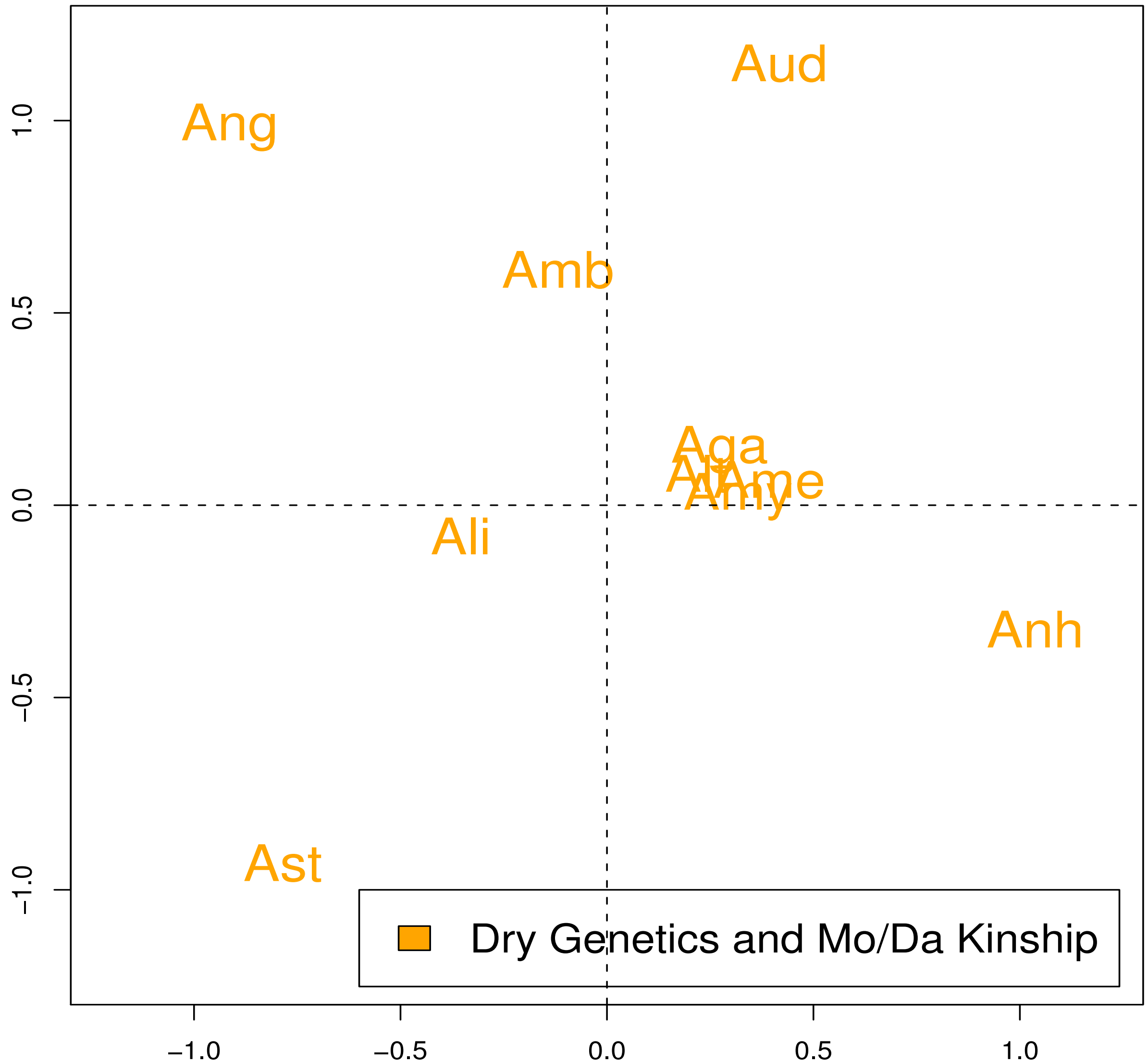
$$\theta_{ij} = \beta_0 + \mathbf{a}_i + \mathbf{a}_j + \gamma_{ij} + \mathbf{z}_i'\mathbf{z}_j$$

Dry Genetic DNA Social Space $\bar{\mathbf{z}}_i$ Posteriors



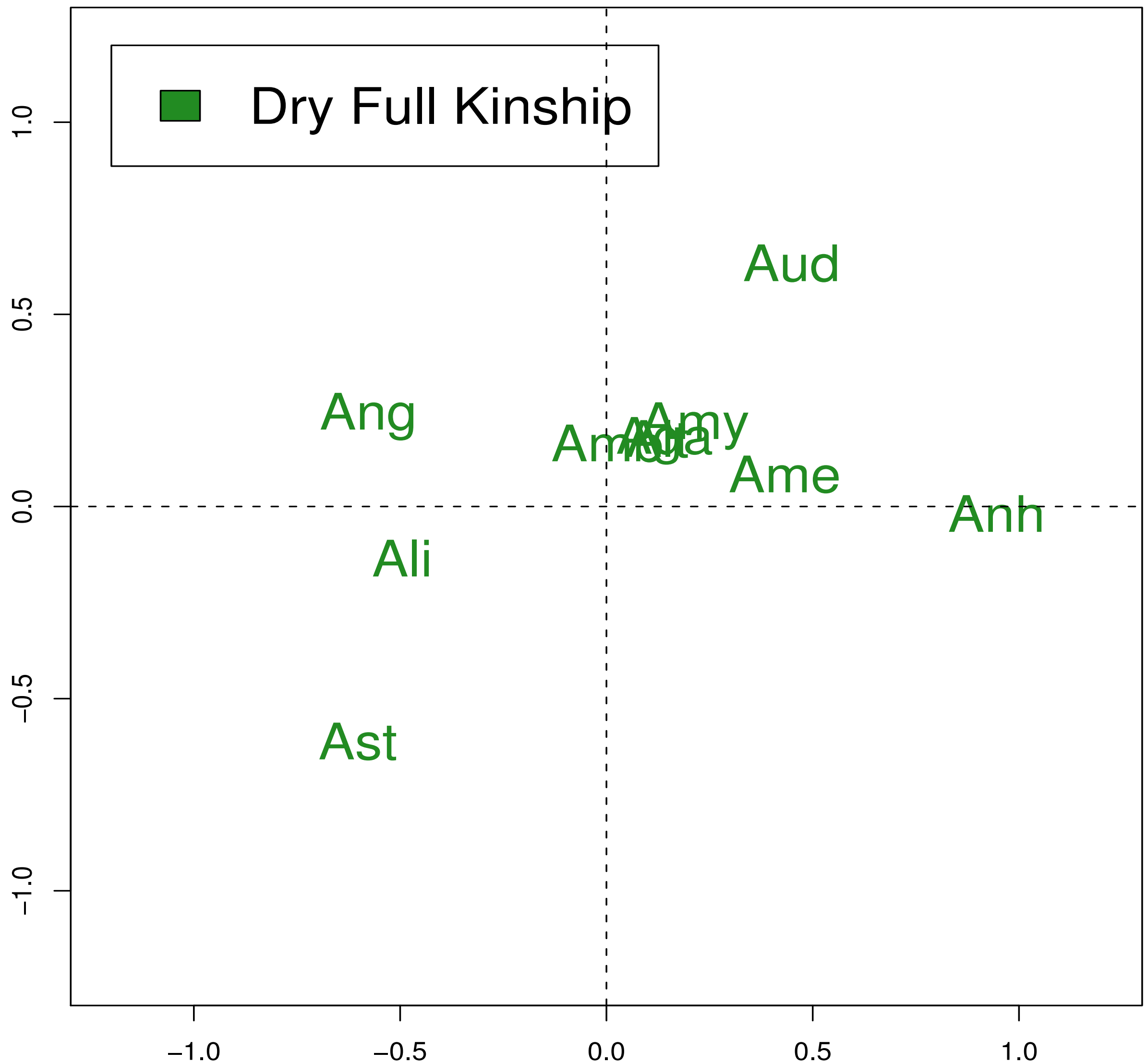
$$\theta_{ij} = \beta_0 + \mathbf{a}_i + \mathbf{a}_j + \beta_{k1}\,\mathbf{k}_{1ij} + \gamma_{ij} + \mathbf{z}_i'\mathbf{z}_j$$

Dry Gen, Mother/Daughter Social Space $\bar{\mathbf{z}}_{\mathbf{i}}$ Posteriors



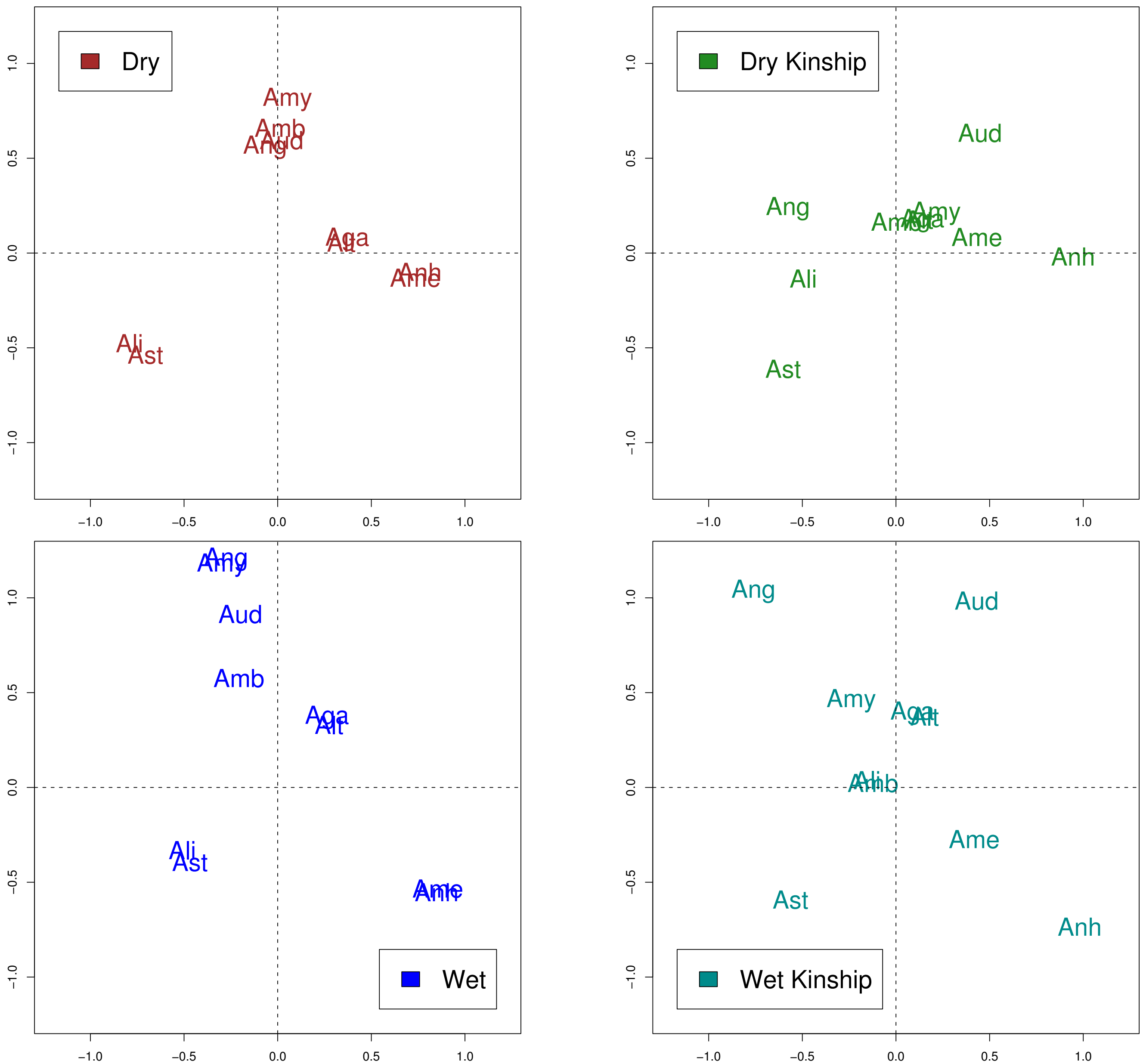
$$\theta_{\mathbf{ij}} = \beta_{\mathbf{0}} + \mathbf{a_i} + \mathbf{a_j} + \beta_{\mathbf{k1}}\,\mathbf{k_{1ij}} + \beta_{\mathbf{k2}}\,\mathbf{k_{2ij}} + \gamma_{\mathbf{ij}} + \mathbf{z_i'z_j}$$

Dry Full Kinship Social Space $\bar{\mathbf{z}}_\mathbf{i}$ Posteriors

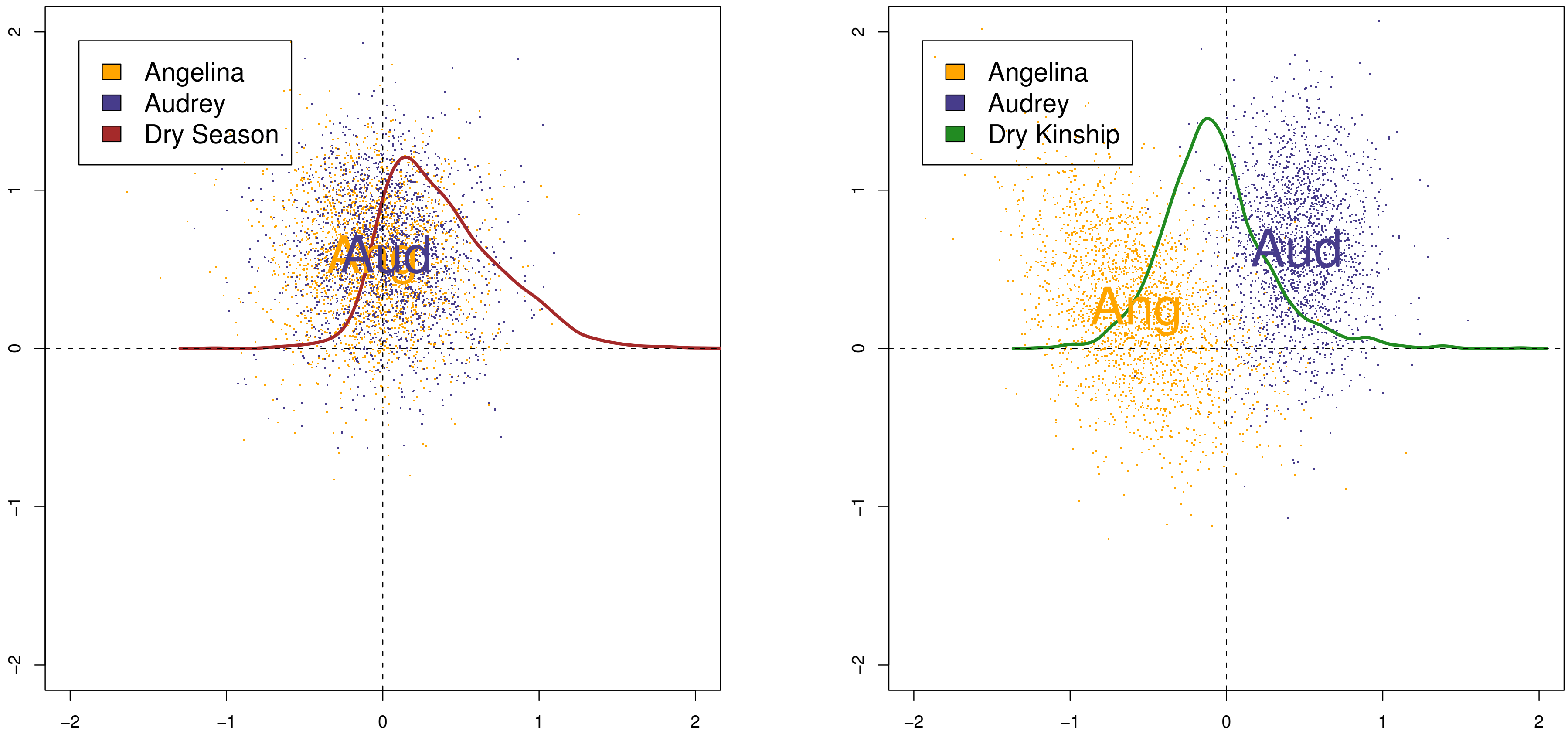


$$\theta_{\mathbf{ij}} = \beta_\mathbf{0} + \mathbf{a_i} + \mathbf{a_j} + \beta_{\mathbf{k1}}\,\mathbf{k_{1ij}} + \beta_{\mathbf{k2}}\,\mathbf{k_{2ij}} + \beta_{\mathbf{k3}}\,\mathbf{k_{3ij}} + \gamma_{\mathbf{ij}} + \mathbf{z_i'z_j}$$

Social Space Posterior Means $\bar{z}_i$



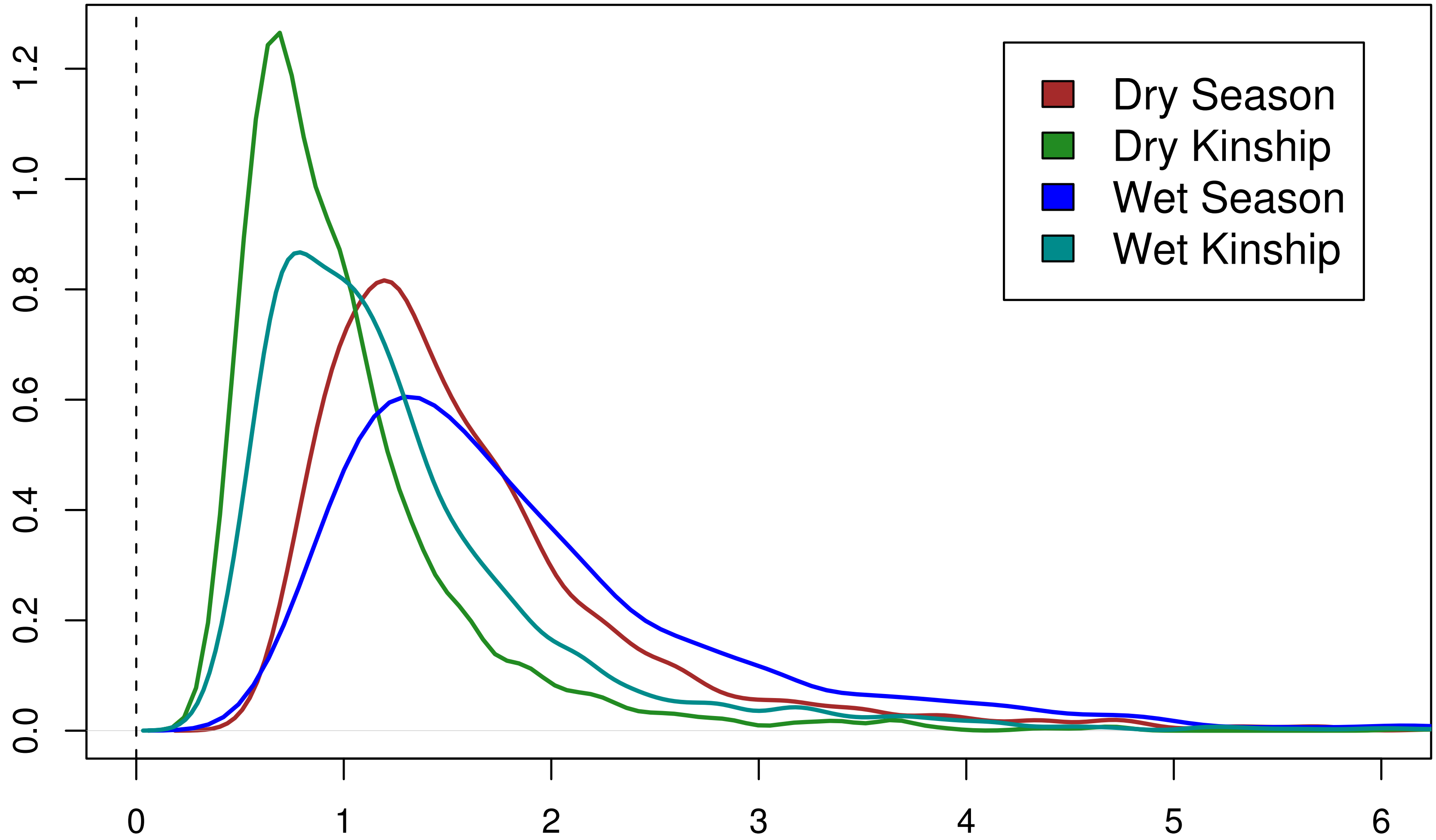
Angelina and Audrey: Two Sisters' Inner Products



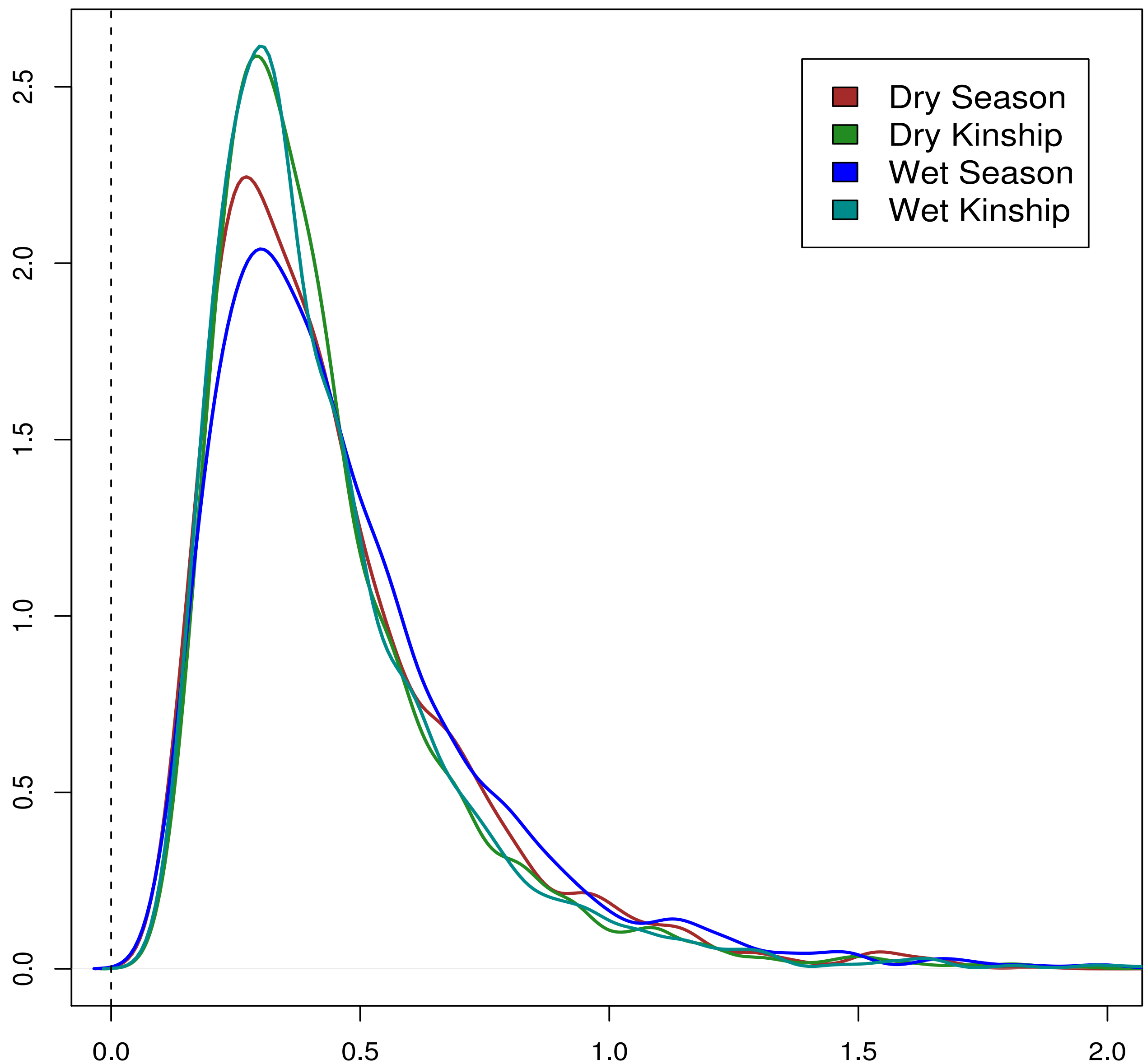
$$\theta_{ij} = \beta_0 + \mathbf{a_i} + \mathbf{a_j} + \beta_k \mathbf{k_{ij}} + \gamma_{ij} + \mathbf{z_i' z_j}$$

Relative Size of the Variance Terms in the Error ϵ_{ij}

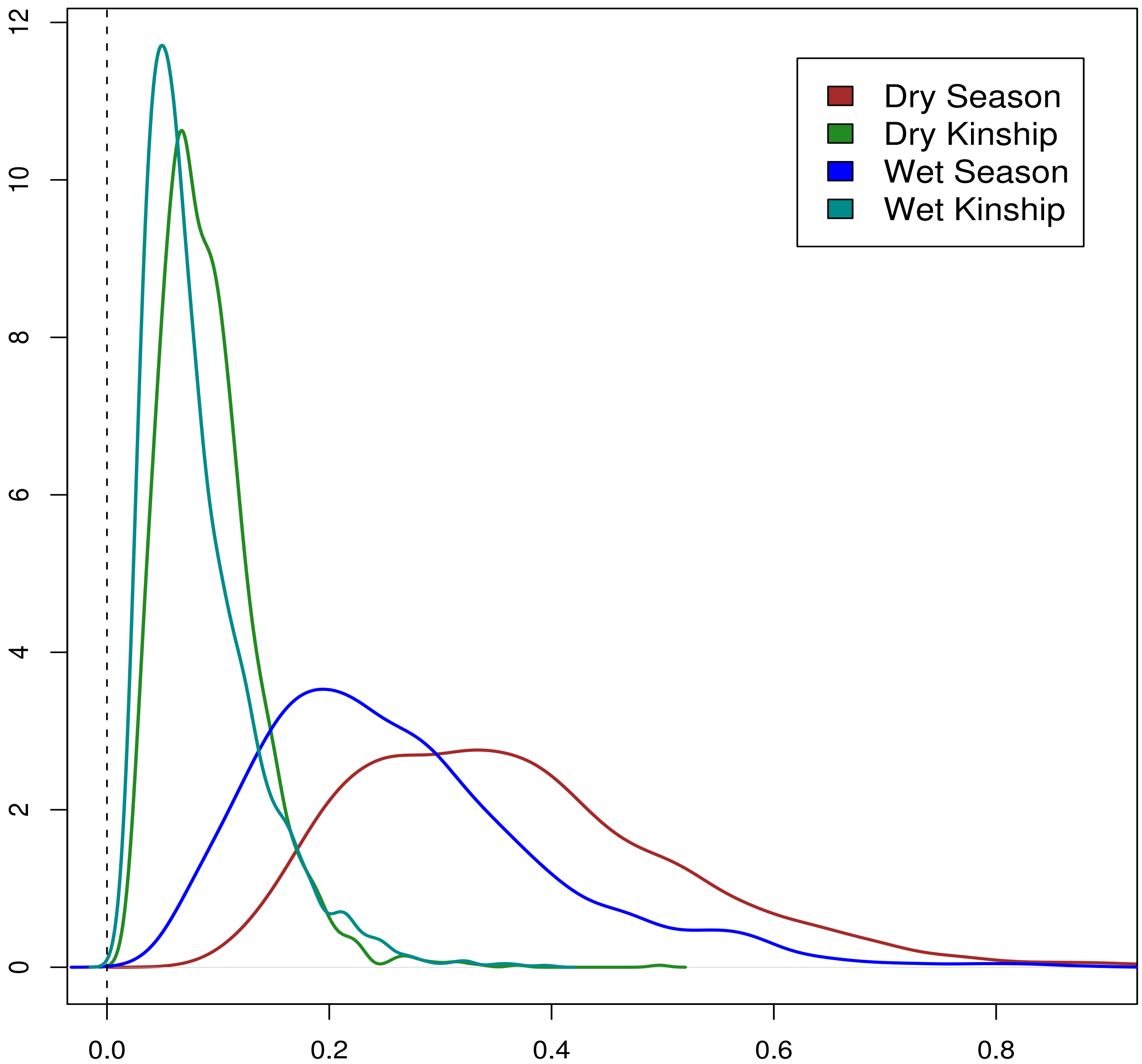
$$\begin{aligned}
\theta_{ij} &= \beta_0 + a_i + a_j + \beta_k\, k_{ij} + \gamma_{ij} + z_i' z_j \\
&= \beta_0 + \beta_k\, k_{ij} + \epsilon_{ij} \\
\epsilon_{ij} &= a_i + a_j + \gamma_{ij} + z_i' z_j \\
\mathrm{E}(\epsilon_{ij}^2) &= 2\sigma_a^2 + \sigma_\gamma^2 + \sigma_{z_1}^4 + \sigma_{z_2}^4
\end{aligned}$$



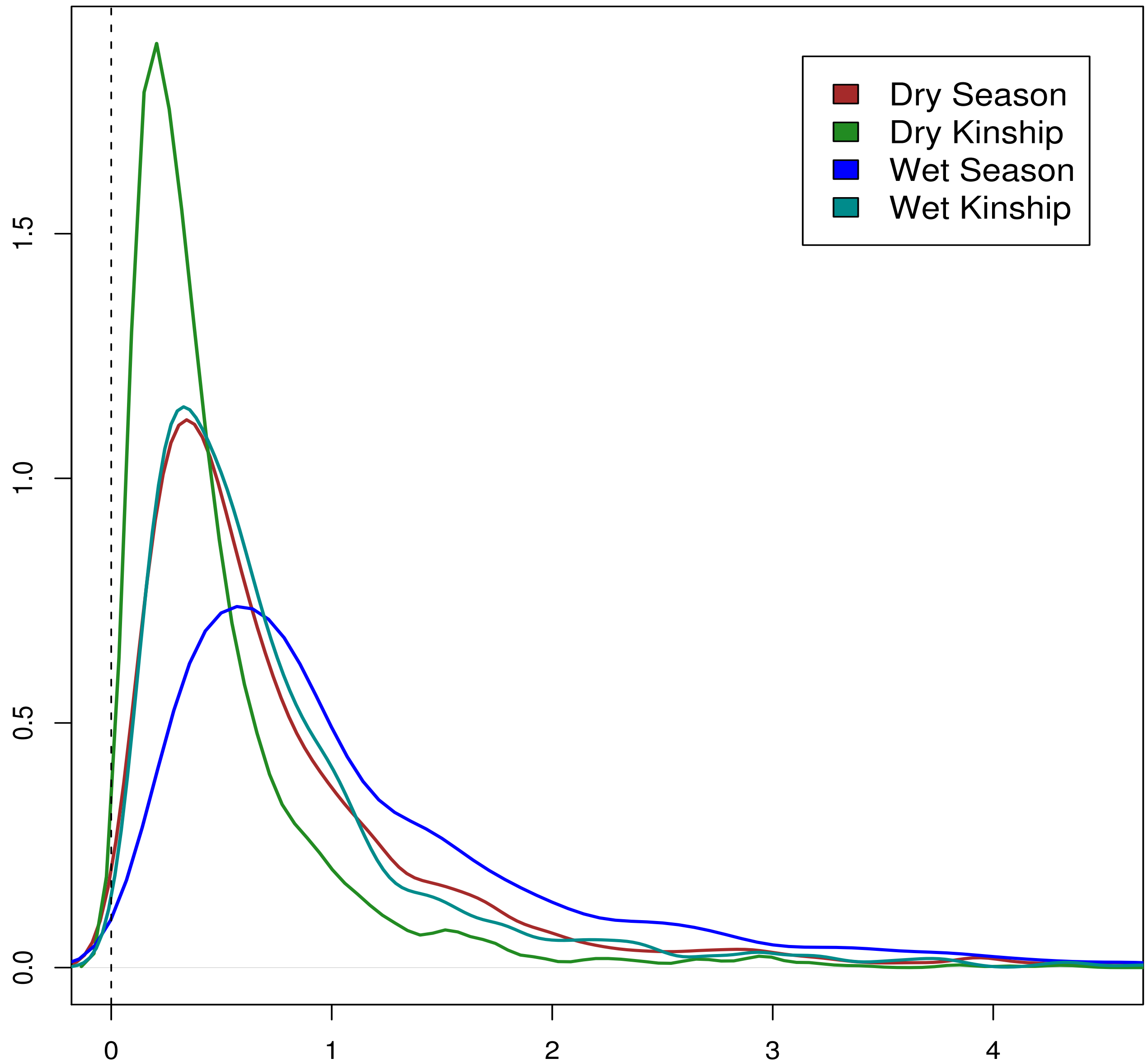
Posterior Sociability Variance $2\sigma_a^2$



Posterior Normal Error σ^2_γ



Posterior Social Space Variance $(\sigma^4_{z_1} + \sigma^4_{z_2})$

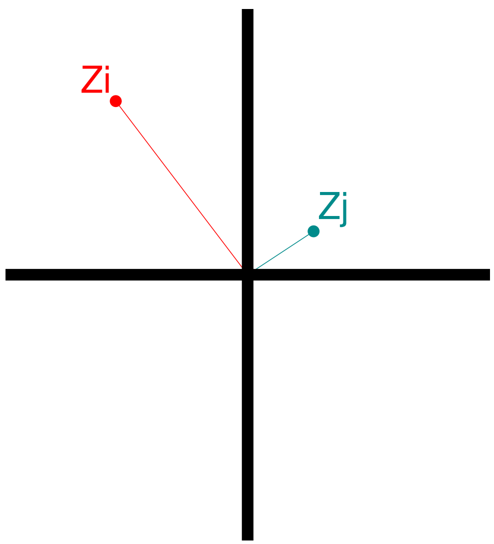


Pickiness in Social Space

- An elephant far away from the origin in social space tends to have highly positive or highly negative inner product pairwise terms in the model.

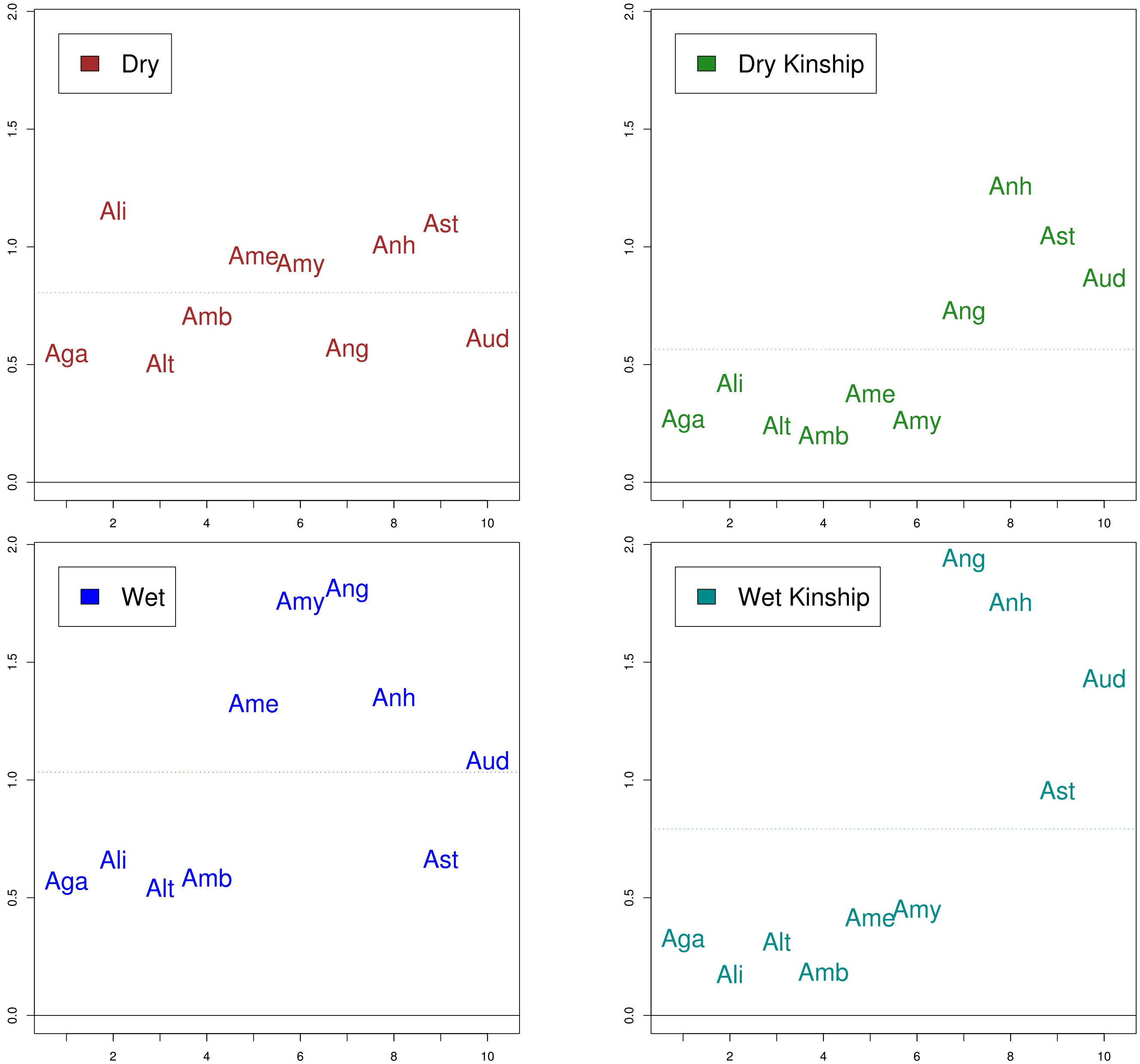
- Elephants close to the origin have small pairwise interaction effects.

- Pickiness is defined as the length of the vector in social space $|\mathbf{z_i}|$.



- Elephant i is "pickier" than elephant j.

Posterior Pickiness $|z_i|$



Conclusions

- The intercept β_0 is greater in the Wet seasons than in the Dry seasons, indicating that the elephants are more gregarious during the Wet season.

- The role of kinships β_k is similar in the Wet and Dry season.

- Mother/Daughter relationships are significant.

- Sister relationships are also very important.

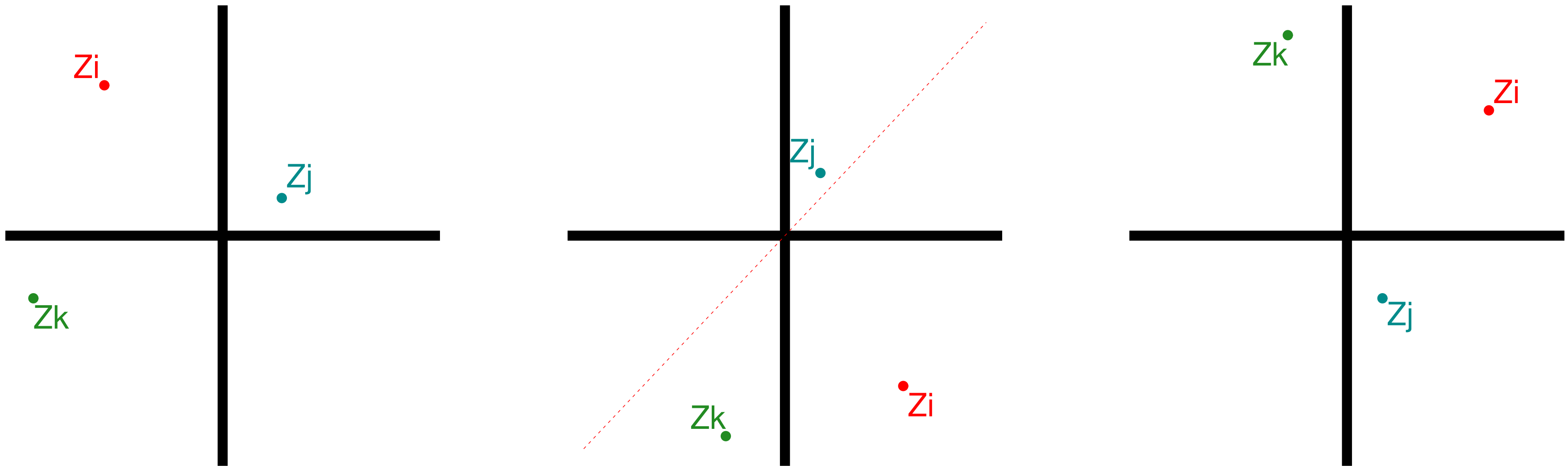
- After accounting for Mother/Daughter and Sister relationships, the DNA relatedness between elephants doesn't really matter.

Amy, Matriarch of Family AA

Pairwise Effects, Cont.

- Only the inner products $z_i' z_j, z_i' z_k, z_j' z_k$ of the vectors z_i, z_j, z_k matter.

Reflections or rotations of social space do not change inner products.

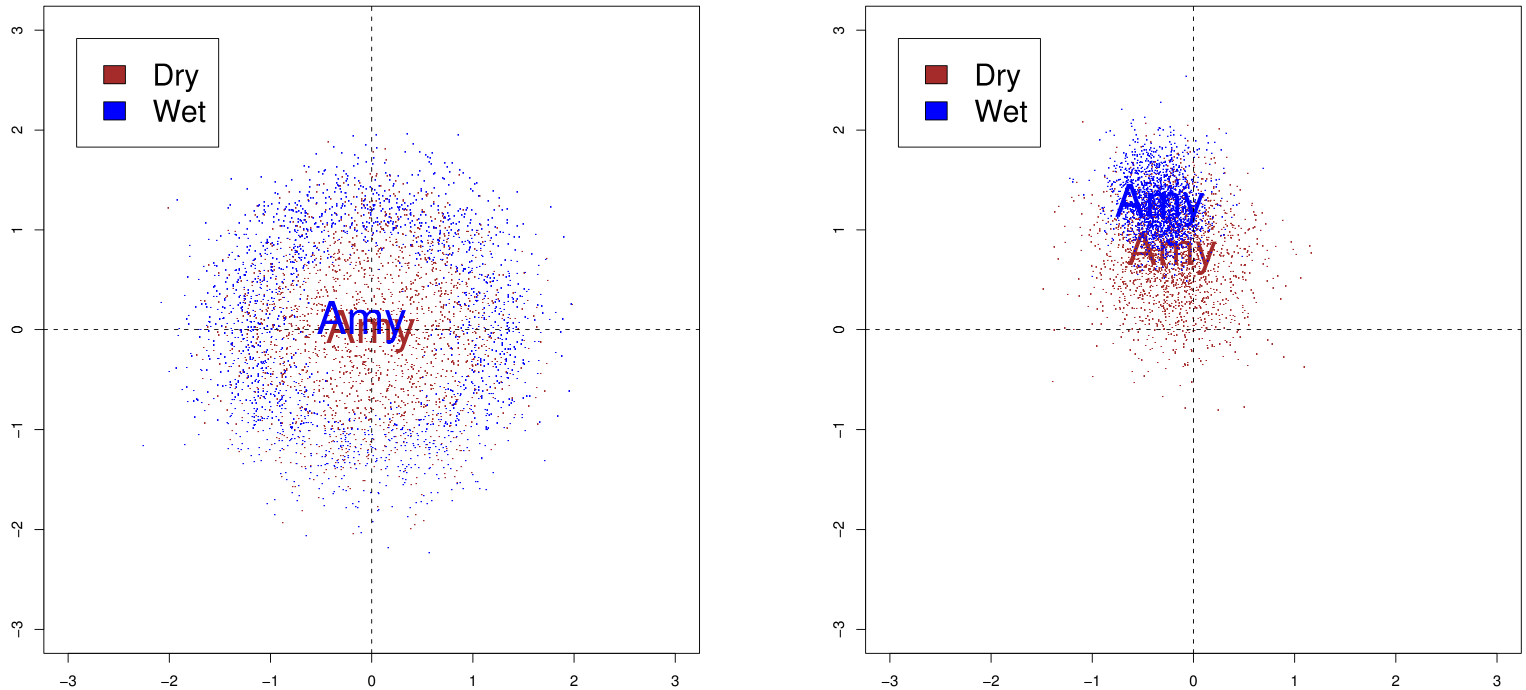


Social Space   Reflection   Rotation

- All 3 social spaces are equivalent.

Procrustean Transformation

- The posterior draws of the social space vectors must be reflected or rotated to give a coherent picture of the posterior distribution.



$\mathbf{Z}$ social space $\mathbf{Z}^*$ transformed social space

- Fix an arbitrary matrix Z_0 of positions in social space, then apply the Procrustean transformation:

$$Z^* = Z_0 Z' \left(Z Z_0' Z_0 Z' \right)^{-\frac{1}{2}} Z$$

Gibbs Sampling

$$\theta_{ij} = \underbrace{\left(\tfrac{1}{2}\beta_0 + a_i\right)}_{\mathbf{s}} + \underbrace{\left(\tfrac{1}{2}\beta_0 + a_j\right)}_{\mathbf{r}} + \beta_k \, \mathrm{g_{ij}} + \gamma_{ij} + z_i' z_j$$

1. Sample linear effects:
   a) Sample $\beta_d, s, r \,|\, \beta_0, \sigma_a^2, \sigma_\gamma^2, \theta, Z$.
   b) Sample $\beta_0 \,|\, s, r, \sigma_a^2$.
   c) Sample $\sigma_a^2, \sigma_\gamma^2 \,|\, \beta_0, s, r$.

2. Sample bilinear effects:
   a) Sample $z_i \,|\, Z_{-i}, \theta, \beta, s, r, \sigma_z^2, \sigma_\gamma^2$.
   b) Sample $\sigma_z^2 \,|\, Z \sim \mathrm{IG}\left(\frac{1}{2} + \frac{nk}{2}, \frac{1}{2} + \frac{\mathrm{tr}(Z'Z)}{2}\right)$.

3. Update θ_{ij} with a Metropolis step:
   a) Propose $\theta_{ij}^* \sim \mathrm{N}\left(\left(\tfrac{1}{2}\beta_0 + a_i\right) + \left(\tfrac{1}{2}\beta_0 + a_j\right) + \beta_k \, \mathrm{k_{ij}} + z_i' z_j \,,\, \sigma_\gamma^2\right)$.
   b) Accept θ_{ij}^* with probability $\left(\frac{p(y_{ij}|\theta_{ij}^*)}{p(y_{ij}|\theta_{ij})} \wedge 1\right)$.

Selecting Dimension k of Social Space

he method of choosing the dimension k of social space depends on the goal of he analysis.

1. Descriptive:
   - Choose $k = 2$ to give easily interpretable results.

2. Assessing model fit: how well does the model explain the data?
   - Various model selection techniques
     - My choice would be to use stochastic search variable selection with point-mass 0 mixture priors on $\sigma^2_{z_1}$, $\sigma^2_{z_2}$, $\sigma^2_{z_3}$, ...
     - Requires proper priors.

3. Make predictions of unobserved data.
   - Cross-validation techniques.
     - Select k based on the predictive performance $= \sum_{l=1}^{4} \sum_{\{i,j\} \in \mathrm{A}_l} \log p(y_{ij} | \hat{\theta}_{ij})$,

where $\hat{\theta}_{ij}$ is the posterior mean excluding pairs in A_l.

Raw Data

ate	Time	Spread	Subgroups?	Amy	Ang	Amb	Aud	Ali	Ast	Aga	Alt	Ame	Anh
01024	11:15	45	NO	1	1	1	1					1	1
01024	11:25	70	NO	1	1	1	1					1	1
01024	11:35	80	NO	1	1	1	1					1	1
01024	11:38	10	NO							1	1		
01024	11:48	10	NO							1	1		
01024	11:58	35	NO	1	1	1	1			1	1	1	1
01030	10:50	55	NO					1	1	1	1	1	1
01030	11:00	45	NO					1	1	1	1	1	1
01030	11:10	100	NO					1	1	1	1	1	1
01030	11:20	250	YES					1	1	1	1		
01030	11:20	250	YES									1	1
01030	11:30		YES					1	1	1	1		
01030	11:30		YES									1	1
10618	11:39	120	YES					1	1				
10618	11:39	120	YES	1		1						1	1
10618	11:49	110	NO	1		1		1	1	1	1	1	1
10618	11:59	120	YES					1	1	1	1		
10618	11:59	120	YES	1		1						1	1
10618	12:09	130	NO	1		1	1	1	1	1	1	1	1

Family AA Dry Observations

RY	Amy	Amy	Ang	Ang	Amb	Amb	Aud	Aud	Ali	Ali	Ast	Ast	Aga	Aga	Alt	Alt	Ame	Ame
	P	A	P	A	P	A	P	A	P	A	P	A	P	A	P	A	P	A
ny P	272	0	237	7	245	2	245	8	154	64	147	61	215	54	205	54	182	68
ny A	0	159	35	152	27	157	27	151	118	95	125	98	57	105	67	105	90	91
ng P	237	7	244	0	224	23	217	36	154	64	142	66	189	80	179	80	162	88
ng A	35	152	0	187	20	164	27	151	90	123	102	121	55	107	65	107	82	99
nb P	245	2	224	23	247	0	220	33	153	65	141	67	201	68	194	65	174	76
nb A	27	157	20	164	0	184	27	151	94	119	106	117	46	116	53	119	73	108
ud P	245	8	217	36	220	33	253	0	149	69	145	63	205	64	197	62	170	80
ud A	27	151	27	151	27	151	0	178	104	109	108	115	48	114	56	116	83	98
li P	154	64	154	64	153	65	149	69	218	0	191	17	147	122	144	115	115	135
li A	118	95	90	123	94	119	104	109	0	213	27	196	71	91	74	98	103	78
st P	147	61	142	66	141	67	145	63	191	17	208	0	148	121	145	114	121	129
st A	125	98	102	121	106	117	108	115	27	196	0	223	60	102	63	109	87	94
ga P	215	54	189	80	201	68	205	64	147	122	148	121	269	0	257	2	193	57
ga A	57	105	55	107	46	116	48	114	71	91	60	102	0	162	12	160	76	105
lt P	205	54	179	80	194	65	197	62	144	115	145	114	257	2	259	0	185	65
lt A	67	105	65	107	53	119	56	116	74	98	63	109	12	160	0	172	74	107
ne P	182	68	162	88	174	76	170	80	115	135	121	129	193	57	185	65	250	0
ne A	90	91	82	99	73	108	83	98	103	78	87	94	76	105	74	107	0	181

Kinship Relatedness

A	Amy	Angelina	Amber	Audrey	Alison	Astrid	Agatha	Althea	Amelia
ny									
ngelina	0.39								
nber	0.46	0.26							
udrey	0.31	0.22	0.11						
lison	0.3	0.02	0.08	0.02					
strid	0.25	0.18	0.02	0.14	0.53				
gatha	0.27	0.08	0.25	-0.15	0.38	0.34			
lthea	0.05	0.05	0.12	-0.01	0.15	0.21	0.46		
nelia	0.35	0.06	-0.09	0.01	0.09	0.2	0.1	0.02	
ngharad	0.25	0.34	0.02	0.2	-0.06	0.1	0.06	-0.04	0.52