

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

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Elephant Social Structure



- Only females form families. Males just run around looking to mate.
- Oldest female is the leader since she is the largest and wisest.
- Elephants within a family tend to be related.

Scientific Questions



- Why do elephants stay in large groups even when food is scarce?
- What role does genetics play in elephant social structure?
- How does one quantify social structure in order to assess whether or not groups are larger in the Wet Season vs. the Dry Season?

Data Collection



- Biologists in Kenya ride into the National Park looking for herds of elephants.
- When a herd is spotted, they write down the names of the elephants present.
- The biologists either stay to observe the family or move on to the next herd.

The Model

- Data is binomial
 - $y_{ij} \sim \text{Bin}(n_{ij}, p_{ij})$
 - 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 \implies Logistic regression
 - $E(y_{ij} | \theta_{ij}) = g(\theta_{ij})$.
 - g is the inverse logit link function.
 - The probability of elephants i and j being together is:

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

- θ_{ij} **is the linear predictor.**

Linear Predictor θ_{ij}

How often are elephants together?

- Intrinsic sociability a_i .
 - Sociable elephants will be observed together with other elephants (in groups) more often than unsociable elephants.
- Common intercept β_0 .
- Genetic relatedness $\beta_g g_{ij}$.
 - DNA samples lead to a measure g_{ij} of how closely elephant i and j are related.
- Normal error γ_{ij} (unexplained error or white noise).
- **Pairwise effect** $z'_i z_j$ between elephants i and j .

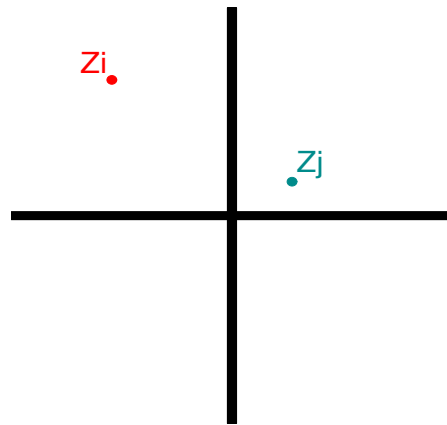
$$\theta_{ij} = \left(\frac{1}{2}\beta_0 + \mathbf{a}_i\right) + \left(\frac{1}{2}\beta_0 + \mathbf{a}_j\right) + \beta_g \mathbf{g}_{ij} + \gamma_{ij} + \mathbf{z}'_i \mathbf{z}_j$$

Pairwise Effect

$\mathbf{z}_i' \mathbf{z}_j$ is the inner product of the positions of elephants i and j in “Social Space”.

- For visual interpretability I choose the dimension of social space $\mathbf{k} = 2$.

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



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

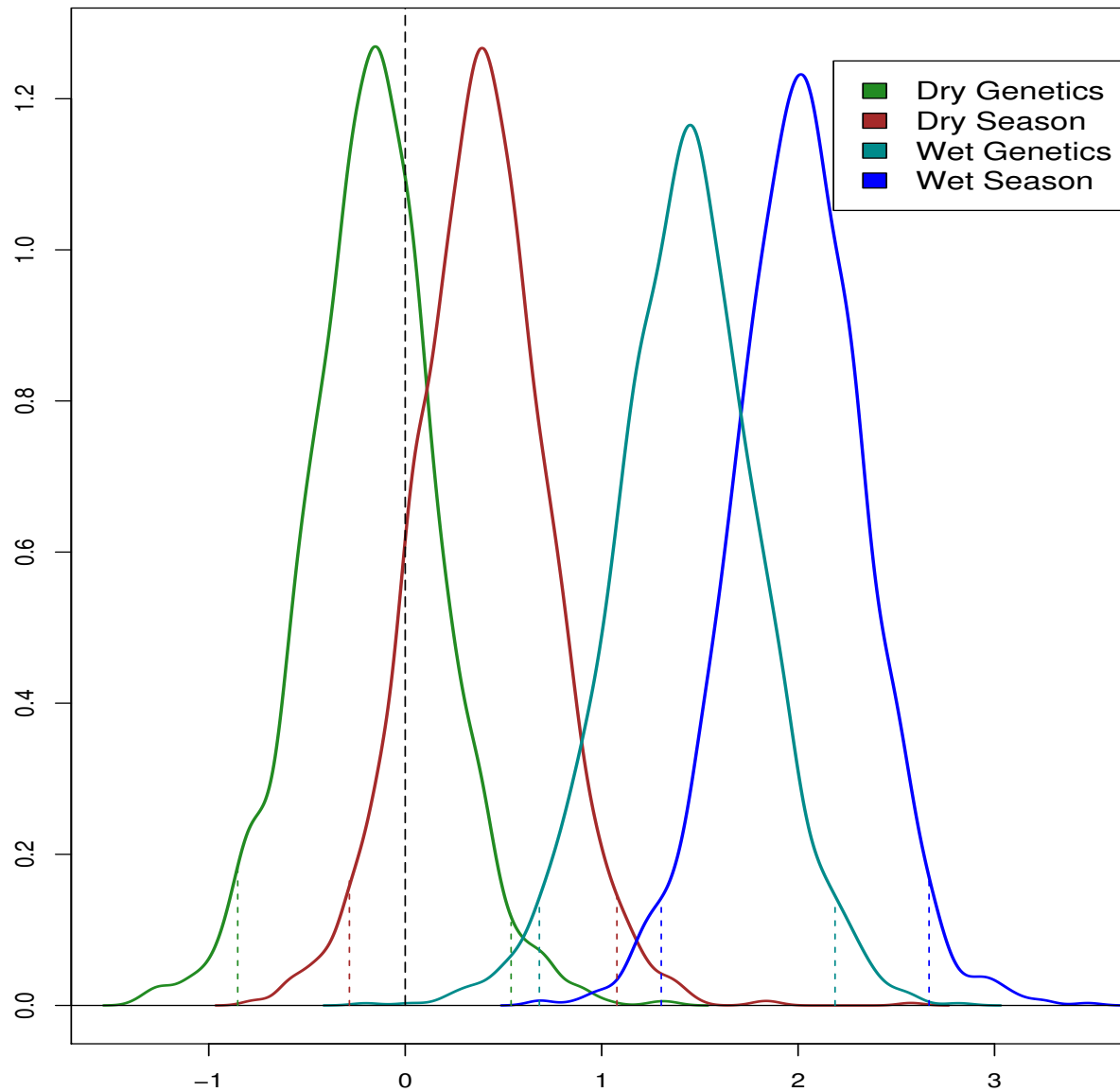
$$\mathbf{z}_j \sim N(\mathbf{0}, \sigma_z^2 \mathbf{I})$$

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

Elephant Family Results

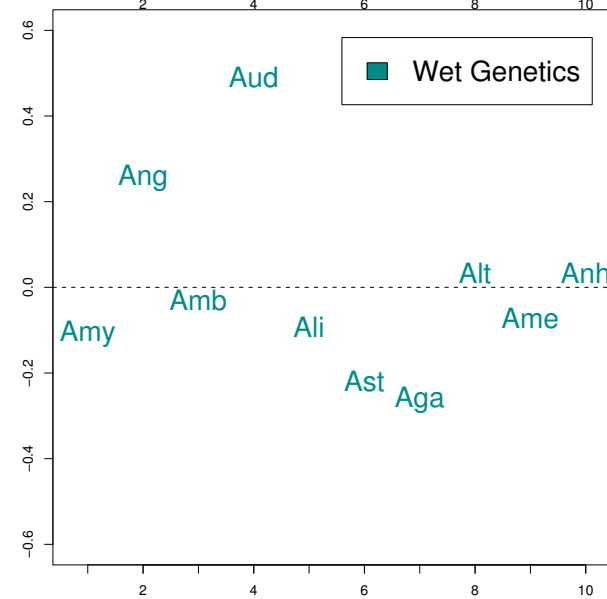
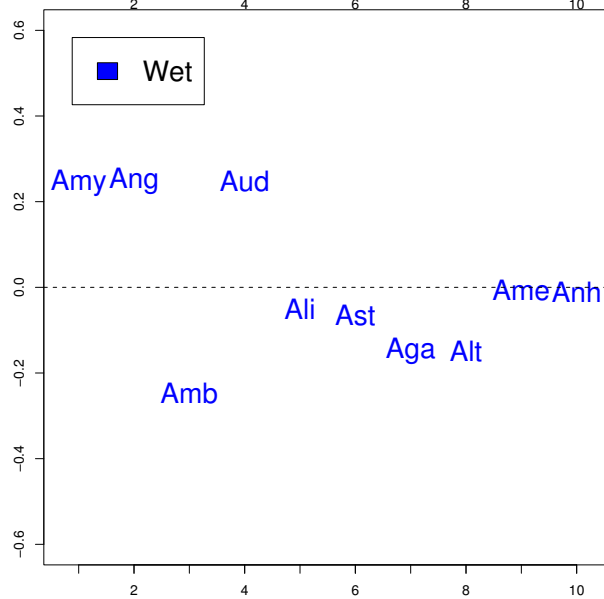
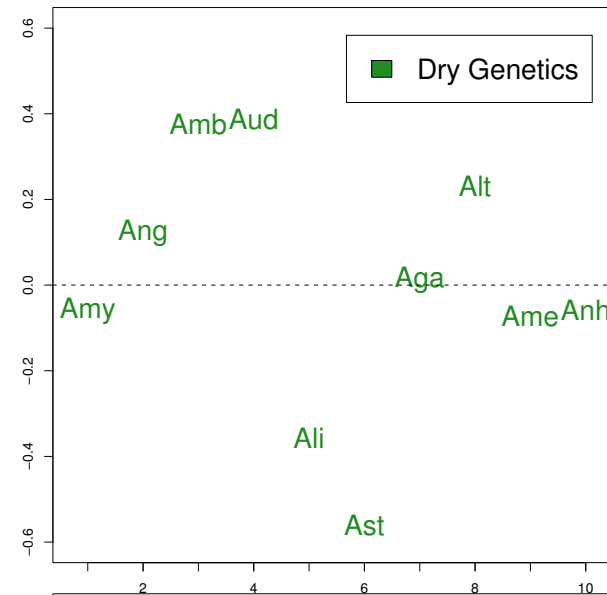
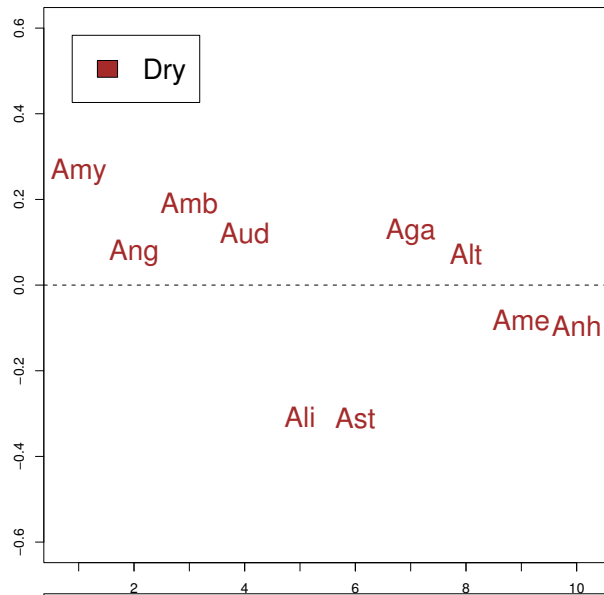


Posterior Intercepts β_0



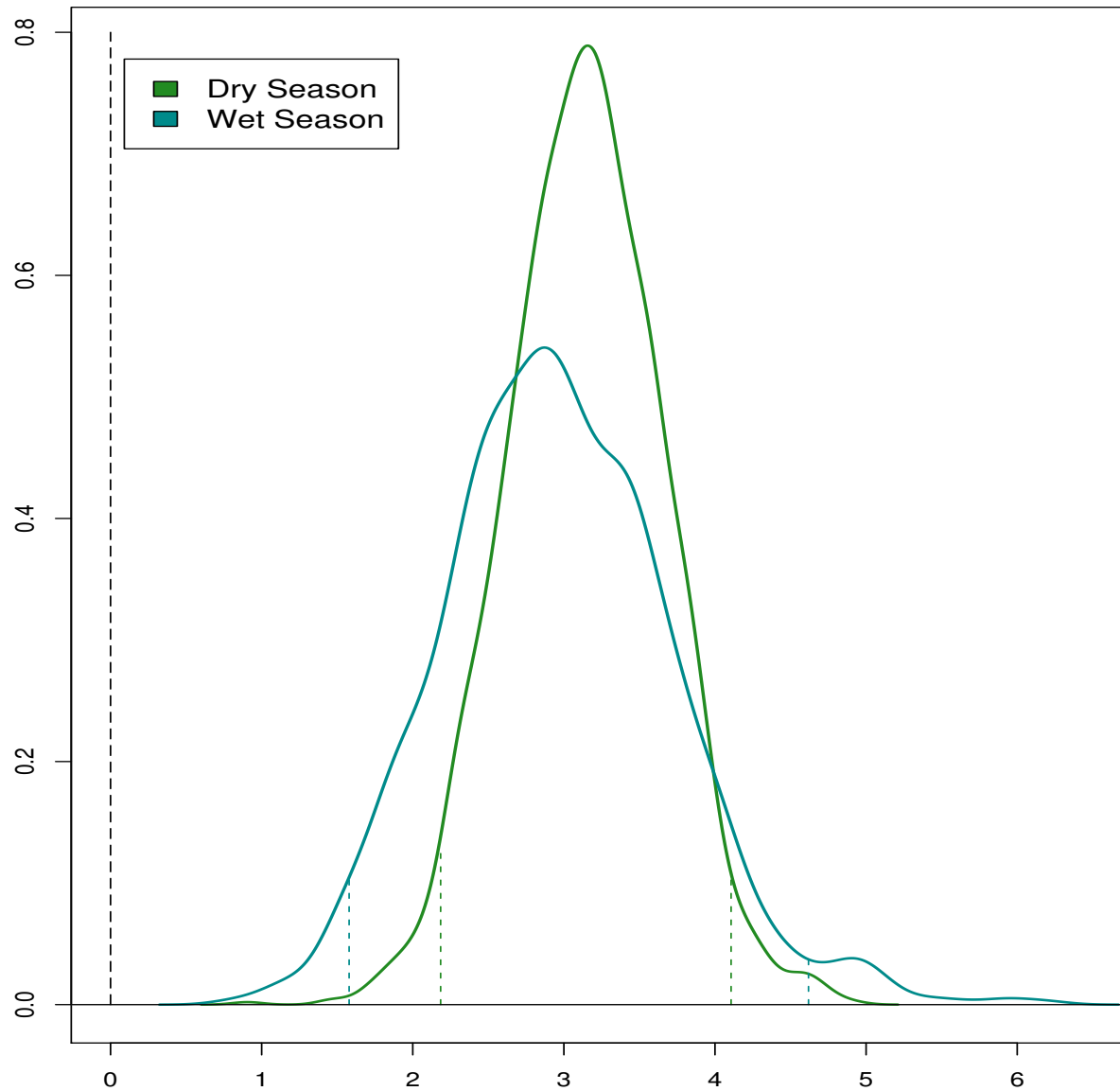
$$\theta_{ij} = \left(\frac{1}{2}\beta_0 + \mathbf{a}_i\right) + \left(\frac{1}{2}\beta_0 + \mathbf{a}_j\right) + \beta_g \mathbf{g}_{ij} + \gamma_{ij} + \mathbf{z}'_i \mathbf{z}_j$$

Posterior Sociabilities \bar{a}



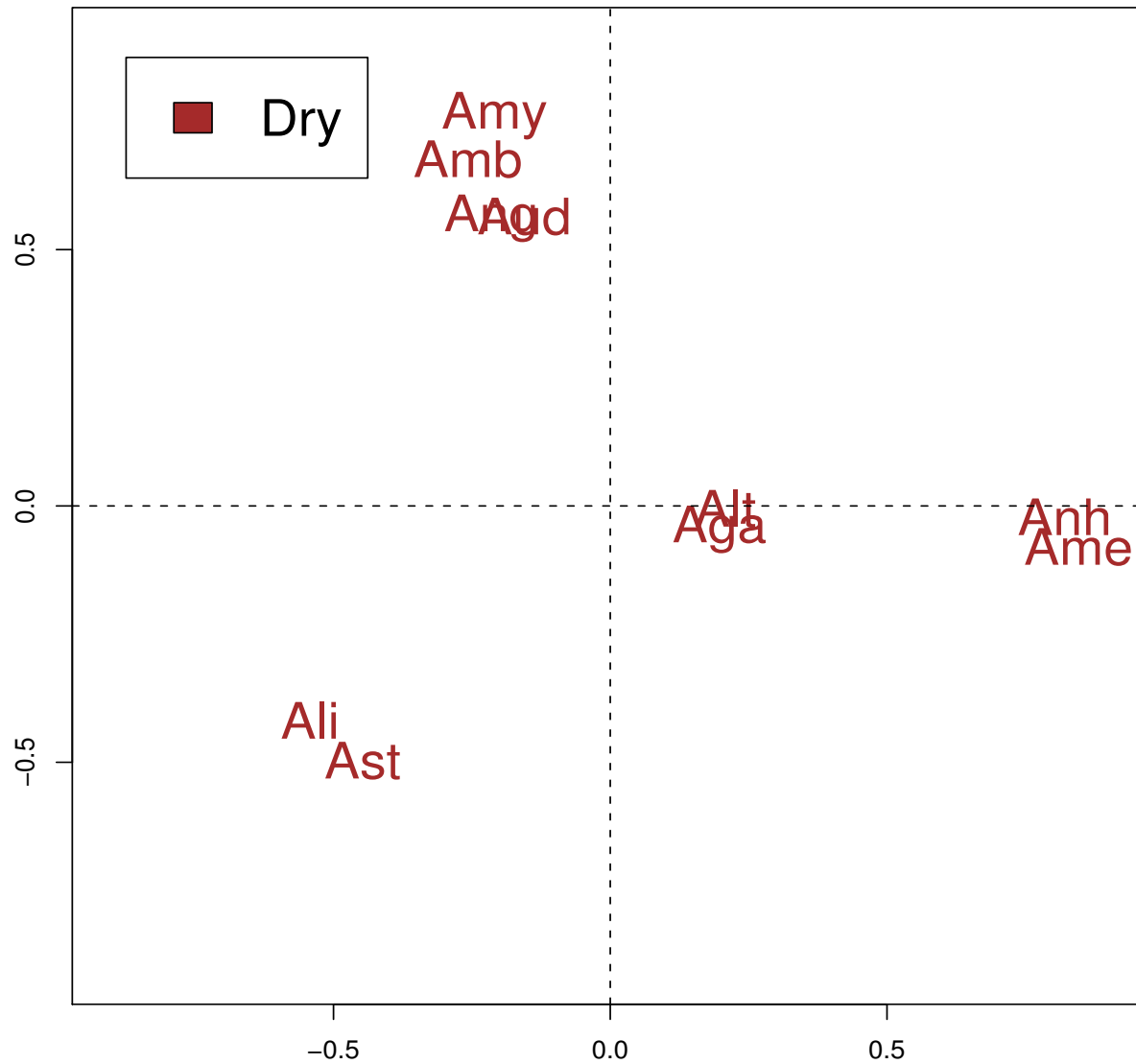
$$\theta_{ij} = \left(\frac{1}{2}\beta_0 + \mathbf{a}_i\right) + \left(\frac{1}{2}\beta_0 + \mathbf{a}_j\right) + \beta_g \mathbf{g}_{ij} + \gamma_{ij} + \mathbf{z}'_i \mathbf{z}_j$$

Posteriors for Genetic Coefficients β_g



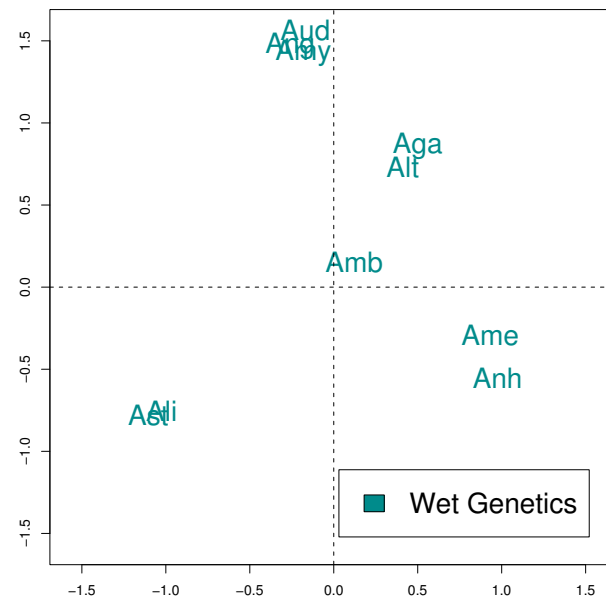
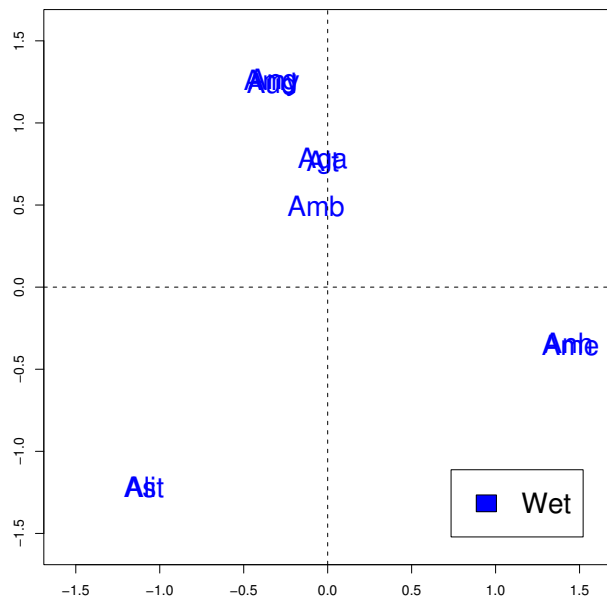
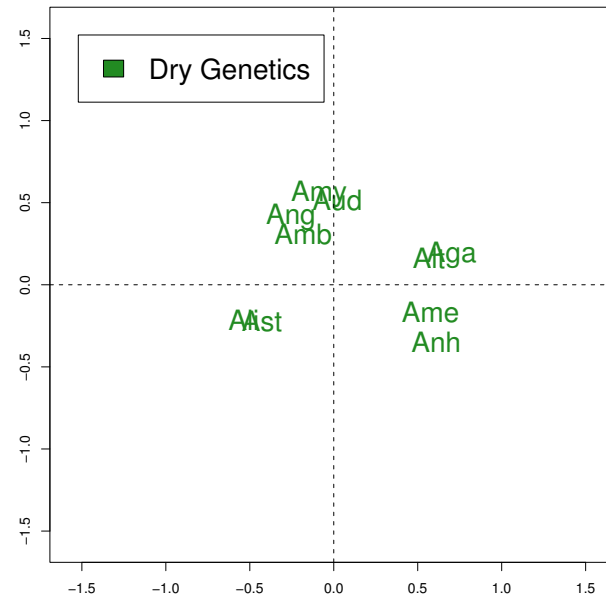
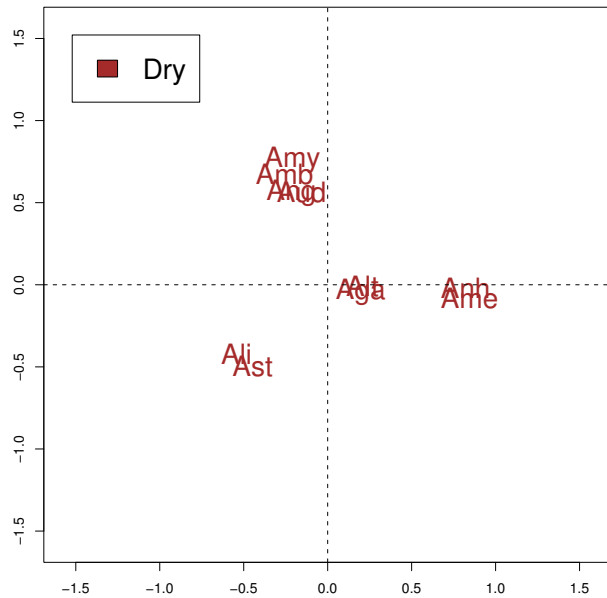
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Dry Season Social Space \bar{z}_i Posteriors



$$\theta_{ij} = \left(\frac{1}{2}\beta_0 + \mathbf{a}_i\right) + \left(\frac{1}{2}\beta_0 + \mathbf{a}_j\right) + \beta_g \mathbf{g}_{ij} + \gamma_{ij} + \mathbf{z}'_i \mathbf{z}_j$$

Social Space Posterior Means \bar{z}_i



$$\theta_{ij} = \left(\frac{1}{2}\beta_0 + \mathbf{a}_i\right) + \left(\frac{1}{2}\beta_0 + \mathbf{a}_j\right) + \beta_g \mathbf{g}_{ij} + \gamma_{ij} + \mathbf{z}'_i \mathbf{z}_j$$

Conclusions

- Some of the posterior sociabilities in Family AA change depending on the season.
- Posterior intercepts β_0 for the Wet seasons are greater than in the Dry seasons, indicating that the elephants are more gregarious during the Wet season.
- Genetic coefficients $\beta_g > 0$ for both Wet and Dry seasons.
- There are clusters of elephants in social space.

Amy, Matriarch of Family AA



Binomial Data Example

The total number of times data were recorded:

$$\text{Dry Season: } N_{\text{Dry}} = 331$$

$$\text{Wet Season: } N_{\text{Wet}} = 171$$

If Amy, Ang, and Ali are observed together, and the others are missing, then:

$$y_{\text{AmyAng}} = y_{\text{AmyAli}} = y_{\text{AngAli}} = 1$$

$$n_{\text{AmyAng}} = n_{\text{AmyAli}} = n_{\text{AngAli}} = 1$$

While for one missing elephant:

$$y_{\text{AmyAme}} = 0$$

$$n_{\text{AmyAme}} = 1$$

Whereas for two missing elephants:

$$y_{\text{AstAme}} = 0$$

$$n_{\text{AstAme}} = 0$$

Binomial Data, Cont.

In this example of five elephants Amy, Angelina, Alison, Astrid, and Amelia at time = t , the \mathbf{y} matrix of successful observations would be:

$$\mathbf{y}_t =$$

	Amy	Ang	Ali	Ast	Ame
Amy	\ddots	1	1	0	0
Ang	1	\ddots	1	0	0
Ali	1	1	\ddots	0	0
Ast	0	0	0	\ddots	0
Ame	0	0	0	0	\ddots

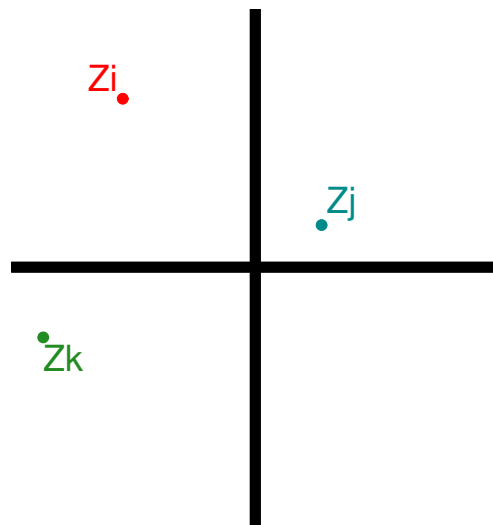
The \mathbf{n}_t matrix of potential observations =

	Amy	Ang	Ali	Ast	Ame
Amy	\ddots	1	1	1	1
Ang	1	\ddots	1	1	1
Ali	1	1	\ddots	1	1
Ast	1	1	1	\ddots	0
Ame	1	1	1	0	\ddots

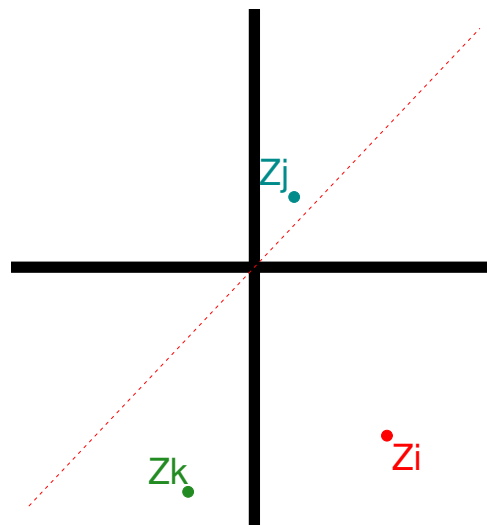
Pairwise Effect, Cont.

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

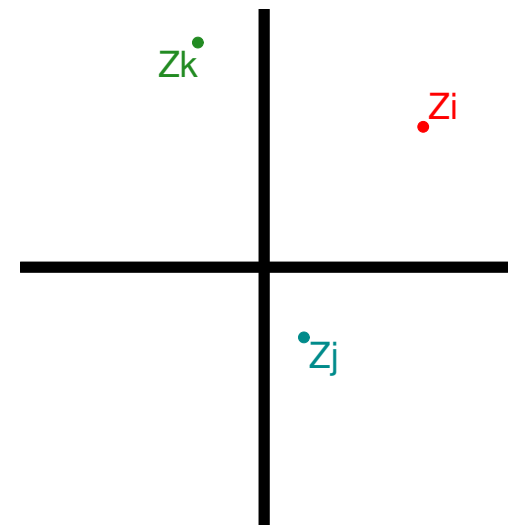
Reflections or rotations of Social Space do not change inner products.



Social Space



Reflection

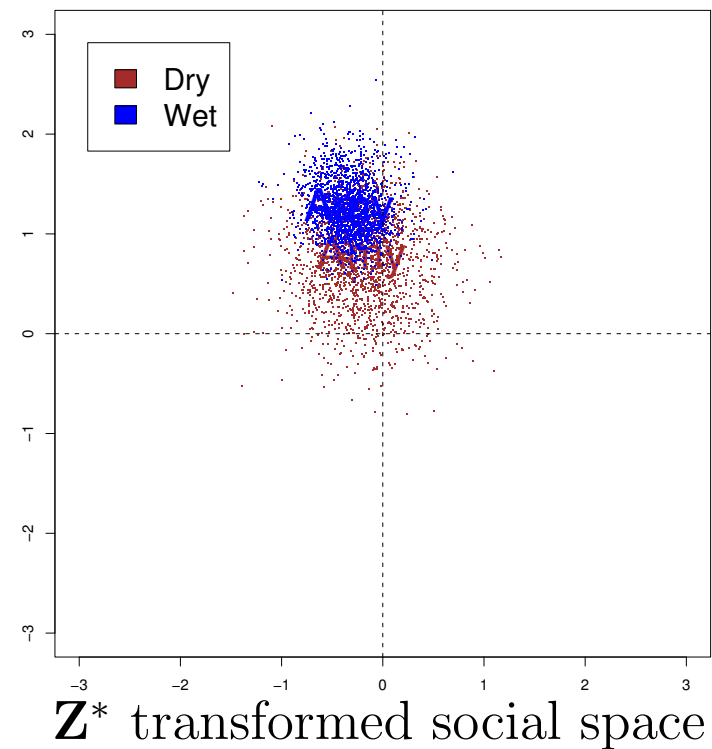
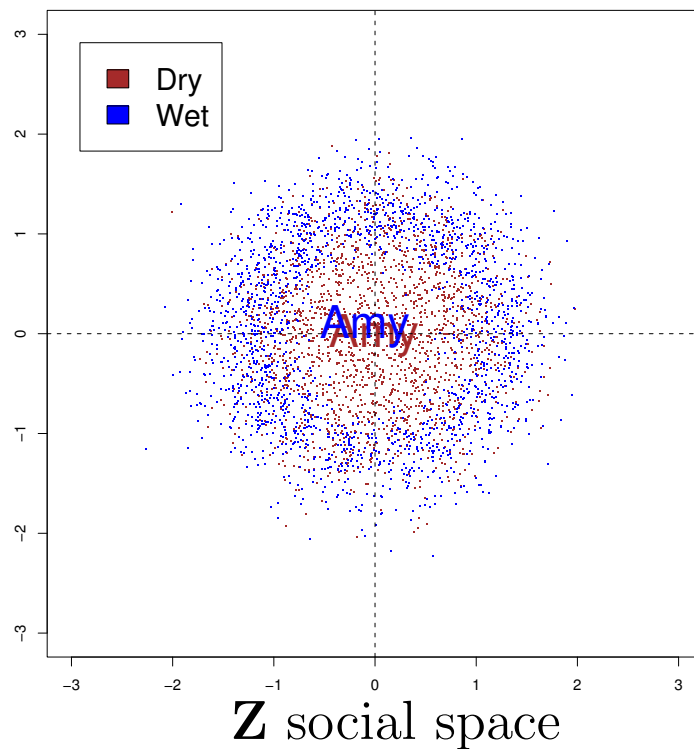


Rotation

- 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.



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

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

Vague Priors

$$\theta_{ij} = \left(\frac{1}{2}\beta_0 + \mathbf{a}_i\right) + \left(\frac{1}{2}\beta_0 + \mathbf{a}_j\right) + \beta_g \mathbf{g}_{ij} + \gamma_{ij} + \mathbf{z}'_i \mathbf{z}_j$$

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

Sociabilities: $a_i, a_j \sim N(0, \sigma_{\text{soc}}^2), \quad \sigma_{\text{soc}}^2 \sim IG\left(\frac{1}{2}, \frac{1}{2}\right)$

Genetic Coefficient: $\beta_g \sim N(0, 100)$

Pairwise error: $\gamma_{ij} \sim N(0, \sigma_{\gamma}^2), \quad \sigma_{\gamma}^2 \sim IG\left(\frac{1}{2}, \frac{1}{2}\right)$

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

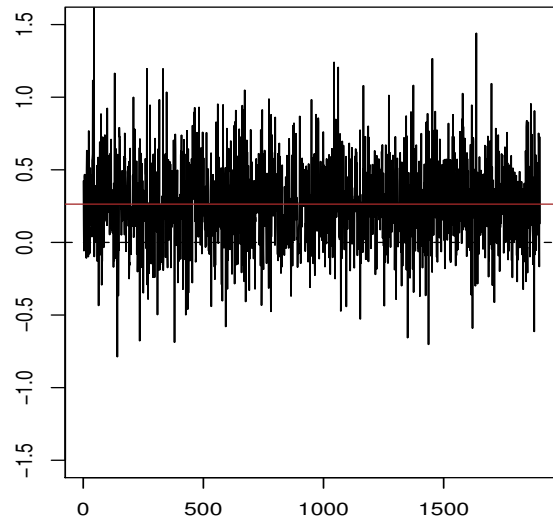
Parameter Estimation

Proceed using Gibbs sampling.

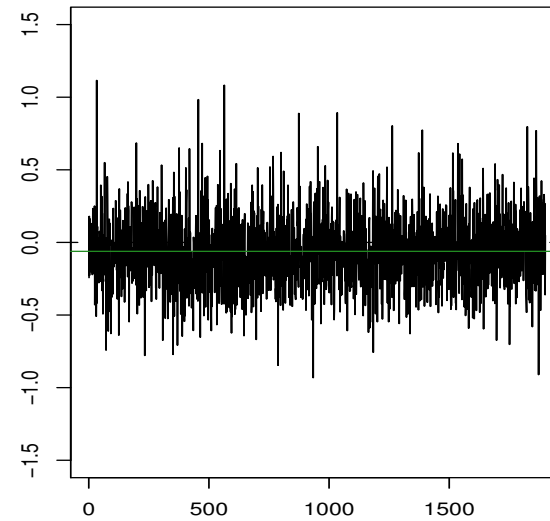
For details see Peter Hoff's article "Bilinear Mixed-Effects Models for Dyadic Data" in the current March 2005 issue of *JASA*.

Amy Sociability MCMC

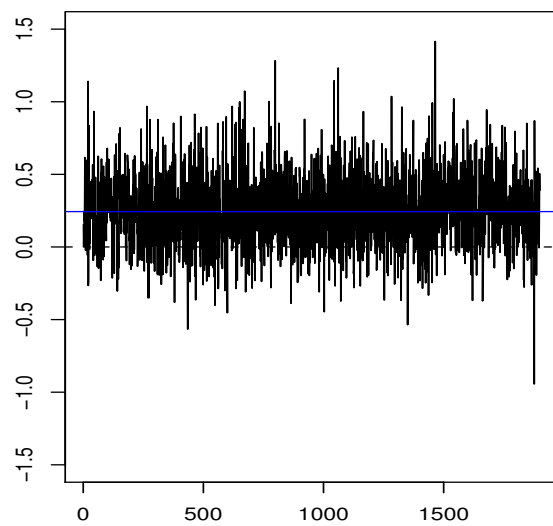
Dry Season



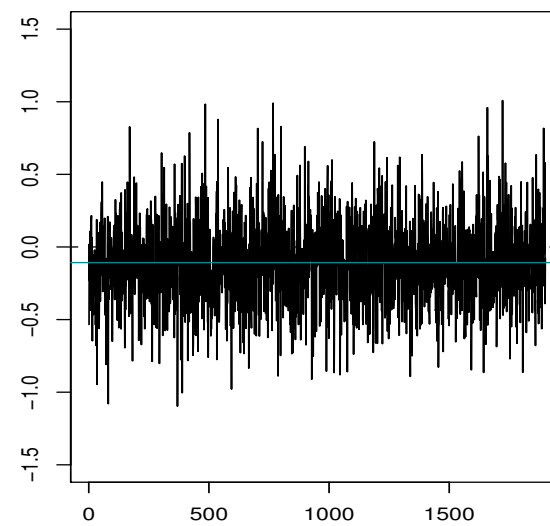
Dry Season with Genetics



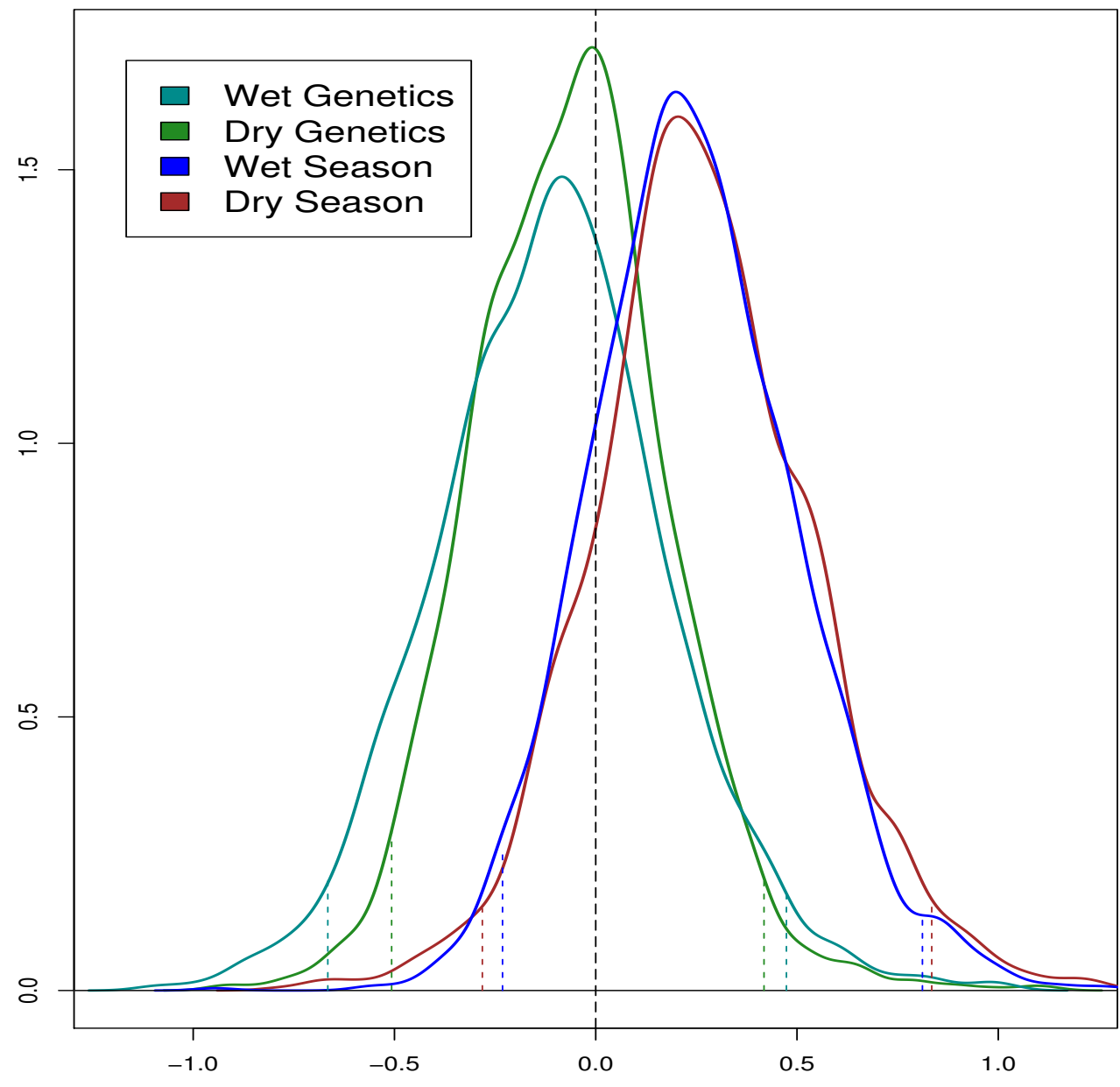
Wet Season



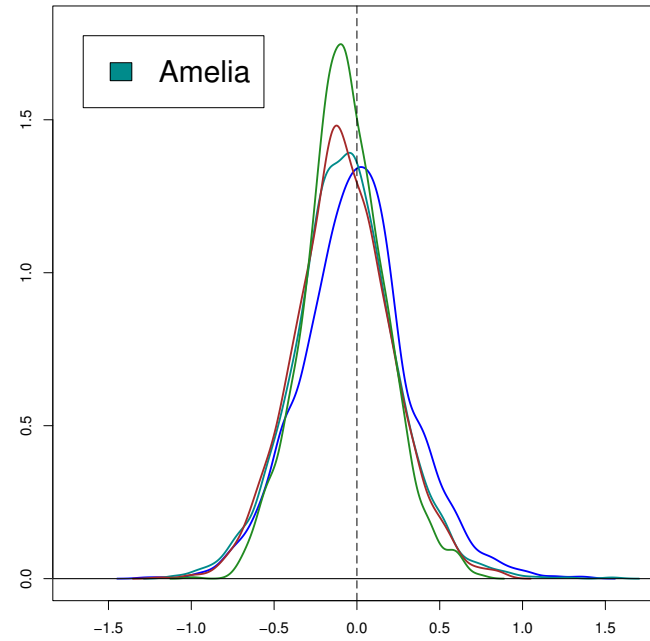
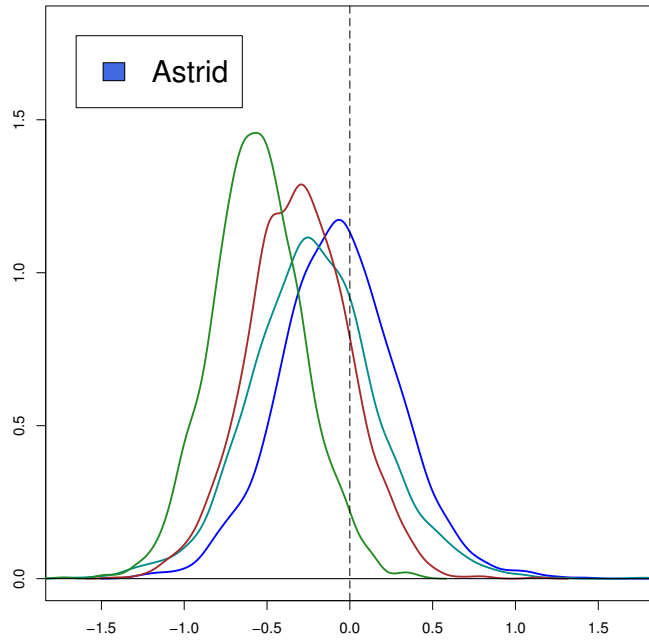
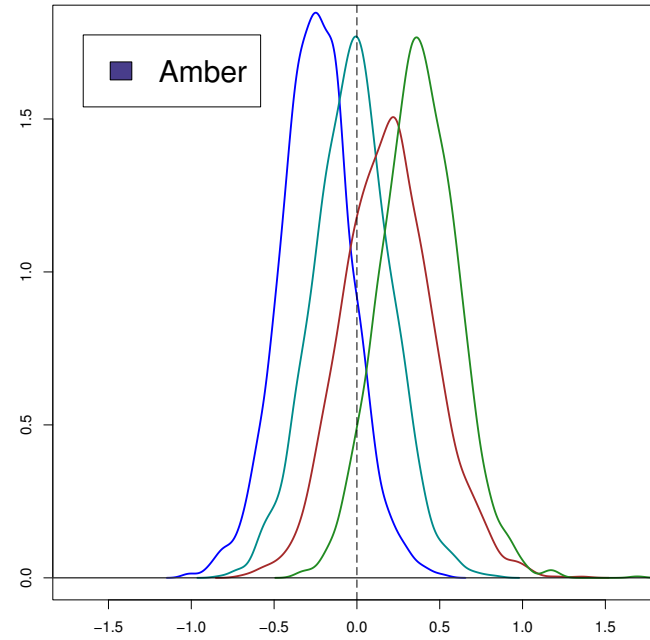
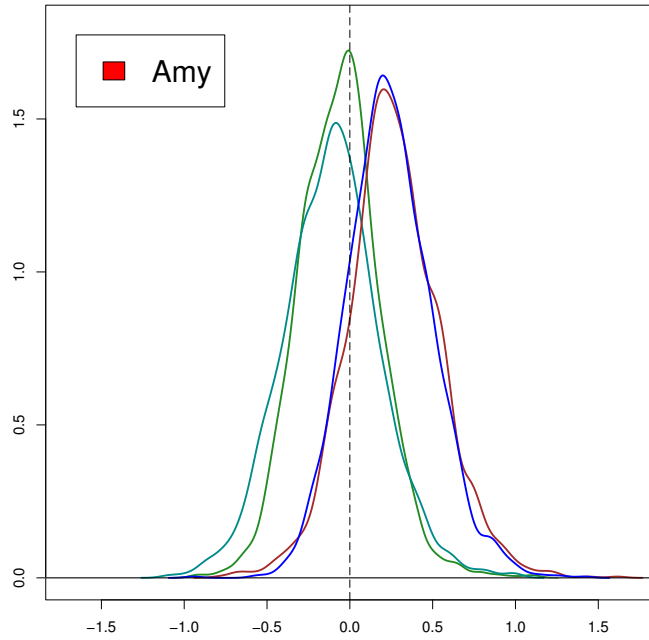
Wet Season with Genetics



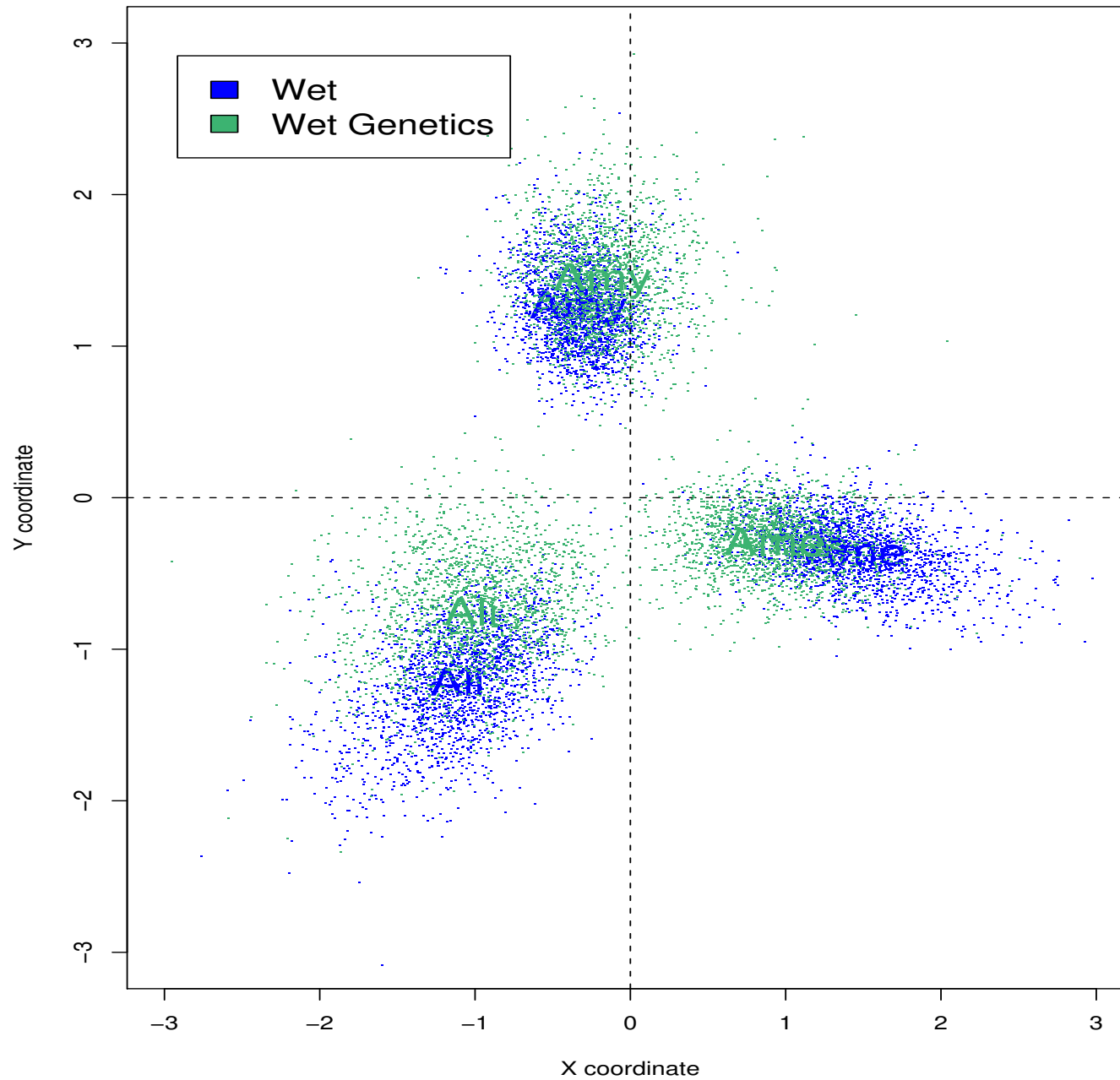
Amy Sociability Posterior Density



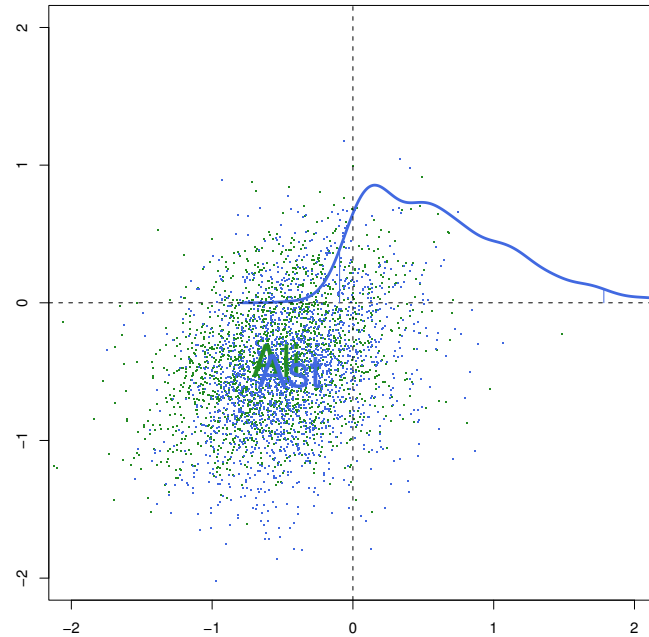
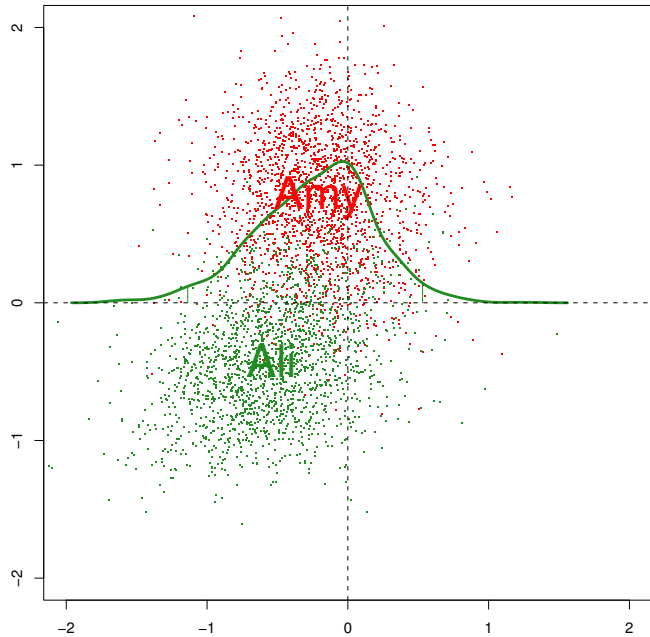
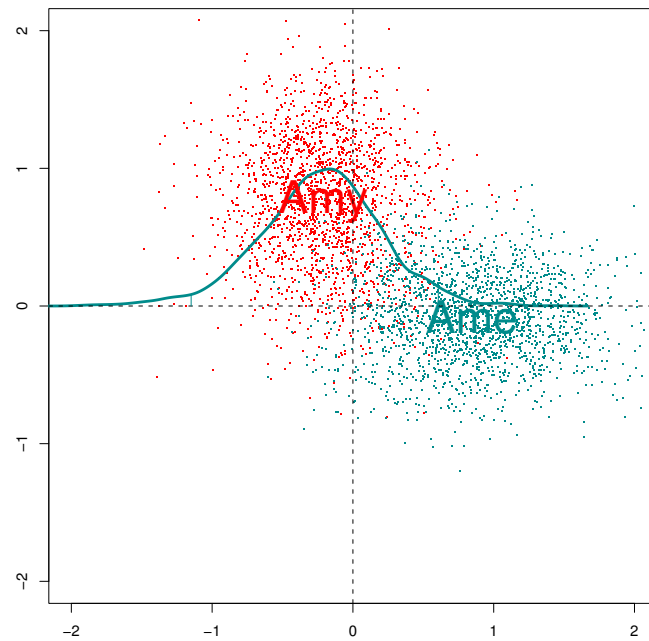
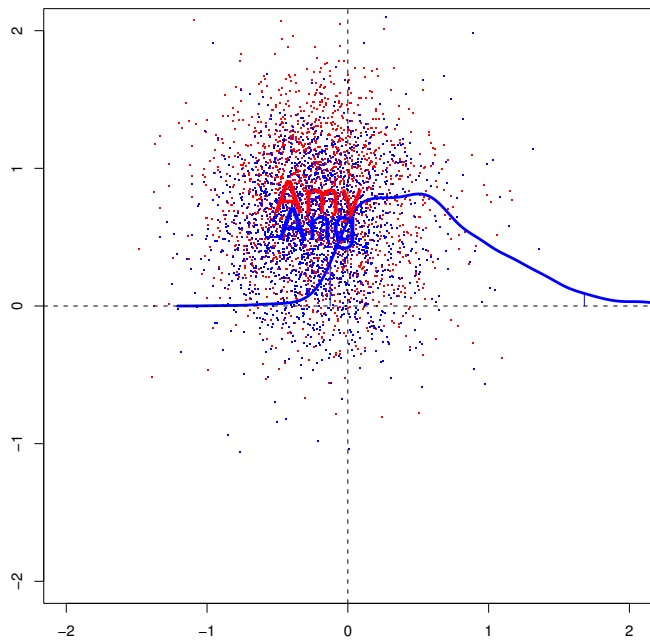
Posterior Sociabilities a_i



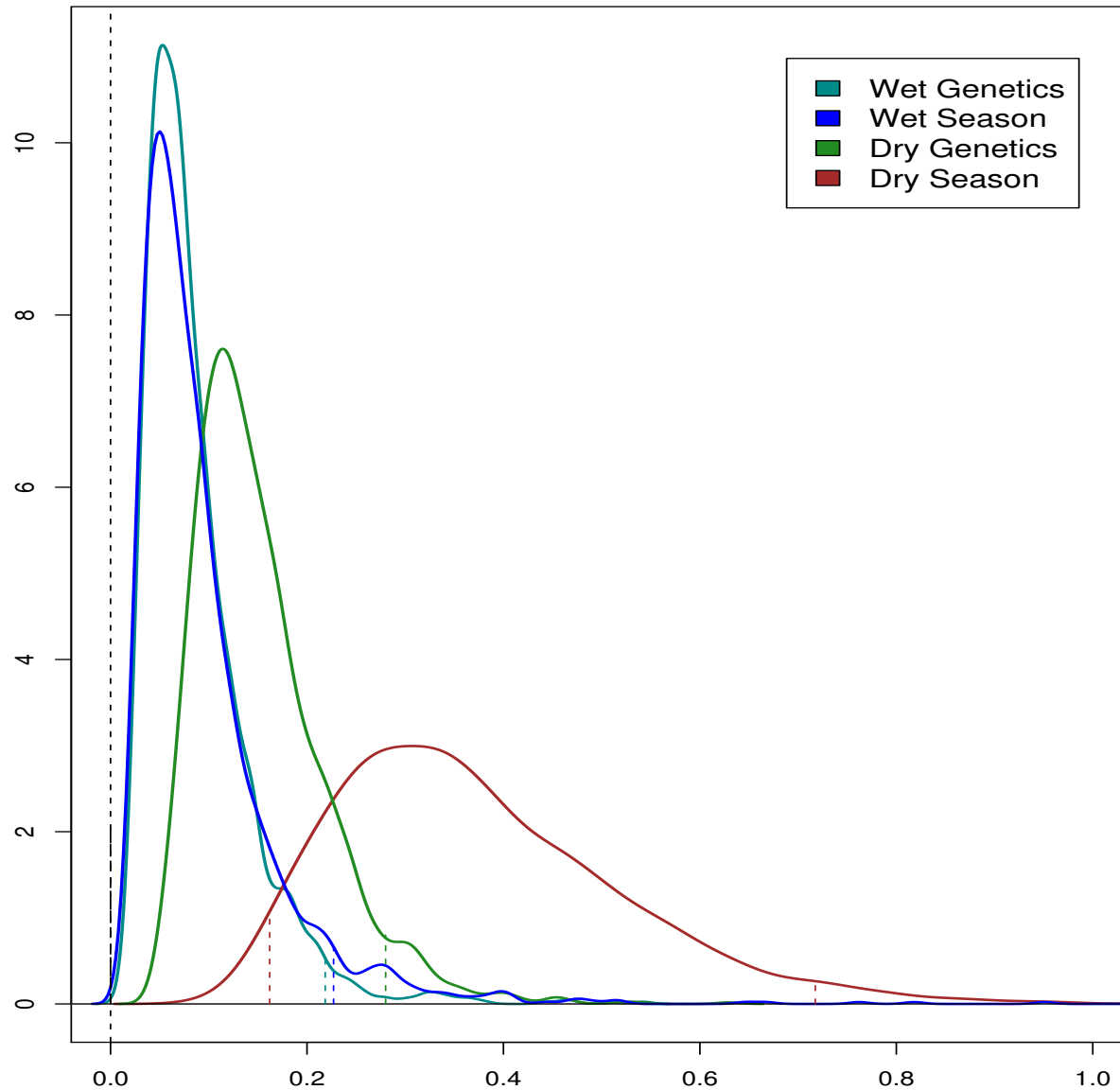
Three Elephants' Social Space Posterior Draws



Posterior Innerproducts $z_i'z_j$



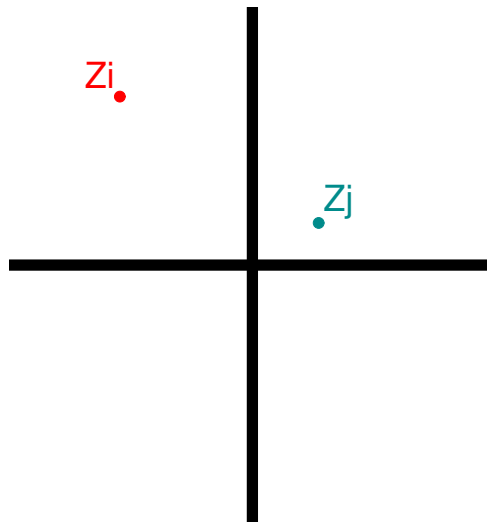
Posterior Normal Error σ_{γ}^2



$$\theta_{ij} = \left(\frac{1}{2}\beta_0 + \mathbf{a}_i\right) + \left(\frac{1}{2}\beta_0 + \mathbf{a}_j\right) + \beta_g \mathbf{g}_{ij} + \gamma_{ij} + \mathbf{z}'_i \mathbf{z}_j$$

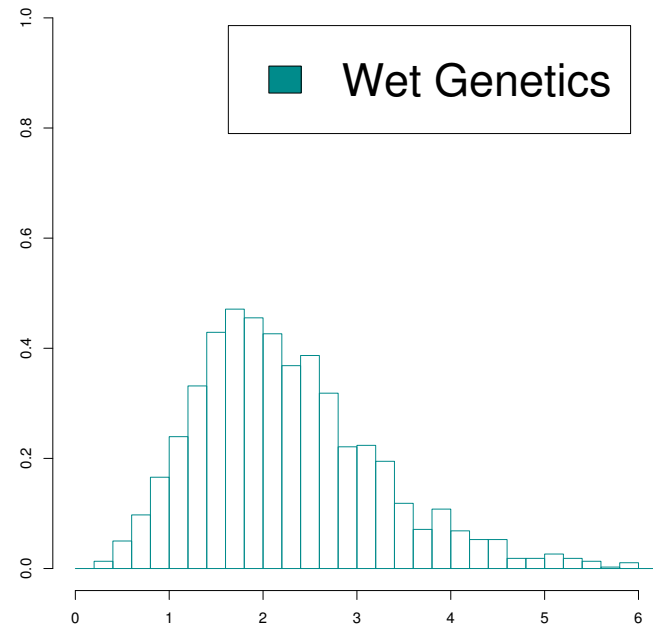
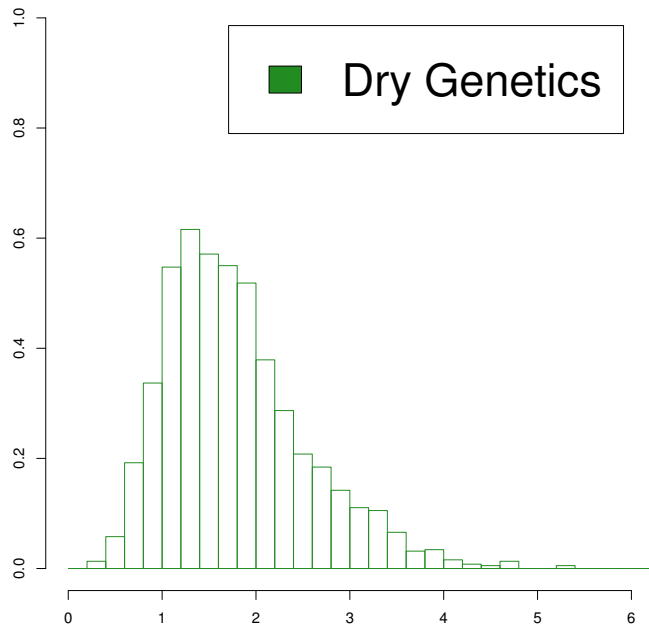
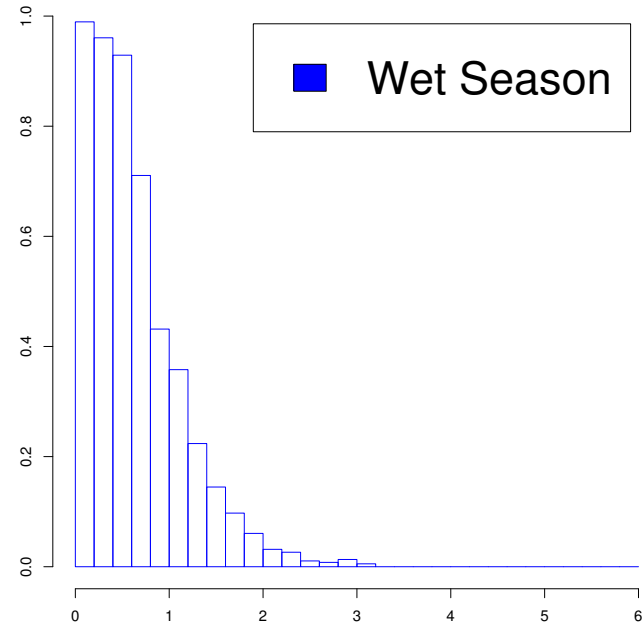
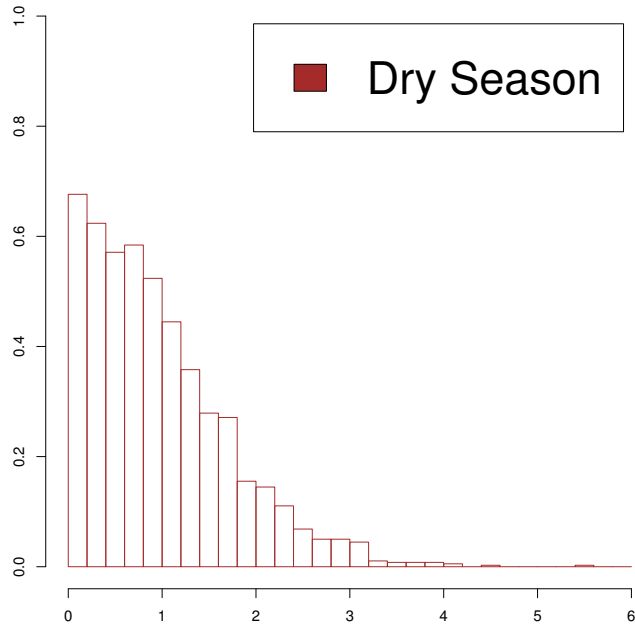
Pickiness in Social Space

- When an elephant is farther from the origin in social space, the inner product term increases and has a larger influence in the model.
- An elephant close to the origin will have a small pairwise effect in the model.
- Pickiness is defined as the length of the vector in social space $|\mathbf{z}_i|$.

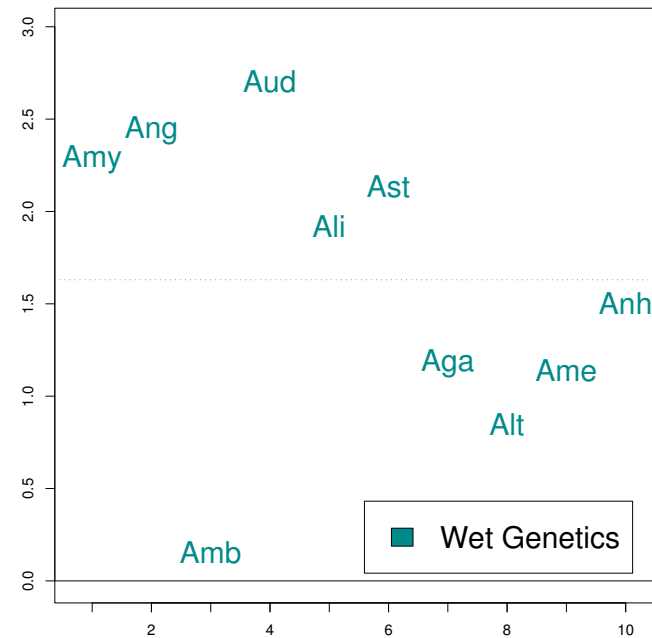
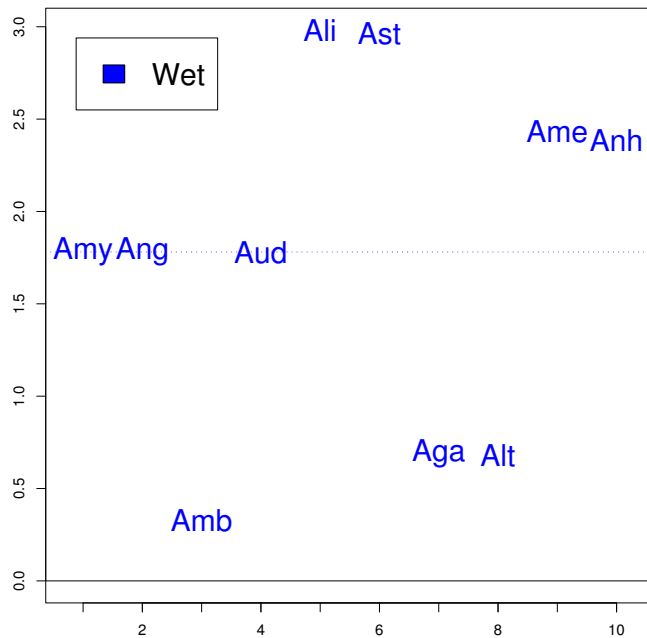
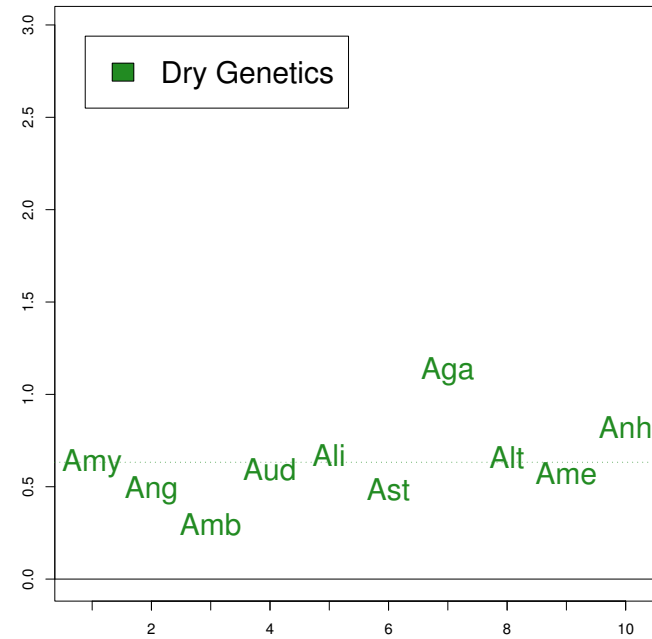
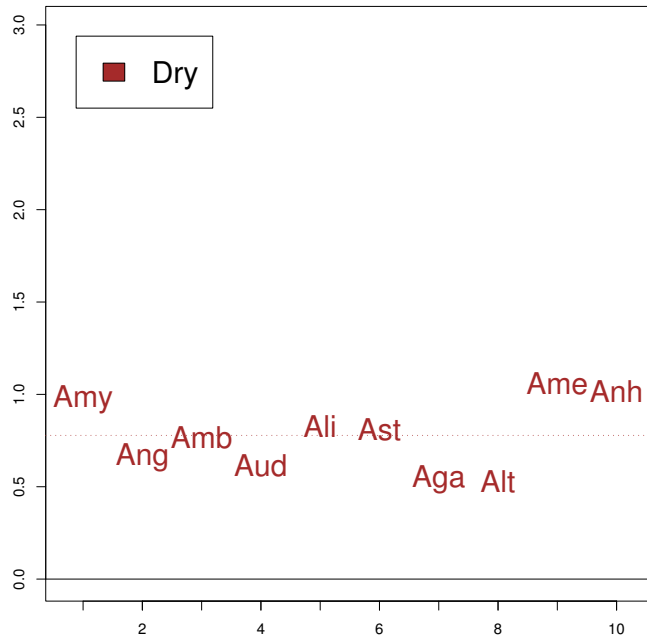


- Elephant i is “pickier” than elephant j .

Amy's Posterior Pickiness



Posterior Pickiness $|z_i|$



Family AA Observations

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

Genetic Relatedness

AA	Amy	Angelina	Amber	Audrey	Alison	Astrid	Agatha	Althea	Amelia
Amy									
Angelina	0.39								
Amber	0.46	0.26							
Audrey	0.31	0.22	0.11						
Alison	0.3	0.02	0.08	0.02					
Astrid	0.25	0.18	0.02	0.14	0.53				
Agatha	0.27	0.08	0.25	-0.15	0.38	0.34			
Althea	0.05	0.05	0.12	-0.01	0.15	0.21	0.46		
Amelia	0.35	0.06	-0.09	0.01	0.09	0.2	0.1	0.02	
Anghared	0.25	0.34	0.02	0.2	-0.06	0.1	0.06	-0.04	0.52