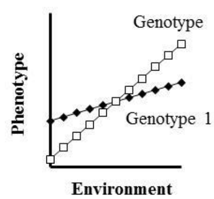
Estimation of GxE in animal breeding populations and implications of GxE for breeding programs

Han Mulder



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Contents

- Types of environments and size of GxE in animals
- Data structures to estimate GxE
- Dealing with GxE in breeding programs
- Statistical methods to estimate GxE in animal breeding
- Practical
  - Designs/data structures
  - Statistical analysis using ASReml

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Learning outcomes

- To design experiments/datasets for estimating genetic correlations between environments
- To understand the effect of G x E on breeding programs
- To use bivariate and random regression models to analyze genotype by environment interaction

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Types of environments and GxE found in animals

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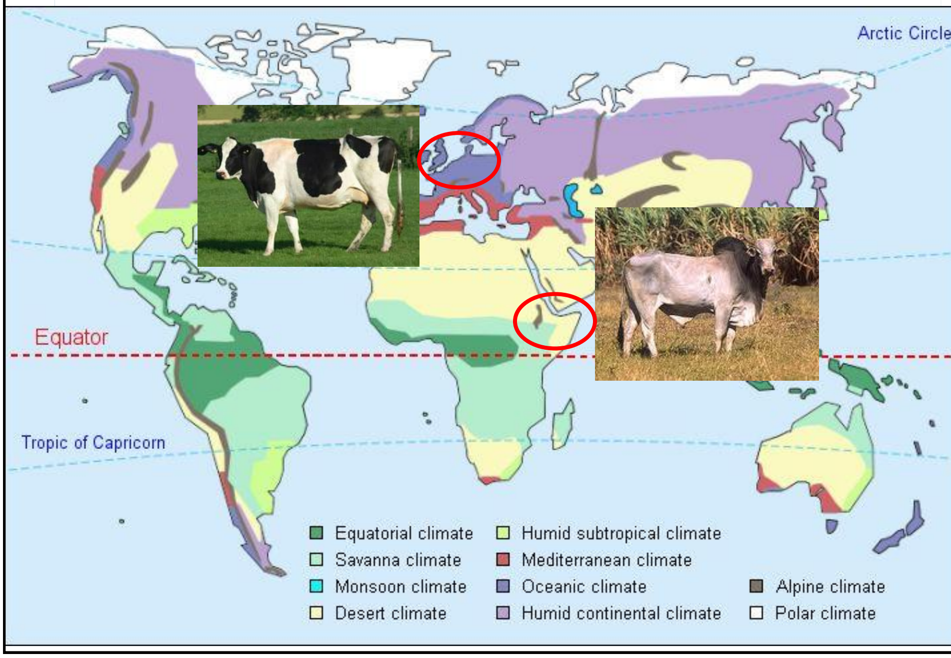

Environment can have many sights!

- Climate
- Housing system
- Nutrition
- Disease pressure
- Stocking density

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Different types of environments

- Mega-environments
  - Different countries, different climate zones
- Macro-environments
  - Different climates within farms
  - Different farm types (organic vs conventional)
- Micro-environments
  - Each animal has a different environments
  - Some animals diseased; others not

Different types of environments

- Types of environments
  - Categorical
    - Farm types
    - Presence or absence of disease
    - → bivariate/multivariate model
  - Continuous
    - Temperature
    - Daylength
    - Rainfall
    - → Reaction norm model

How to quantify size of GxE?

- In animal breeding: aim is genetic improvement of populations by selection
  - GxE causing reranking has biggest impact
- The degree of GxE is judged by the genetic correlations between environments
  - How much is the genetic correlation deviating from 1.0?

How large is G x E in livestock?

- In dairy cattle (many studies)
  - Production: >0.8
  - Fertility/longevity: 0.5-1.0
- In pigs (fewer studies)
  - 0.5-1.0 between environments with stress and without stress (e.g. disease, heat stress)
  - 0.6-1.0 between farms with different health status
- In poultry (very few studies)
  - 0.6-1.0 between nucleus and commercial environments

How large is G x E in aquaculture?

- Extensive review
  - Different species
  - Different traits
  - Different environments: temperature, diet, location, rearing and stocking density

Sae-Lim et al., 2015. Reviews in Aquaculture 7:1-25

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Table 5 Unweighted and weighted mean genetic correlations, number of observations (N), minimum (min) and maximum (max) by species and environments for growth traits

Species	Variable	Macro-environment[†]					Reference
		REAR	TEMP	DIET	DENT	LOCAT	
Nile tilapia	Mean[‡]	$0.77^{0.89}$				$0.71^{0.66}$	Eknath *et al.* (2007); Khaw *et al.* (2009); Thodesen *et al.* (2011); Bentsen *et al.* (2012); Khaw *et al.* (2012); Trọng *et al.* (2013); Luan (2010); Luan *et al.* (2008)
	N	57	–	–	–	3	
	Min–max	0.07 to 0.99				0.45 to 0.87	
Tilapia shiranus	Mean	$0.77^{0.80}$	–	–	–	–	Maluwa *et al.* (2006)
	N	3					
	Min–max	0.63 to 0.95					
Rainbow trout	Mean	$0.47^{0.46}$	0.36^{NA}	$0.86^{0.90}$	0.77^{NA}	–	McKay *et al.* (1984); Sylvén *et al.* (1991); Bagley *et al.* (1994); Kause *et al.* (2003, 2006); Pierce *et al.* (2008); Le Boucher *et al.* (2011a); Sae-Lim *et al.* (2013)
	N	25	2	23	10		
	min–max	0.15 to 0.86	0.18–0.54	0.55 to 1.00	0.56 to 0.90		
Atlantic cod	Mean	$0.89^{0.90}$	–	–	–	$0.89^{0.89}$	Kolstad *et al.* (2006b)
	N	2				2	
	Min–max	0.83 to 0.94				0.82 to 0.95	
Common carp	Mean	$0.84^{0.85}$	–	–	–	–	Ninh *et al.* (2011)
	N	3					
	Min–max	0.81 to 0.88					
European seabass	Mean	$0.73^{0.87}$	0.49^{NA}	$0.78^{0.99}$	0.51^{NA}	–	Saillant *et al.* (2006); Dupont-Nivet *et al.* (2008, 2010); Le Boucher *et al.* (2011b)
	N	18	1	7	1		
	Min–max	0.21 to 0.99	0.49	0.51 to 0.99	0.51		
Pacific white shrimp	Mean	$0.87^{0.93}$	–	–	$0.84^{0.83}$	–	Gitterle *et al.* (2005); Castillo-Juárez *et al.* (2007)
	N	14			3		
	Min–max	0.65 to 0.99			0.80–0.86		
Chinook Salmon	Mean	0.56^{NA}	–	–	–	–	Winkelman and Peterson (1994)
	N	6					
	Min–max	0.45 to 0.64					
Pacific oyster	Mean	$0.74^{0.89}$	–	–	–	$0.81^{0.84}$	Dégremont *et al.* (2007); Swan *et al.* (2007)
	N	16				27	
	Min–max	0.11 to 0.97				0.02 to 0.97	
Blue Mussel	Mean	–	–	–	–	0.58^{NA}	Mallet *et al.* (1986)
	N					1	
	Min–max					0.58	
European whitefish	Mean	–	–	0.97^{NA}	–	–	Quinton *et al.* (2007a)
	N			1			
	Min–max			0.97			
Common sole	Mean	$0.42^{0.40}$	–	–	–	–	Mas-Muñoz *et al.* (2013)
	N	2					
	Min–max	0.27 to 0.56					
Asian seabass	Mean	0.99^{NA}	–	–	–	–	Domingos *et al.* (2013)
	N	2					
	Min–max	0.98 to 0.99					
Red tilapia	Mean	$0.72^{0.78}$	–	–	–	–	Thodesen *et al.* (2013)
	N	7					
	Min–max	0.24 to 1.00					

Sae-Lim et al., 2015. Reviews in Aquaculture 7:1-25

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Data structures to estimate G x E

Data structures to estimate G x E

- Categorical environments

- Measure genotype in different environments
  - Ideal design: animal itself or clones
  - Often animals perform in only one environment

- In animal breeding: no clones, no experiments!
  - Extensive databases with animal phenotypes and pedigree
  - High-density SNP-genotypes

How to estimate G x E?

- Usually pedigree links
  - Use of additive genetic relationships
  - E.g. half-sisters in different environments
  - Grand-offspring in different environments
  - E.g. less related individuals
- Use of genomic relationships
  - Example Silva et al. (2014; J. Anim. Sci. 92:3825-3834)

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What kind of design is really needed?

- How much does the design affect the standard error on estimated genetic correlation?
  - How many families do we need with offspring in both environments?
    - N
  - How large should families be?
    - Number of offspring per environment: n
  - What is the effect of the heritability?
    - h^2

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Standard error to estimate genetic correlation: Robertson (1959; Biometrics)

- Other formula
- $\mathrm{se}\left(r_g\right) \approx \sqrt{\frac{\left[1+nt(1-r_g^2)\right]^2+r_g^2}{(N-1)n^2t^2}}$
- t =intraclass correlation, e.g. $t = 0.25h^2$ for half-sibs

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Bijma and Bastiaansen (2014, GSE)

- $\mathrm{se}\left(r_g\right) \approx \sqrt{\frac{\frac{1}{r_{IH,x}^2 r_{IH,y}^2}+(1+\frac{0.5}{r_{IH,x}^4}+\frac{0.5}{r_{IH,y}^4}-\frac{2}{r_{IH,x}^2}-\frac{2}{r_{IH,y}^2})r_g^2+r_g^4}{(N-1)}}$
- $r_{IH,x}^2$= reliability of EBV in environment x = accuracy squared

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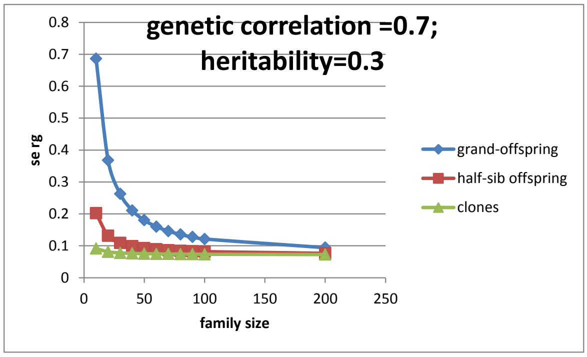
The effect of family size on se(rg)



100 families

- Need many more grand-offspring than half-sib offspring/clones
- Clones is most efficient, but not feasible in livestock

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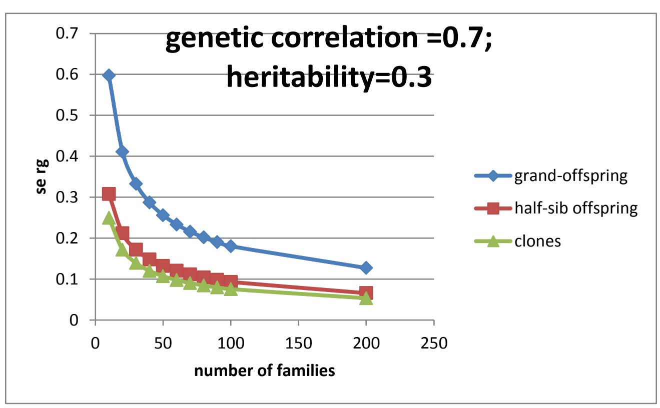
Bijma and Bastiaansen, 2014

The effect of number of families on se(rg)

50 offspring per family per environment



Need 50-100 families to get accurate estimate of genetic correlation

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Bijma and Bastiaansen, 2014

Summary

- Large datasets required to estimate genetic correlations between environments
  - 50-100 families
  - Each with 50-100 offspring
- Clones slightly better than half-sibs, grand-offspring is quite a bit worse than half-sibs

Deal with GxE in breeding programs

Different situations:
1. Nucleus and commercial environment

- Typically selection environment (SE) and production environment (PE) different
  - SE: higher health status, less diseases, optimal management
  - PE: higher disease pressure, lower management level, in pigs and poultry crossbred animals

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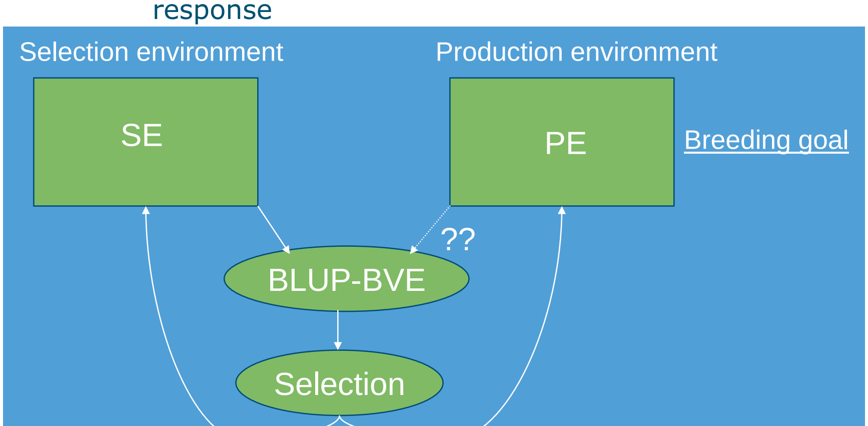
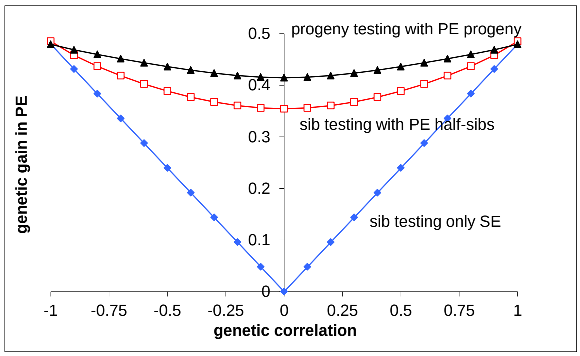
G x E: nucleus and production environment

- Only information from nucleus, but breeding goal is commercial environment
  - Genetic gain in commercial environment is correlated response



G x E: nucleus and production environment

- Use of sib/progeny information from commercial environment



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Mulder and Bijma, 2004; J. Anim. Sci.

Different situations: 2. Multiple production environments

- Breeding organization are international
- Multiple production environments
  - Different climates
  - Within countries different types of farms
    - Organic and conventional
    - Management level
    - Barn type
    - Disease status
    - Grazing and non-grazing

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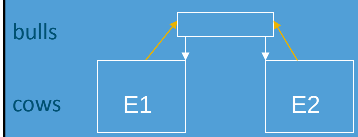
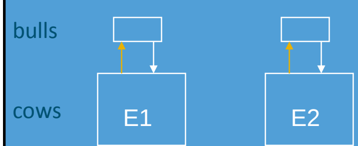
G x E: How many lines/breeding programs?

Breeding strategies

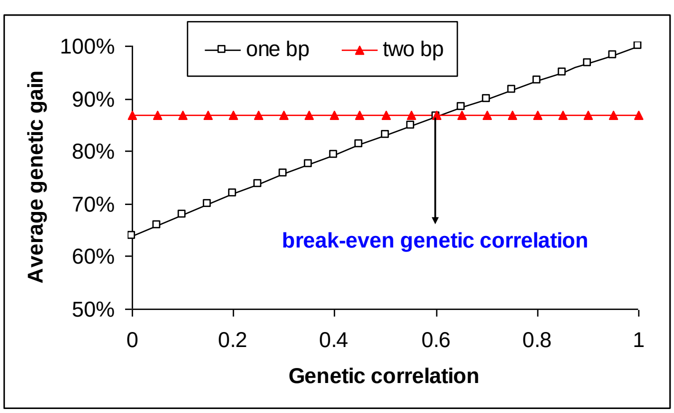


One breeding program
- all 400 bulls tested in both environments: 50 daughters in each environment
- increase average performance



Two breeding programs
- 200 bulls tested in one environment: 100 daughters in one environment
- Each bp: increase performance in environment of testing

G x E: How many lines/breeding programs?



Mulder et al., 2006; J. Dairy Sci.

G x E and multi-trait selection

- Between environments
  - G x E per trait
  - Heterogeneity of genetic variances
  - Breeding goal differences
  - Different genetic correlations between traits
- **Genetic correlation between breeding goals**
- $r_{H,kl} = \frac{\mathbf{v_k'Gv_l}}{\sqrt{\mathbf{v_k'Gv_k v_l'Gv_l}}}$
- $\mathbf{G}$: full genetic variance-covariance matrix between all traits in the breeding goals of environment k and l
- $\mathbf{v_k}$: economic values for environment k
- $\mathbf{v_l}$: economic values for environment l

(Mulder, 2007)

Summary

- G x E lowers genetic gain, but more genetic diversity is conserved
- Nucleus and production environment
  - Minimize environmental difference
  - Use phenotypes of sibs or progeny in multivariate breeding value estimation
- Different production environments
  - If rg>0.6-0.7 then single breeding program (provided that information of sibs/progeny is collected in both environments)
  - If rg<0.6-0.7, then different breeding programs needed

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Statistical methods to estimate GxE in animal breeding

Statistical methods to estimate G x E in animal breeding populations

- We use pedigree relationships and we use BLUP
- Main interest in additive genetic effects or breeding values
- Most common models to analyze G x E
  - Bivariate/multivariate models
  - Reaction norm/random regression models

BLUP

- $y = \mu + herd + animal + e$
- y = phenotype
- μ = fixed mean
- $herd$ = fixed effect for herd
- $animal$ = random additive genetic effect = EBV
- e = residual

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BLUP mixed model equations

- $\mathbf{y} = \mathbf{Xb} + \mathbf{Za} + \mathbf{e}$
- $\mathbf{X}$=design matrix to link phenotypes to fixed effects, e.g. which cow is in which herd
- $\mathbf{b}$=vector with solutions for fixed effects
- $\mathbf{Z}$=design matrix to link phenotypes to EBV
- $\mathbf{a}$=vector with EBV for all animals
- $\begin{bmatrix} \mathbf{X'X} & \mathbf{X'Z} \\ \mathbf{Z'X} & \mathbf{Z'Z} + \lambda\mathbf{A}^{-1} \end{bmatrix} \begin{bmatrix} \mathbf{b} \\ \mathbf{a} \end{bmatrix} = \begin{bmatrix} \mathbf{X'y} \\ \mathbf{Z'y} \end{bmatrix}$
- $\lambda = \frac{\sigma_e^2}{\sigma_a^2}$
- $\mathbf{A}^{-1}$=inverse of additive genetic relationship matrix

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Breeding values Holstein bulls

	kg milk	%fat	%protein	kg fat	kg protein	total merit index milk	total merit index NVI
Bookem	+1552	-0.29	-0.11	+37	+43	+275	+299
G-Force	+771	+0.16	+0.13	+48	+39	+271	+246
Atlantic	+298	-0.06	+0.14	+7	+23	+110	+245
Titanium	+645	+0.21	+0.01	+47	+23	+199	+234
Snowman	+2576	-0.37	-0.29	+69	+57	+415	+228

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Bivariate model to estimate GxE

- $\begin{bmatrix}\mathbf{y}_1\\ \mathbf{y}_2\end{bmatrix} = \begin{bmatrix}\mathbf{X}_1 & \mathbf{0}\\ \mathbf{0} & \mathbf{X}_2\end{bmatrix}\begin{bmatrix}\mathbf{b}_1\\ \mathbf{b}_2\end{bmatrix} + \begin{bmatrix}\mathbf{Z}_1 & \mathbf{0}\\ \mathbf{0} & \mathbf{Z}_2\end{bmatrix}\begin{bmatrix}\mathbf{a}_1\\ \mathbf{a}_2\end{bmatrix} + \begin{bmatrix}\mathbf{e}_1\\ \mathbf{e}_2\end{bmatrix}$
- $\begin{bmatrix}\mathbf{a}_1\\ \mathbf{a}_2\end{bmatrix} \sim \mathrm{N}\left[\begin{matrix}\mathbf{0}\\ \mathbf{0}'\end{matrix}, \mathbf{A} \otimes \begin{bmatrix}\sigma^2_{a1} & \sigma_{a1,a2}\\ symmetric & \sigma^2_{a2}\end{bmatrix}\right]$
- $\begin{bmatrix}\mathbf{e}_1\\ \mathbf{e}_2\end{bmatrix} \sim \mathrm{N}\left[\begin{matrix}\mathbf{0}\\ \mathbf{0}'\end{matrix} \begin{matrix}\mathbf{I}_1 I\sigma^2_{e1} & \mathbf{0}\\ \mathbf{0} & \mathbf{I}_2\sigma^2_{e2}\end{matrix}\right]$
- no residual covariances between environments if animals are in one environment
- $\boldsymbol{rg} = \boldsymbol{r_a} = \frac{\sigma_{a1,a2}}{\sigma_{a1}\sigma_{a2}}$

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Reaction norm models

- $y = fixed\ effects + bx + a_{int} + a_{sl}x + e$
- Fixed reaction norm: bx
- $\begin{bmatrix} \mathbf{a_{int}} \\ \mathbf{a_{sl}} \end{bmatrix} \sim \mathrm{N}\begin{bmatrix} \mathbf{0} \\ \mathbf{0}' \end{bmatrix}, \mathbf{A} \otimes \begin{bmatrix} \sigma^2_{aint} & \sigma_{aint,asl} \\ symmetric & \sigma^2_{asl} \end{bmatrix}$
- **A** = matrix with all additive genetic relationships
- Heterogeneity of residual variance accounted for using 3-10 groups each with their own residual variance

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Issues with reaction norms models

1. Which covariate to use?
   1. External environmental factor
   2. Internal data derived parameter
2. Scaling and (Legendre) polynomials
3. Model comparison
4. Interpretation of results

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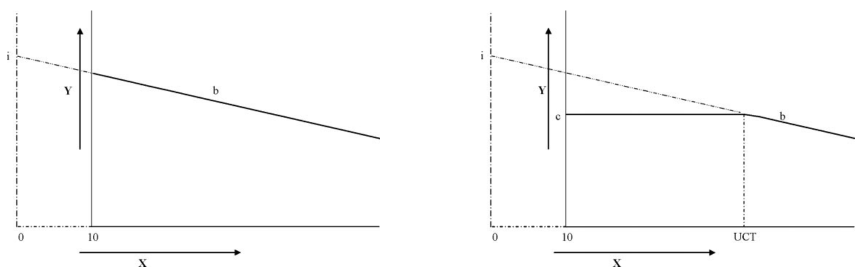
1. Which covariate to use?

External and internal environmental factors

- External environmental factors
  - Temperature
  - Day length
  - Rainfall
  - Salinity, oxygen (fish)
  - ...
- Internal derived environmental factors
  - Finlay-Wilkinson regression
  - Mean performance
  - Herd-year-season estimated effect

Temperature

- Temperature may affect phenotypes only above a certain temperature, the so-called upper critical temperature



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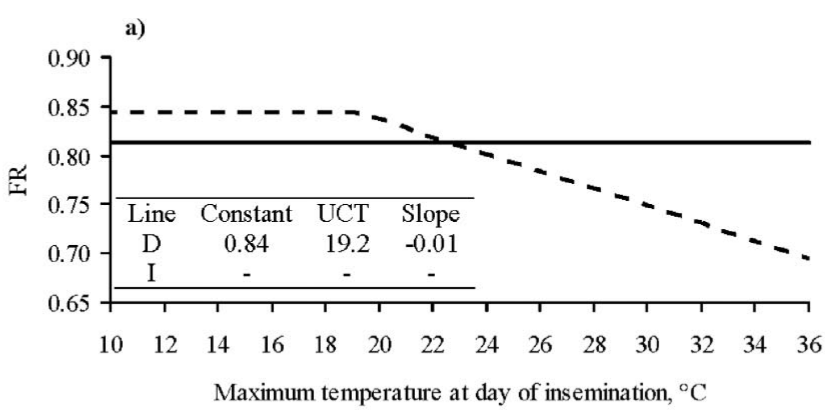
Bloemhof et al., 2008. J. Anim. Sci. 86:3330–3337

Upper critical temperature: Farrowing rate at first insemination



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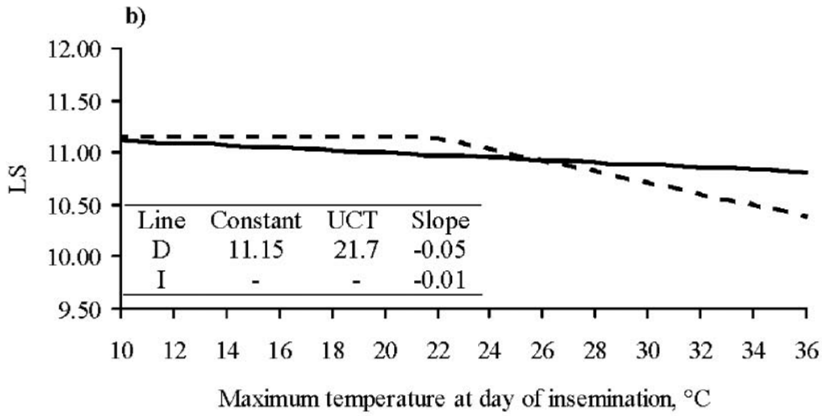
Bloemhof et al., 2008. J. Anim. Sci. 86:3330–3337

Upper critical temperature: litter size



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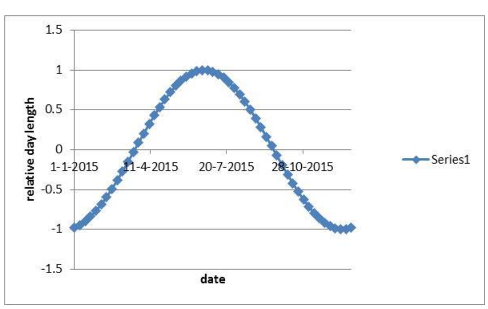
Bloemhof et al., 2008. J. Anim. Sci. 86:3330–3337

Day length

- Day length is according to a sinus function



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Sevillano et al., 2016. J. Anim. Sci.

Internal data derived parameter: The use of herd-year-season estimates

- In many studies, it is difficult to categorize farms
  - No access to external data
  - HYS gives indication of management level, but may also contain the genetic level of the herd
- Strategy
  - Estimated herd-year-season effects on the same data using mixed model
  - Add to the data set and use random regression
  - Use of data twice = tricky

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Possible solutions

- Derive environmental parameters (EP) from other traits
  - Calus et al. (2003; J. Dairy Sci. 86: 3756-3764)
- Use other animals to calculate the EP
- Use many animals to estimate EP, dependency is smaller
  - Avoid very small HYS classes
  - Include all parities

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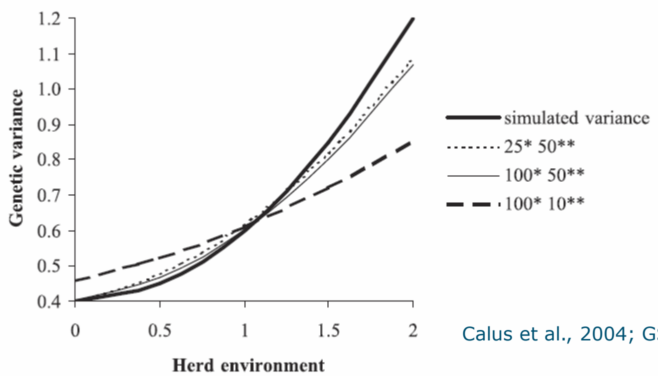
Consequences for estimation of G x E

- Reaction norm models tend to underestimate G x E
  - Underestimation of the genetic variance in slope
  - Correlations closer to 1.0 than the true value



Calus et al., 2004; GSE 36:489-507

Possible solution

- Bayesian approach
  - The x-variable is simultaneously sampled with the breeding values and the other effects in the model

Table 1. Mean and SE of estimates (based on posterior means) of (co)variance components over 20 replicate simulations

Model[1]	$\sigma^2_{a_0}$	$\sigma^2_{a_h}$	$\sigma_{a_0 a_h}$	σ^2_e
Realized[2]	100.4 ± 0.040	1.01 ± 0.002	5.11 ± 0.065	298.3 ± 0.016
M1[3]	101.7 ± 1.102	1.02 ± 0.034	5.04 ± 0.101	297.1 ± 0.872
M2[4]	99.3 ± 1.051	1.01 ± 0.013	5.00 ± 0.080	298.5 ± 0.868
M3[5]	111.5 ± 1.440	0.58 ± 0.020	3.68 ± 0.105	305.5 ± 0.702

[1] $\sigma^2_{a_0}$ = variance of the level; $\sigma^2_{a_h}$ = variance of the slope of additive genetic reaction norm; σ_{a_0,a_h} = covariance between the level and the slope; and σ^2_e = residual variance.
[2] The variance components were calculated from the realized values of the simulation.
[3] Model with unknown covariate of reaction norm (the proposed approach).
[4] Model using true herd-year effect as covariate of reaction norm.
[5] Model using phenotypic mean of herd-year as covariate of reaction norm.

Su et al., J. Anim. Sci. 84:1651-1657

2. Scaling and (Legendre) polynomials

Do we need polynomials?

- Linear reaction norm
  - No need for use of polynomials
  - Would give equivalent results
- Higher order reactions norms
  - Yes, performance of REML or Gibbs much better

Linear reaction norm models without polynomials

- Scaling of covariate mean = 0, variance 1.0
  - The correlation between intercept and slope has a meaning when selection is performed in the average environment
  - Variance of 1.0 makes it feasible to compare estimates of genetic variance in slope when using different covariates

Higher reaction norms: Legendre polynomials

- They are orthogonal
  - Lower correlations between regression coefficients – faster convergence
- Scale the EP to be between -1 and 1
- $x_l = -1 + 2 * \left(\frac{EP_l - EP_{min}}{EP_{max} - EP_{min}}\right)$

(Schaeffer, Random regression models: http://www.aps.uoguelph.ca/~lrs/ABModels/NOTES/RRM14a.pdf

Legendre polynomials

- Legendre polynomial coefficient order n>1, recursive equation:
- $P_0 = 1$
- $P_1 = x$
- $P_{n+1}(x) = \frac{1}{n+1}((2n+1)xP_n(x) - n(P_{n-1}(x))$
- $\phi_n(x) = \left(\frac{2n+1}{2}\right)^{0.5} P_n(x)$

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(Schaeffer, Random regression models: http://www.aps.uoguelph.ca/~lrs/ABModels/NOTES/RRM14a.pdf

Example polynomial coefficients

x	x scaled	P0	P1	P2	$\phi 0$	$\phi 1$	$\phi 2$
100	0.33	1.00	0.33	-0.33	0.71	0.41	-0.53
200	0.67	1.00	0.67	0.17	0.71	0.82	0.26
300	1.00	1.00	1.00	1.00	0.71	1.22	1.58
-100	-0.33	1.00	-0.33	-0.33	0.71	-0.41	-0.53
-200	-0.67	1.00	-0.67	0.17	0.71	-0.82	0.26
-300	-1.00	1.00	-1.00	1.00	0.71	-1.22	1.58
0	0.00	1.00	0.00	-0.50	0.71	0.00	-0.79

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3. Model comparison

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Significance of model

- Likelihood ratio test
- H0: model with only intercept
- H1: model with intercept and slope
- The likelihood ratio:
- $D = 2logL(full\ model) - 2logL(reduced\ model)$
- If the hypothesis contains a parameter on the boundary, then D follows a mixture of Chi-square distributions

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Which degrees of freedom?

- Suppose the model under H0 estimates:
- $G = \begin{bmatrix} \sigma^2_{aint} & 0 \\ 0 & 0 \end{bmatrix}$
- The model under H1:
- G= $\begin{bmatrix} \sigma^2_{aint} & \sigma_{aint,asl} \\ symmetric & \sigma^2_{asl} \end{bmatrix}$
- The large sample distribution is:
- Mixture of χ^2_1 and χ^2_2

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Visscher, 2006; Twin research and human studies 9: 490-495
Stram and Lee, 1994; Biometrics 50:1171-1177

In more general terms

- Model H0:
- $G = \begin{bmatrix} \mathbf{D_0} & 0 \\ 0 & 0 \end{bmatrix}$
- $\mathbf{D_0}$ is a matrix with dimension q * q
- Model H1:
- $G = \mathbf{D_1} = \begin{bmatrix} \mathbf{D_0} & d12 \\ d21 & d22 \end{bmatrix}$
- $\mathbf{D_1}$ is a matrix with dimension (q+1) * (q+1)
- The large sample distribution is:
- Mixture of χ^2_q and χ^2_{q+1}

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Stram and Lee, 1994; Biometrics 50:1171-1177

Other model comparisons

- Akaike's information criterion:
- $AIC = -2LogL + 2t$
- t = number of variance parameters in the model

- Bayesian information criterion (more conservative):
- $BIC = -2LogL + 2tlog(v)$
- v = residual degrees of freedom

- AIC/BIC are not tests for significance
- AIC/BIC favour the most parsimonious model

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Other model comparisons

- Check the genetic parameters obtained from reaction norm model with a bivariate model

- Reaction norm models may lead to:
  - Extreme heritabilities in extreme environments
  - Low genetic correlation between extreme environments

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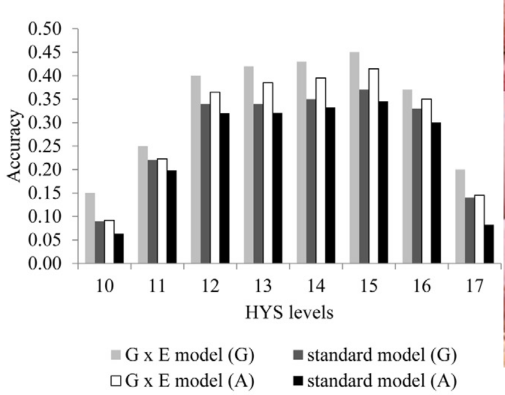
Other model comparisons

- Predictive ability
- Cross-validation
  - Predict the phenotype or adjusted phenotype in the validation set

Accuracy of genomic and pedigree breeding values



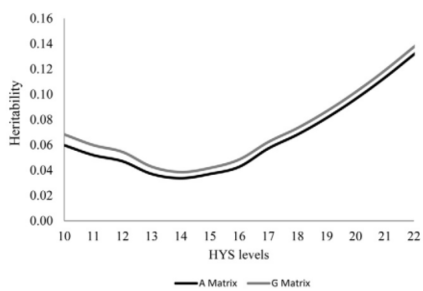
Silva et al., 2014; J. Anim. Sci. 92:3825–3834

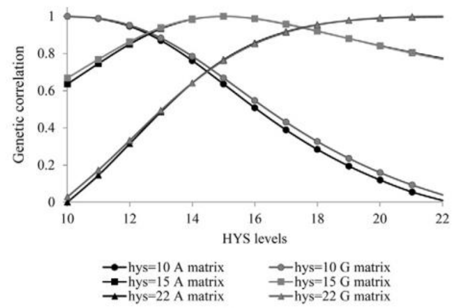
4. Interpretation of results

Calculation of genetic parameters

- Genetic variance-covariance matrix between different environments
- $\mathbf{H} = \mathbf{\Phi G \Phi}'$
- $\mathbf{G}$ = matrix estimated (co)variances for the different orders of the polynomial
- $\mathbf{\Phi}$ =matrix with ϕ values for the orders of the polynomial for the environments of interest.

Genetic parameters using genomic or pedigree relationship matrix (litter size)





Trait: litter size
Environments: Large White sows in 22 countries

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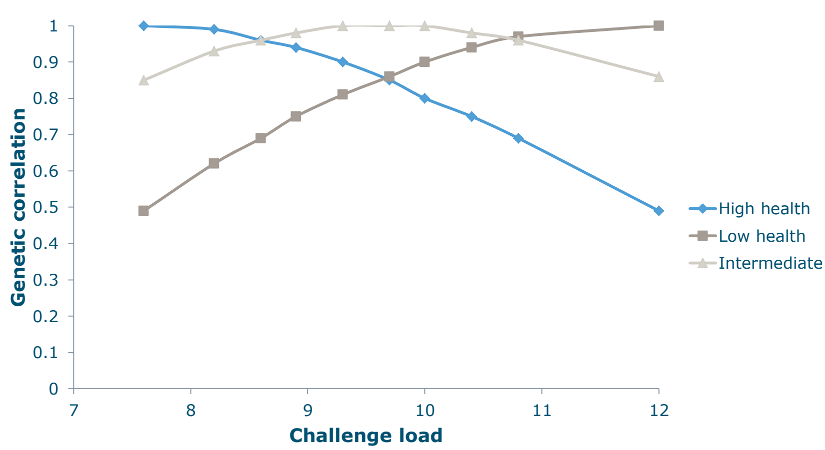
Silva et al., 2014; J. Anim. Sci. 92:3825–3834

Genetic correlations between different environments



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Herrero-Medrano et al., 2015; J. Anim. Sci. 93:1494-1502

Running ASREML with reaction norms

- ASREML mean model iteration1
- animal !P
- sire
- dam
- herd
- hys
- Am
- Asl
- Av
- x #!-1 # you can shift the intercept if you want
- E
- Pheno

- ped.dat !make
- cows_asreml.dat !MAXIT 100

- Pheno ~ mu !r animal animal.x
- 1 1 1
- 10000
- animal 2
- 2 0 US 0.3 0.0 0.05
- animal

Running ASReml

- Use ASREML-W

- Or with a batch-file

Summary

- Bivariate models and reaction norm models can be used to estimate G x E
- Reaction norm models are more complex
  - Heritabilities and genetic correlations for every set or pair of environments
- Different environmental parameters can be used
  - Be careful when using HYS

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