Genomic Selection: Promise And Concerns

William Muir
Purdue University

Poultry Genetics, Breeding and Biotechnology

Edited by W.M. Muir and S.E. Aggrey

CABI Publishing
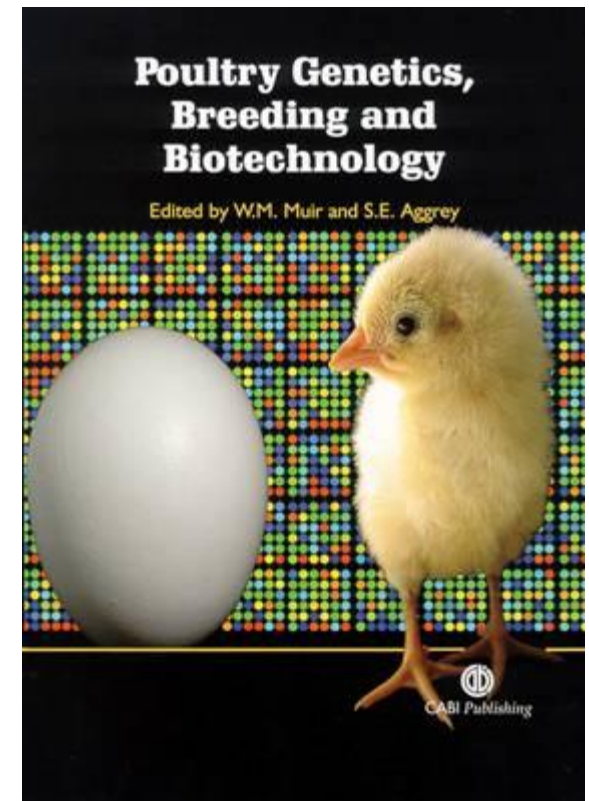
Efficiency of MAS Relative to Individual Selection

Proportion of genetic variation explained by the markers
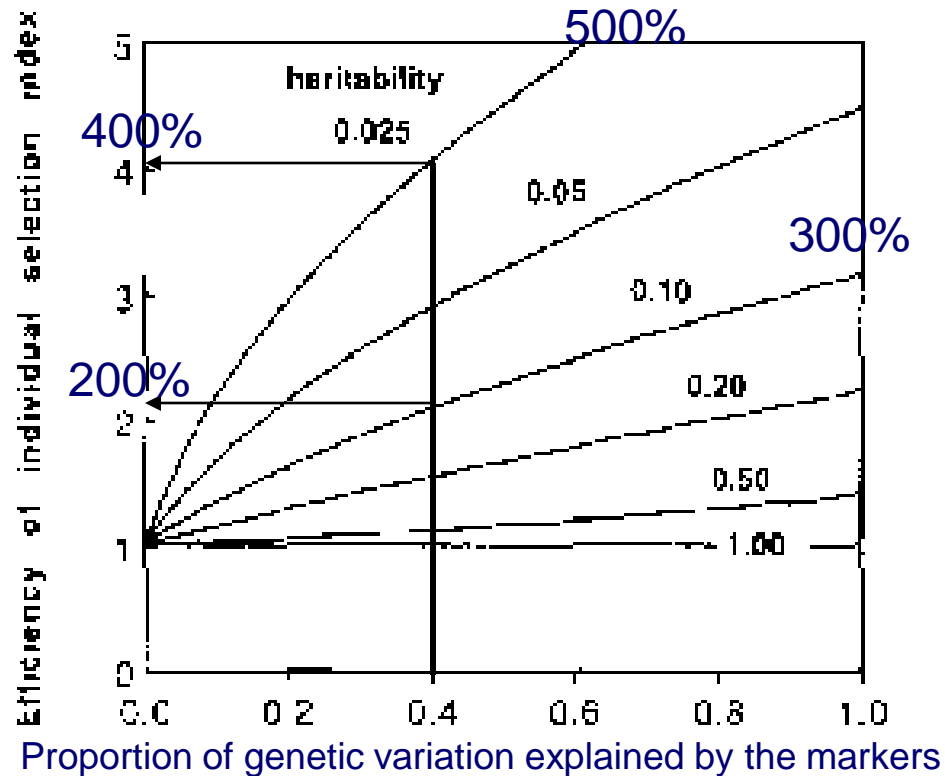
Lande and Thompson (1990)

Problem: Cannot identify QTL that account for even moderate proportion of genetic variation with lowly heritable traits
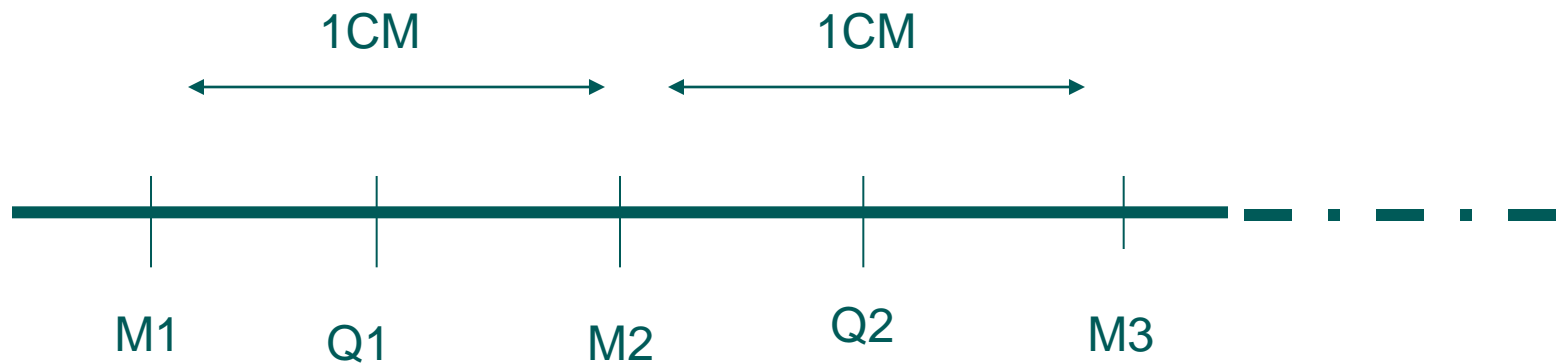
Detection of QTL

- Also requires phenotypic data
- Low Heritability Traits
  - Cannot Establish Marker-QTL associations
  - MAS is Most Needed for Such Traits

PARADOX

Potential Solution

- Genome Wide MAS (GMAS)
  - Meuwissen et al 2001
  - Uses all Markers
  - Dense
    - Every 1cM

Implementation (Meuwissen et al, 2001)

- Combine All Data In Mixed Model
  - QTL effect Assumed Sampled From Distribution
  - Random Effect

Estimation

$$Y = XB + ZG + \varepsilon$$

where G_i represents the genetic effect of the ith haplotype, Z_i is an incidence matrix and has a 0, 1, 2 for the number of haplotypes of type G_i present in the jth animal

Prediction

$$\widehat{Y}_j = GEBV = \sum_i Z_i \hat{G}_i$$

Estimation

- Requires Multiple Generations of Data
  - All Individuals
    - Genotyped at All Loci (Z matrix)
    - Phenotypes Measured for All Traits (Y Matrix)
      - As Many Traits as Desired
    - Fixed Effects (Age, Sex, Block, etc)
      - Recorded
      - (X Matrix)

$$Y = XB + ZG + \varepsilon$$

Maximum Likelihood Estimation of B and G

$$\begin{bmatrix} \mathbf{X'X} & \mathbf{X'Z} \\ \mathbf{Z\,X'} & \mathbf{Z'Z} + \dfrac{\sigma_e^2}{\sigma_g^2}\mathbf{I} \end{bmatrix} \begin{bmatrix} \boldsymbol{\beta} \\ \mathbf{G} \end{bmatrix} = \begin{bmatrix} \mathbf{X'Y} \\ \mathbf{Z'Y} \end{bmatrix}$$

Assumes that genetic variance associated with each marker is equal to the total genetic variance divided by the total number of makers (Bayesian Ridge Regression)

How Well Does it Work?

Compare Accuracy of
Genomic EBV (GEBV) With
BLUP EBV (BEBV)
Using Gene Level Simulations

Assumptions are Critical

- All MAS requires Linkage Disequilibrium (LD)
  - What is LD
  - How is it generated

Linkage Disequilibrium

Genotype/Haplotype   Frequency

$$\frac{m^A \qquad Q^B}{m^a \qquad Q^b}$$ Coupling Phase   p(AB/ab)

$$\frac{m^A \qquad Q^b}{m^a \qquad Q^B}$$ Repulsion Phase   p(Ab/aB)

LD=p(AB/ab)-p(Ab/aB)

Any factor changing the relative frequency of coupling *vs.* repulsion phase impacts LD

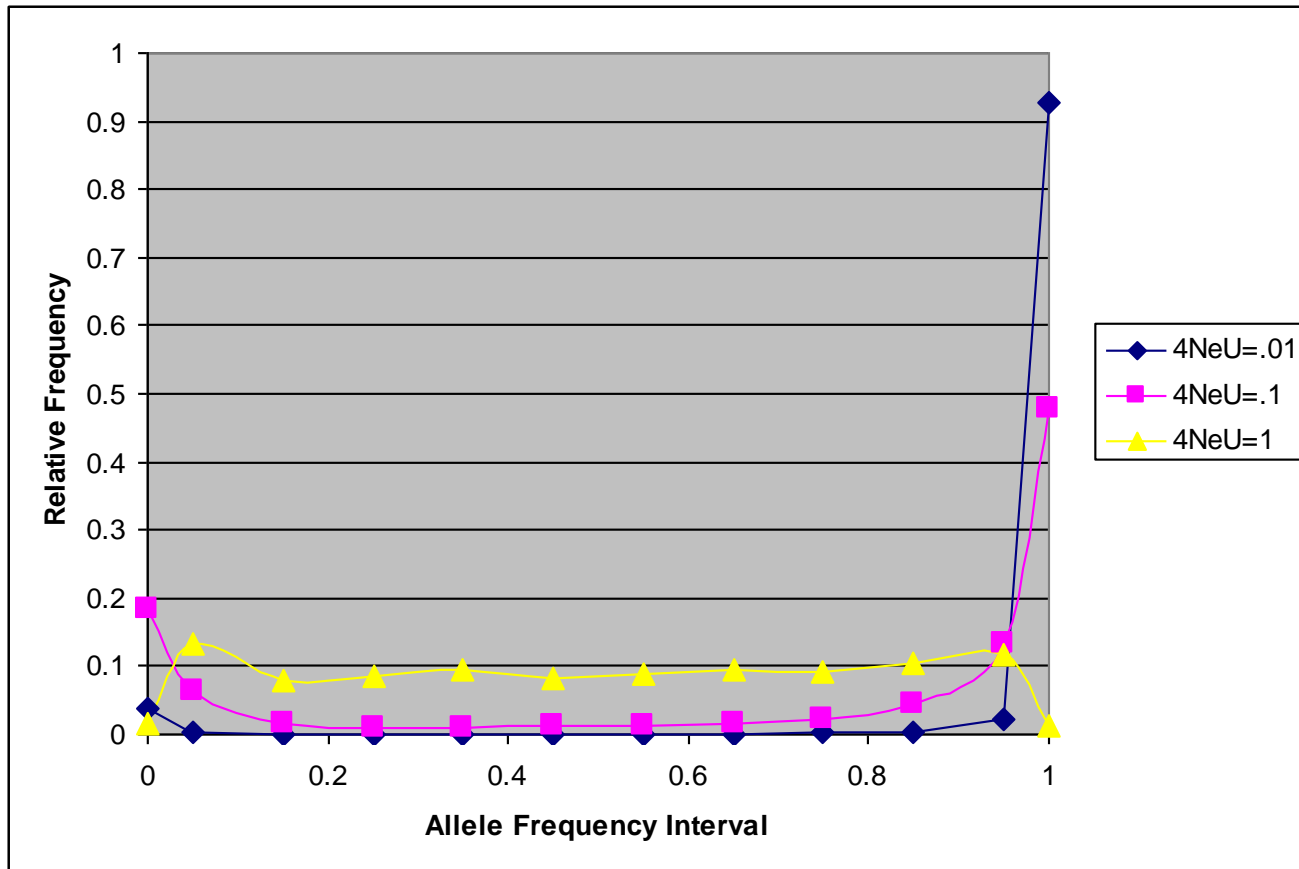# LD Generation

- All forces that change allele frequencies
  - Mutation
  - Migration
  - Selection
  - Genetic Drift

Starting Conditions

- Hardy-Weinberg Equilibrium
  - Within and between loci
  - Generate LD by Random Drift
- Mutation-Drift Equilibrium
  - Pre-existing LD
  - LD has not decayed from original mutation event
  - Dependent on mutation rates (types of makers) and population size

Mutation Drift Equilibrium (MDE)
N_e=100 Generations=1000

Ne=100

QTL
↓
u=2.5x10^{-5}

u=2.5x10^{-4}

u=2.5x10^{-3}
↑
Markers

Markers=Uniform
Distribution
all Polymorphic

QTL=4%
Polymorphic
Steady State

Generations of Training
Duration and Accuracy of Prediction

	Generation	Genotype		Phenotype	Predict Breeding Value	Accuracy
Training Generations	0	Z	and	Y	$\widehat{Y}_0$	r_0
	1	Z		Y	$\widehat{Y}_1$	r_1
	t	Z		Y	$\widehat{Y}_t$	r_t
Prediction Generations	t+1	Z	And	No Phenotypic Data	$\widehat{Y}_{t+1}$	r_{t+1}
	t+2	Z			$\widehat{Y}_{t+2}$	r_{t+2}
	.	Z				
	t+n	Z			$\widehat{Y}_{t+n}$	r_{t+n}

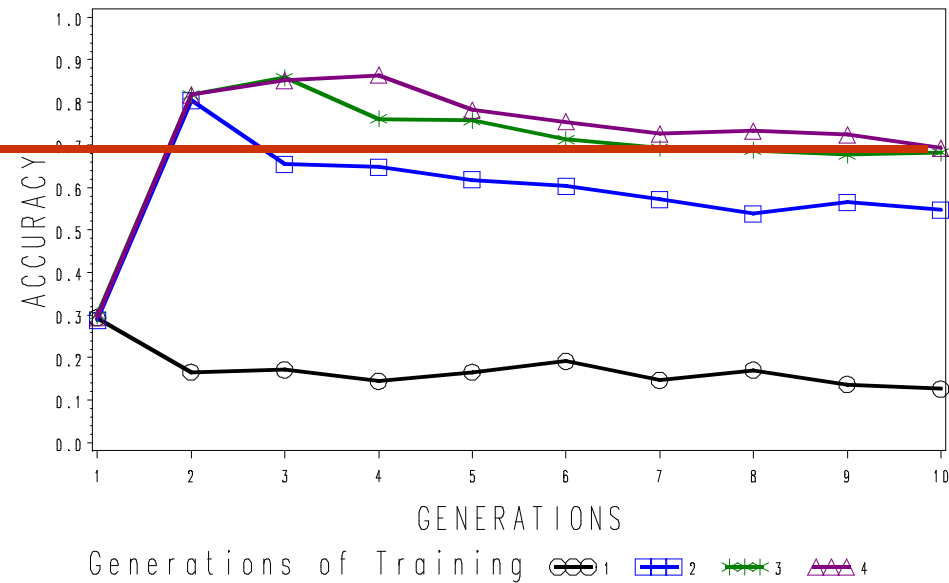Accuracy=Correlation Between Predicted and True Breeding Value

Results

GEBV
Accuracy with $h^2 = .5$

Starting in HWE

Starting in MDE
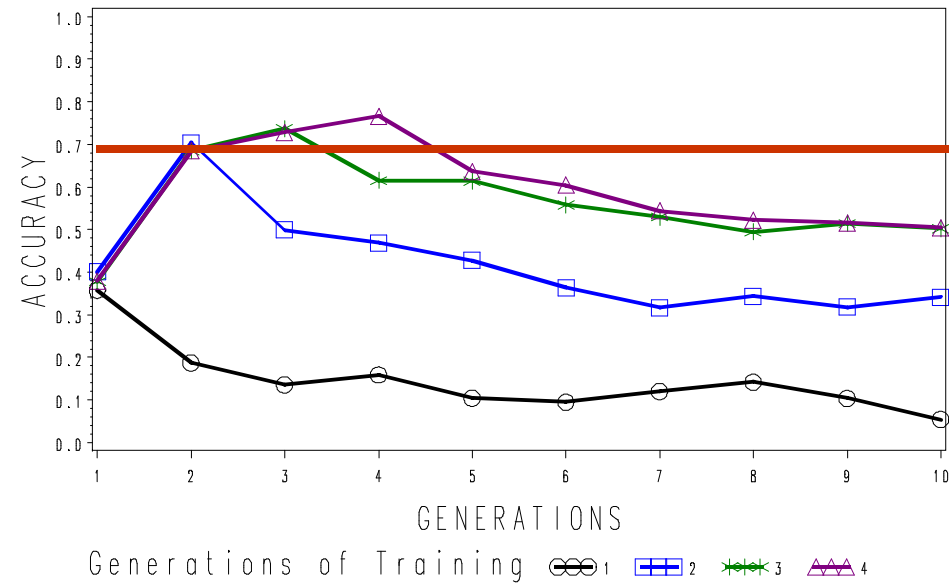
N=128, N_e=16

GEBV
Accuracy with h^2=.1
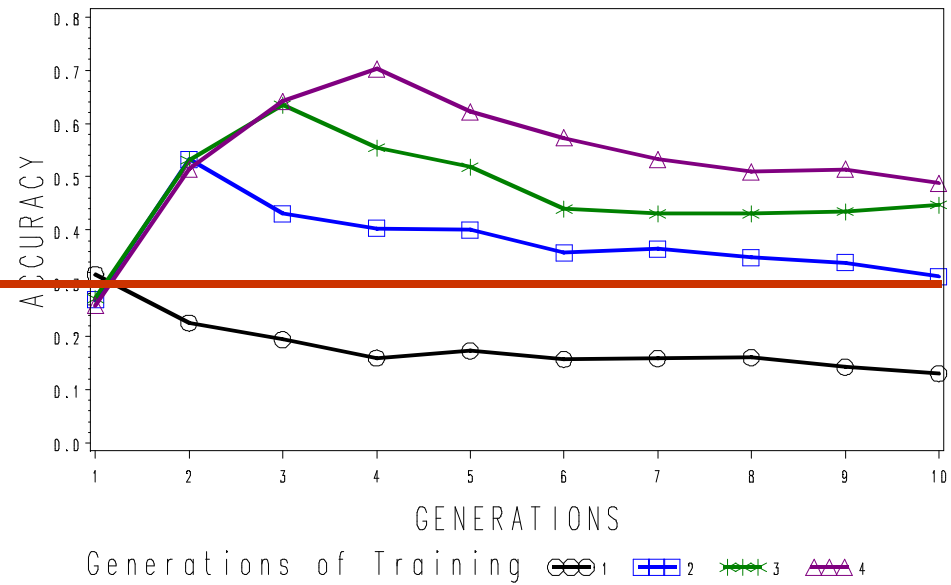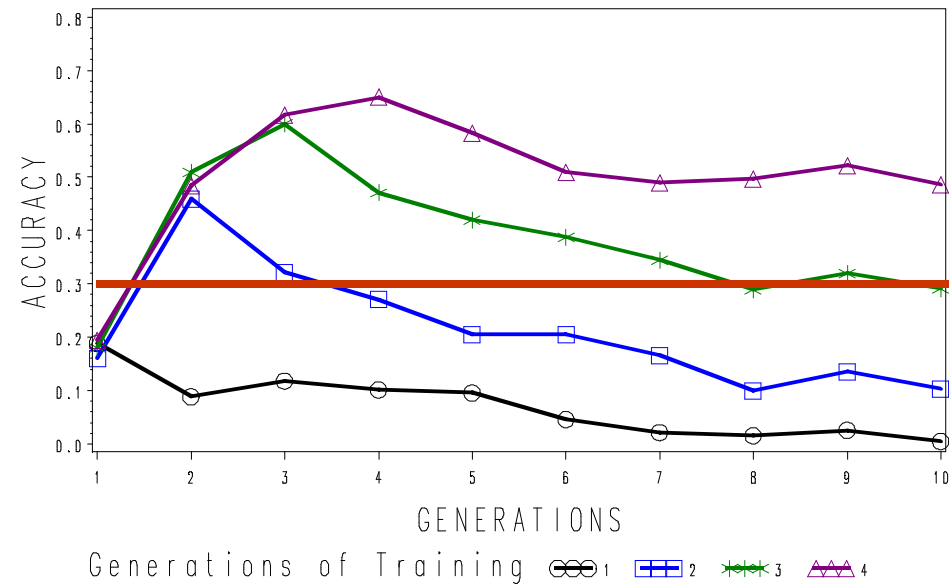
Effect of Random vs. Directional Selection on Accuracy

Starting in HWE
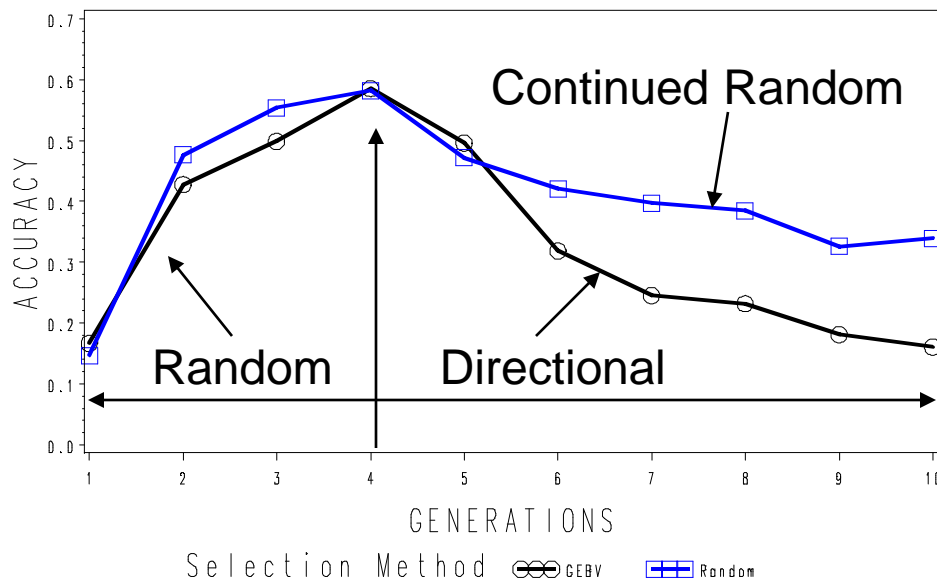
Starting in MDE
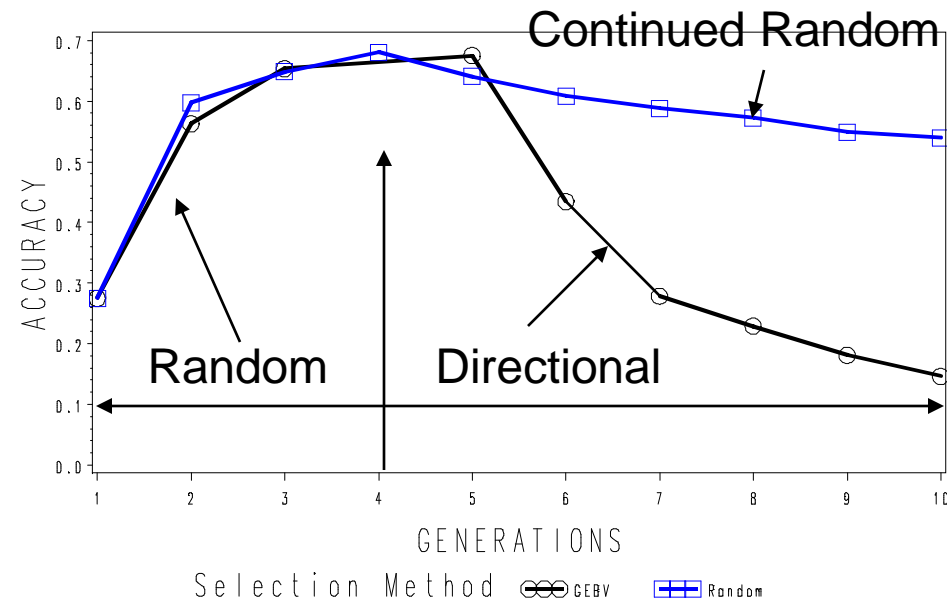
h²=.1 N=256, Ne=32, 100/100 Marker/QTL loci distributed on 100cM.

(average over 60 replicates, SEM=.02).

Alternative Approach Genomic Relationship Matrix

- Assumes
  - Dense markers evenly spaced across the genome
  - Assumes markers are in LD with QTL affecting trait(s) of interest
  - Alike in State (AIS) alleles were at one time a result of a single mutation, thus IBD when traced back in evolutionary time
  - Each marker account for an equal proportion of genetic variance (infinitesimal model)
  - Genetic Effects are Normally Distributed

Compute (AIS) relationship matrix (G)

$$TA_k = 2 \frac{\sum_{i=1}^{2} \sum_{j=1}^{2} I_{ij}}{4}$$

$$\mathbf{G} = \sigma_{A*}^{2} \mathbf{G}^{*}$$

$$\sigma_{A*}^{2}$$

TA_k=total allelic relationship at kth locus
TA_k=2x coefficient of relationship
(Malecot. 1948)

Is the additive genetic variance associated with the markers for the trait

$$G_{xy}^{*} = \frac{\sum_{k=1}^{L} TA_k}{L} = \frac{2 \sum_{i=1}^{L} \left(\frac{\sum_{i=1}^{2} \sum_{j=1}^{2} I_{ij}}{4} \right)}{L}$$

$$\sigma_{A*}^{2} < \sigma_{A}^{2}$$

Note: with low marker density the markers may not capture any genetic variance

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LOCUS

Individual	A 1	A 2	B 1	B 2	C 1	C 2	D 1	D 2	E 1	E 2
1	2	2	1	1	1	2	1	1	2	2
2	1	2	1	2	2	2	1	2	1	1
3	1	2	1	1	1	2	1	2	1	2
4	2	2	1	1	2	2	1	1	2	1
5	2	1	1	2	2	2	1	1	2	1
6	2	2	1	1	2	2	1	1	2	1

Pedigree

Individuals (X,Y)

	A	B	C	D	E	Total	rxy
x=1	2 2	1 1	1 2	1 1	2 2		
y=1	2 2	1 1	1 2	1 1	2 2		
sum	4	4	2	4	4		
shared alleles	2	2	1	2	2	9	1.8
x=1	2 2	1 1	1 2	1 1	2 2		
y=2	1 2	1 2	2 2	1 2	1 1		
sum	2	2	2	2	0		
shared alleles	1	1	1	1	0	4	0.8

AIS   G=GRM

	1	2	3	4	5	6
1	1.8	0.8	1.2	1.6	1.2	1.6
2	0.8	1.4	1	1.2	1.2	1.2
3	1.2	1	1.2	1.2	1.8	1.2
4	1.6	1.2	1.2	1.8	1.4	1.8
5	1.2	1.2	1	1.4	1.4	1.4
6	1.6	1.2	1.2	1.8	1.4	1.8

IBD   PEDIGREE   A

1	1	0	0.5	0.5	0.5	0.5
2	0	1	0.5	0.5	0.5	0.5
3	0.5	0.5	1	0.5	0.5	0.5
4	0.5	0.5	0.5	1	0.5	0.5
5	0.5	0.5	0.5	0.5	1	0.5
6	0.5	0.5	0.5	0.5	0.5	1

Parents assumed not related (False)   Parents assumed non inbred (false)   Full sibs assumed = relationship (false)

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G* Computed Directly from M

Individual	LOCUS										
	A		B		C		D		E		
	1	2	1	2	1	2	1	2	1	2	22=1
1	2	2	1	1	1	2	1	1	2	2	12=0
2	1	2	1	2	2	2	1	2	1	1	11=-1
3	1	2	1	1	1	2	1	2	1	2	
4	2	2	1	1	2	2	1	1	2	1	
5	2	1	1	2	2	2	1	1	2	1	
6	2	2	1	1	2	2	1	1	2	1	

	M N individuals x p markers							**M'** p markers x N individuals				
1	1	-1	0	-1	1			1	0	0	1	0	1
2	0	0	1	0	-1			-1	0	-1	-1	0	-1
3	0	-1	0	0	0			0	1	0	1	1	1
4	1	-1	1	-1	0			-1	0	0	-1	-1	-1
5	0	0	1	-1	0			1	-1	0	0	0	0
6	1	-1	1	-1	0								

0.8	-0.2	0.2	0.6	0.2	0.6		1.8	0.8	1.2	1.6	1.2	1.6
-0.2	0.4	0	0.2	0.2	0.2		0.8	1.4	1	1.2	1.2	1.2
0.2	0	0.2	0.2	0	0.2		1.2	1	1.2	1.2	1	1.2
0.6	0.2	0.2	0.8	0.4	0.8		1.6	1.2	1.2	1.8	1.4	1.8
0.2	0.2	0	0.4	0.4	0.4		1.2	1.2	1	1.4	1.4	1.4
0.6	0.2	0.2	0.8	0.4	0.8		1.6	1.2	1.2	1.8	1.4	1.8

MM'/5   G*

dimension nxn   Note that 1+**MM'**/5=**G***

The are the same

Mixed Model Equations

$$\begin{bmatrix} \mathbf{X}'\mathbf{R}^{-1}\mathbf{X} & \mathbf{X}'\mathbf{R}^{-1}\mathbf{Z} \\ \mathbf{Z}'\mathbf{R}^{-1}\mathbf{X} & \mathbf{Z}'\mathbf{R}^{-1}\mathbf{Z}+\mathbf{G}^{-1} \end{bmatrix}\begin{bmatrix} \mathbf{b} \\ \mathbf{u} \end{bmatrix} = \begin{bmatrix} \mathbf{X}'\mathbf{R}^{-1}\mathbf{Y} \\ \mathbf{Z}'\mathbf{R}^{-1}\mathbf{Y} \end{bmatrix}$$

Simplifications If $\quad \mathbf{R} = \mathbf{I}\sigma_e^2$

$$\mathbf{G} = \sigma_{A*}^2 \mathbf{M}'\mathbf{M}/L$$

$$\begin{bmatrix} \mathbf{X}'\mathbf{X} & \mathbf{X}'\mathbf{Z} \\ \mathbf{Z}'\mathbf{X} & \mathbf{Z}'\mathbf{Z}+\dfrac{\sigma_e^2}{\sigma_{A*}^2}\left(\mathbf{M}\mathbf{M}'/L\right)^{-1} \end{bmatrix}\begin{bmatrix} \mathbf{b} \\ \mathbf{u} \end{bmatrix} = \begin{bmatrix} \mathbf{X}'\mathbf{Y} \\ \mathbf{Z}'\mathbf{Y} \end{bmatrix}$$

Note one can multiply both sides of the second equation by **G** to avoid an inverse

Example

$$\mathbf{Y} = \begin{bmatrix} 7 \\ 9 \\ 10 \\ 6 \\ 9 \\ 11 \end{bmatrix} \quad \mathbf{X} = \begin{bmatrix} 1 \\ 1 \\ 1 \\ 1 \\ 1 \\ 1 \end{bmatrix} \quad b = \begin{bmatrix} \mu_0 \end{bmatrix} \quad Z = \begin{bmatrix} 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 \end{bmatrix} \quad \mathbf{u} = \begin{bmatrix} u_1 \\ u_2 \\ u_3 \\ u_4 \\ u_5 \\ u_6 \end{bmatrix}$$

$$\mathbf{M} = \begin{bmatrix} 1 & -1 & 0 & -1 & 1 \\ 0 & 0 & 1 & 0 & -1 \\ 0 & -1 & 0 & 0 & 0 \\ 1 & -1 & 1 & -1 & 0 \\ 0 & 0 & 1 & -1 & 0 \\ 1 & -1 & 1 & -1 & 0 \end{bmatrix} \quad \mathbf{MM'}/L = \begin{bmatrix} .8 & -.2 & .2 & .6 & .2 & .6 \\ -.2 & .4 & 0 & .2 & .2 & .2 \\ .2 & 0 & .2 & .2 & 0 & .2 \\ .6 & .2 & .2 & .8 & .4 & .8 \\ .2 & .2 & 0 & .4 & .4 & .4 \\ .6 & .2 & .2 & .8 & .4 & .8 \end{bmatrix} \quad \begin{array}{l} \sigma_A^2 = 10 \\ \sigma_{A*}^2 = 5 \\ \sigma_\varepsilon^2 = 20 \end{array}$$

Note, only ½ the additive genetic variance was captured by the markers   24

Y				Z				V(A)=	5
7		1	0	0	0	0	0	V(A)=	5
9		0	1	0	0	0	0	V(E)=	20
10		0	0	1	0	0	0		
6		0	0	0	1	0	0	XX	
9		0	0	0	0	1	0	6	
11		0	0	0	0	0	1		

X		**MM'/5**						XY	
1		0.8	-0.2	0.2	0.6	0.2	0.6	52	
1		-0.2	0.4	0	0.2	0.2	0.2		
1		0.2	0	0.2	0.2	0	0.2		
1		0.6	0.2	0.2	0.8	0.4	0.8		
1		0.2	0.2	0	0.4	0.4	0.4		
1		0.6	0.2	0.2	0.8	0.4	0.8		

V(A*)G*Z'X			V(A*)GZ'Z+V(E)I					V(A*)GZ'Y	
11		24	-1	1	3	1	3	89	
4		-1	22	0	1	1	1	37	
4		1	0	21	1	0	1	34	
15		3	1	1	24	2	4	126	
8		1	1	0	2	22	2	68	
15		3	1	1	4	2	24	126	

							b		52
6	1	1	1	1	1	1	b		52
11	24	-1	1	3	1	3	u1		89
4	-1	22	0	1	1	1	u2		37
4	1	0	21	1	0	1	u3		34
15	3	1	1	24	2	4	u4		126
8	1	1	0	2	22	2	u5		68
15	3	1	1	4	2	24	u6		126
			LHS					RHS	

		LHS						RHS		
b		0.238268	-0.00798	-0.01022	-0.01037	-0.00629	-0.00886	-0.00629	52	8.762384
u1		-0.07865	0.045659	0.005799	0.001807	-0.00248	0.001686	-0.00248	89	-0.25929
u2		-0.03389	0.003561	0.047264	0.001527	-0.00087	-0.00061	-0.00087	37	0.094488
u3	='	-0.03092	-0.00058	0.001379	0.04919	-0.00075	0.001505	-0.00075	34	=' -0.02194
u4	='	-0.11254	-0.00078	0.003063	0.003334	0.046655	0.001074	-0.00335	126	-0.1648
u5		-0.06107	0.000807	0.000747	0.003012	-0.0015	0.048432	-0.0015	68	-0.05796
u6		-0.11254	-0.00078	0.003063	0.003334	-0.00335	0.001074	0.046655	126	-0.1648

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Equivalent Model
Estimation of Marker effects

$$
\begin{bmatrix} \mathbf{X'}_{1,N}\,\mathbf{X}_{N,1} & \mathbf{X}_{1,N}{'}\mathbf{M}_{N,p} \\ \mathbf{M'}_{p,N}\,\mathbf{X}_{N,1} & \mathbf{M}_{p,N}^{'}\mathbf{M}_{N,p} + \dfrac{\sigma_e^2}{\left(\dfrac{\sigma_{A*}^2}{L}\right)}\mathbf{I} \end{bmatrix}\begin{bmatrix} \boldsymbol{\beta}_{1,1} \\ \mathbf{g}_{p,1} \end{bmatrix} = \begin{bmatrix} \mathbf{X'}_{1,N}\,\mathbf{Y}_{N,1} \\ \mathbf{M'}_{p,N}\,\mathbf{Y}_{N,1} \end{bmatrix}
$$

Dimension pxp

Each Marker effects is solved for

Model of Meuwissen et al (2001)

$$
\hat{u}_i = GEBV_i = \mathbf{Mg} = \sum_j M_{ij}\hat{g}_j
$$

		M'							M					
1	0	0	1	0	1			1	-1	0	-1	1	
-1	0	-1	-1	0	-1			0	0	1	0	-1	
0	1	0	1	1	1			0	-1	0	0	0	
-1	0	0	-1	-1	-1			1	-1	1	-1	0	
1	-1	0	0	0	0			0	0	1	-1	0	
		MM'						1	-1	1	-1	0	
3	-3	2	-3	1				M'X		M'Y			Y	X
-3	4	-2	3	-1				3		24			7	1
2	-2	4	-3	-1				-4		-34			9	1
-3	3	-3	4	-1				4		35			10	1
1	-1	-1	-1	2				-4		-33			6	1
		I						0		-2			9	1
1	0	0	0	0									11	1
0	1	0	0	0										
0	0	1	0	0				V(A)=	5				X'X	
0	0	0	1	0				V(E)=	20				6	
0	0	0	0	1										
		LHS								RHS			X'Y	
6	3	-4	4	-4	0	B				52			52	
3	23	-3	2	-3	1	g1				24				
-4	-3	24	-2	3	-1	g2				-34				
4	2	-2	24	-3	-1	g3	='			35				
-4	-3	3	-3	24	-1	g4				-33				
0	1	-1	-1	-1	22	g5				-2				

		inverse(LHS)						RHS		
B		0.238268	-0.02055	0.030921	-0.03165	0.029414	0.002238	52		8.762384
g1		-0.02055	0.046795	0.002074	-0.00012	0.002068	-0.00194	24		-0.08491
g2	='	0.030921	0.002074	0.047116	-0.00139	-0.00057	0.001958	-34	='	0.021935
g3		-0.03165	-0.00012	-0.00139	0.047031	0.00085	0.002119	35		0.012177
g4		0.029414	0.002068	-0.00057	0.00085	0.047091	0.002059	-33		0.070134
g5		0.002238	-0.00194	0.001958	0.002119	0.002059	0.045822	-2		-0.08231

		M					g			
u1		1	-1	0	-1	1	-0.08491		-0.25929	
u2		0	0	1	0	-1	0.021935		0.094488	
u3	='	0	-1	0	0	0	0.012177	='	-0.02194	same as before
u4		1	-1	1	-1	0	0.070134		-0.1648	
u5		0	0	1	-1	0	-0.08231		-0.05796	
u6		1	-1	1	-1	0			-0.1648	

Genomic Selection in Poultry, Results with Broilers and Comparison with Traditional BLUP

Acknowledgements

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Potential Benefits

- Reduced Generation Interval
  - Select breeders as chicks
  - Housing and feed savings
- Increased accuracy
  - Low heritability traits
- Alternative for difficult or expensive traits to measure
  - Feed efficiency
  - Carcass composition
  - Disease resistance
  - Can address animal wellbeing concerns

Design of experiment

- Lines
  - Male line
  - Female line
- Traits of selection
  - Breast Meat (high h^2)
  - Weight   (medium h^2)

Methods for estimation of breeding values (EBVs and GEBVs)

- EBV's
  - BLUP (multi-trait)
- GEBVs
  - GBLUP (multi-trait)
  - Single Step (ssGBLUP)
    - Aguilar, I., I. Misztal, D. L. Johnson, A. Legarra, S. Tsuruta *et al.* 2010 Hot topic: A unified approach to utilize phenotypic, full pedigree, and genomic information for genetic evaluation of Holstein final score. Journal Of Dairy Science **93**: 743-752.
    - Legarra, A., I. Aguilar, and I. Misztal, 2009 A relationship matrix including full pedigree and genomic information. Journal Of Dairy Science **92**: 4656-4663.
  - Advantages
    - Corrects for multi-trait selection bias
      - Vitezica, Z. G., I. Aguilar, I. Misztal, and A. Legarra, 2011 Bias in genomic predictions for populations under selection. Genetics Research **93**: 357-366.
    - Utilizes records from ungenotyped animals
      - Concurrent
      - Ancestral

EBVs and GEBVs combined using an index

- Equal weight to all traits
- Standardized relative to additive variance (standard deviation)

GBLUP and BLUP Training

- Two training generations
  - no selection
  - used historical phenotypes
  - Banked DNA samples
- Numbers genotyped (GBLUP)
  - 2,500 each line
- Phenotypes
  - BLUP and GBLUP
  - 280,000 each line

Selection Program-GEBV

- Tiered
  - Tier 1
    - 800 **Genotyped** and Phenotyped
  - Tier 2
    - 200 Phenotyped
- Plays into strength of ssGBLUP
  - Uses all records
- Only birds from Tier 1 selected based on index
- Number selected
  - 20 Males
  - 200 Females

Selection Program BLUP

- Tiered
  - Tier 1 (800) phenotyped
  - Tier 2 (200) phenotyped
- Only birds from Tier 1 selected based on index
- Number selected
  - 20 Males
  - 200 Females

Duration

- 3 generations of selection
- Generation 4
  - Expanded to 4,000
  - Phenotyped only
    - Progeny test of Generation 3
    - Bases for comparison between methods

Accuracy

- Correlation between the true and predicted breeding values
  - Don't know true EBV

- Equivalent formula
  - Legarra, A., C. Robert- Granie´, E. Manfredi, and J. M. Elsen. 2008. Performance of genomic selection in mice. Genetics **180**: 611-618
  - Chen, C. Y., I. Misztal, I. Aguilar, A. Legarra, and W. M. Muir, 2011 Effect of different genomic relationship matrices on accuracy and scale. Journal Of Animal Science **89**: 2673-2679
  - Does not require true value of EBV to be known
  - Requires heritability to be known
  - Calculation of EBV does not include phenotypes of the generations they were estimated in
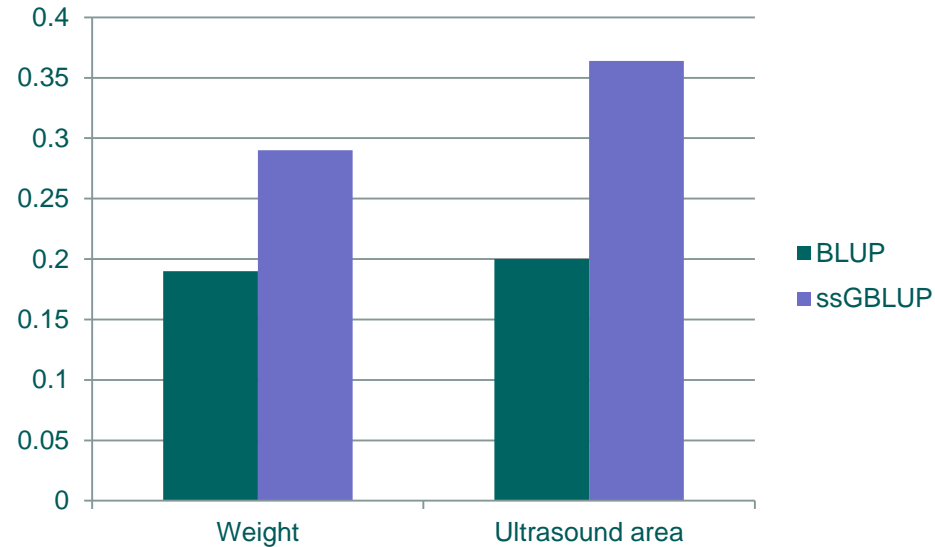
$$r\left(EBV, \hat{EBV}\right)$$

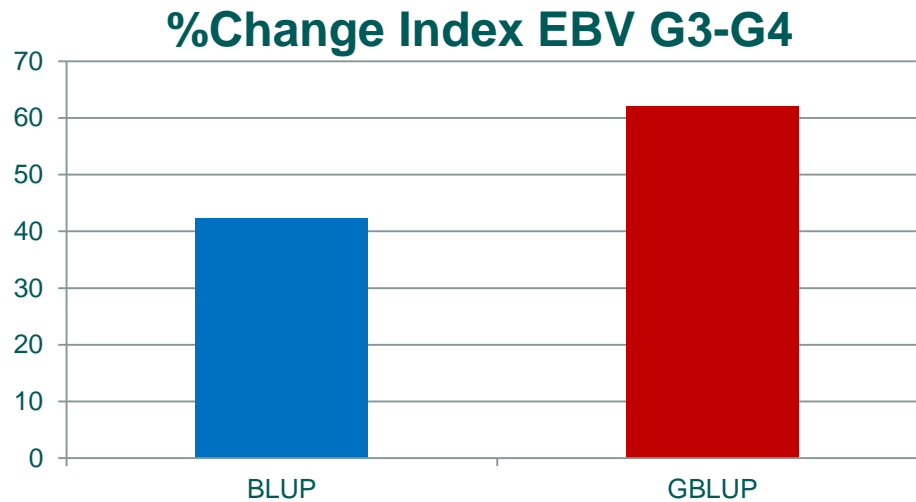$$\frac{r(\hat{EBV}, Y)}{h}$$

Results

Generations 3-4

Accuracy

Chen, C. Y., I. Misztal, I. Aguilar, A. Legarra, and W. M. Muir, 2011 Effect of different genomic relationship matrices on accuracy and scale. Journal Of Animal Science **89**: 2673-2679

Genetic Trend Female Line Index

%Change Index EBV G3-G4

Genetic Trend
Male Line Index

%Change Index EBV G3-G4

Challenges

GBLUP lines

- Some mismatch in early generations between DNA samples, pedigree, phenotypes

- Impact

$$\Delta G = \text{accuracy} * \text{intensity} * \sigma_a$$

  – Reduced selection intensity in GBLUP lines
    - Mismatches were random
    - Proportion of those selected was therefore at random
  – Reduced accuracy in GBLUP program
    - Training and SNP effects were updated each generation including current generation
    - Inaccurate SNP effects (phenotype- genotype relationships were incorrect)

Opportunities

- Blood sampling on a large scale by farm workers in a chicken house.
  - Sample identification and tracking
  - Bar-coding, portable scanners and printers suitable for a chicken house
- Timely pedigree checking
  - Parent and offspring pedigree checking where possible
  - Full sib pedigree checking when parent information is not available
- Sample processing and genotyping to allow timely error checking
  - Timing is critical in chicken breeding (weeks not months)
  - Ability to keep selection candidates for pedigree verification if necessary
  - Space for storing selection candidates
  - Very different to cattle breeding..less space, less time

Conclusions

- GBLUP more accurate than BLUP
- Genetic trends reflect increased accuracy of GBLUP
- GBLUP at a minimum was able to keep up with BLUP☺
- Quality control essential for translation of technology to applications
- For some traits, especially those measured late in life, being as good as BLUP is good enough

Conclusions

- Results are very encouraging
- Company will continue GBLUP program, particularly for
  - low heritability traits
  - Traits difficult or expensive to measure
  - Traits measured late in life cycle