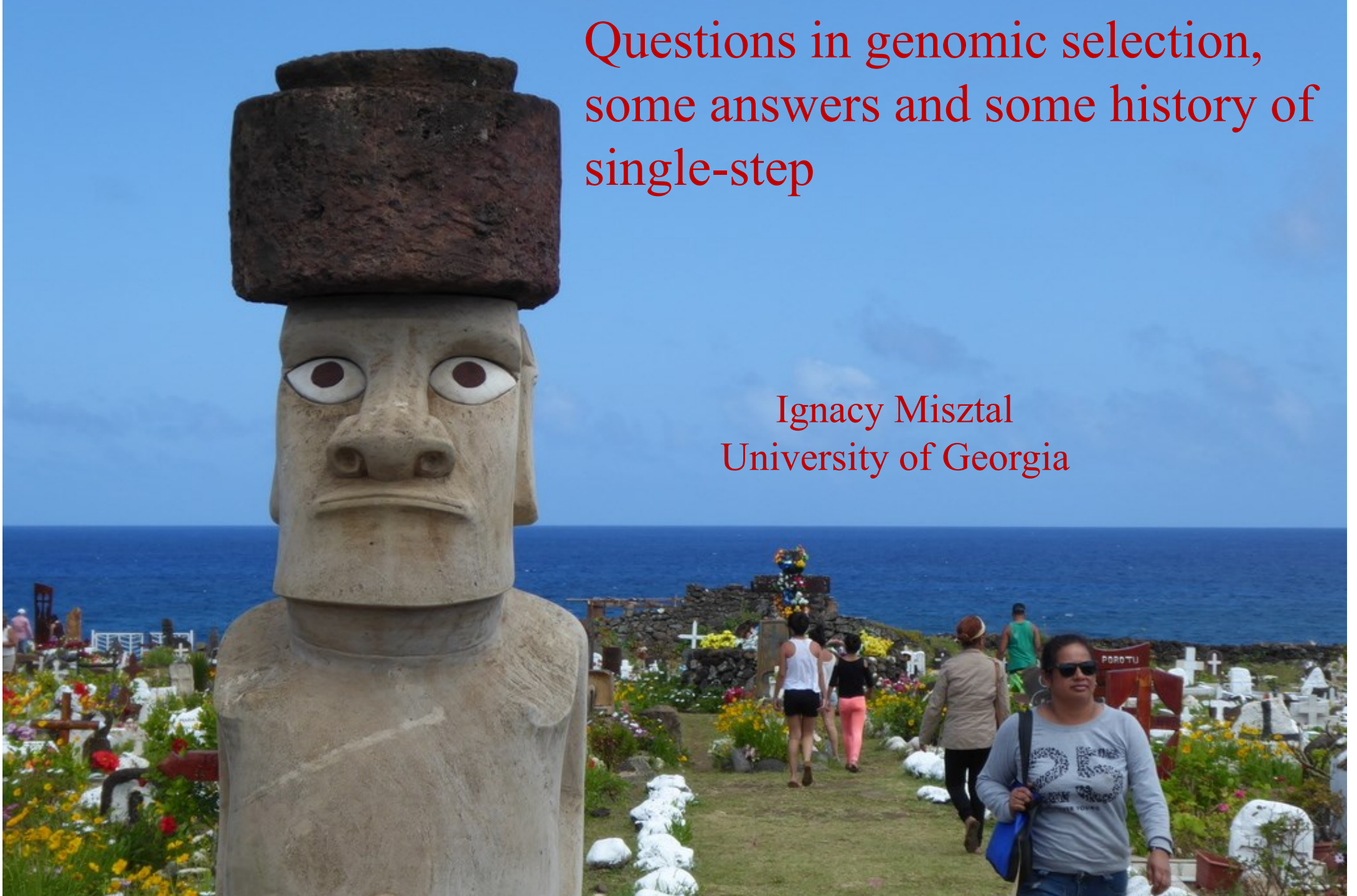


Questions in genomic selection, some answers and some history of single-step

Ignacy Misztal
University of Georgia



Questions in genomic selection

- SNP are genes, markers or something else?
- Good accuracy at 30k SNP , standard 50-60k, a bit better at 700k
 - What is magic with 50K?
 - Why not more noise at 600K
 - Causative SNP?
- Stability problems with GRM
 - At about 5k, usually blended with A
- OK accuracy with few genotyped animals 1k-2k
 - Good in farm
 - Rise with extra genotypes slow
 - Discrepancy between simulation and field-data results

Inversion by recursion

$$u_i \mid u_1, u_2, \dots, u_{i-1} = \mathbf{p}_i' \mathbf{u} + \varphi_i \quad \text{Generic recursion}$$

$$\mathbf{u} = \mathbf{P}\mathbf{u} + \mathbf{\Phi}$$

$$\text{var}(\mathbf{u})^{-1} = (\mathbf{I} - \mathbf{P})' \text{var}(\mathbf{\Phi})^{-1} (\mathbf{I} - \mathbf{P}) \quad \text{Cost low only if P sparse}$$

For pedigree relationships (Henderson, 1976):

$$u_i = 0.5u_{s_i} + 0.5u_{d_i} + \varphi_i \quad \text{P very sparse}$$

Is limited recursion applicable to genomic relationships?

Algorithm for proven and young animals (APY)

For young animals

=0 in GBLUP

$$u_i \mid u_1, u_2, \dots, u_{i-1} = \sum_{j=\text{"proven"}} p_{ij} u_j + \sum_{j=\text{"young"}} p_{ij} u_j + \varepsilon_i$$

Misztal et al. (2014)

$$\mathbf{G}^{-1} = \begin{bmatrix} \mathbf{G}_{pp}^{-1} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} \end{bmatrix} + \begin{bmatrix} -\mathbf{G}_{pp}^{-1} \mathbf{G}_{py} \\ \mathbf{I} \end{bmatrix} \mathbf{M}^{-1} \begin{bmatrix} \mathbf{G}_{yp} \mathbf{G}_{pp}^{-1} & \mathbf{I} \end{bmatrix}$$

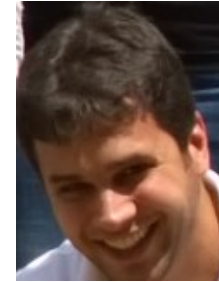
\mathbf{Z}_p – genotypes for proven animals



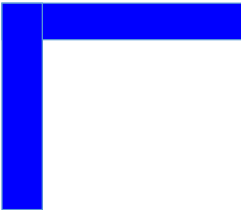

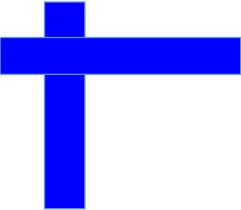
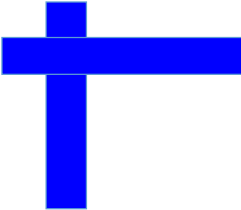

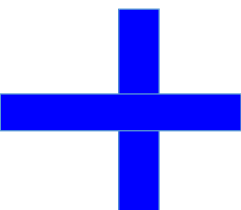
\mathbf{Z}_y – genotypes for young animals

$$m_i = g_{ii} - \mathbf{z}_i' \mathbf{Z}_p' \mathbf{G}_{pp}^{-1} \mathbf{Z}_p \mathbf{z}_i$$

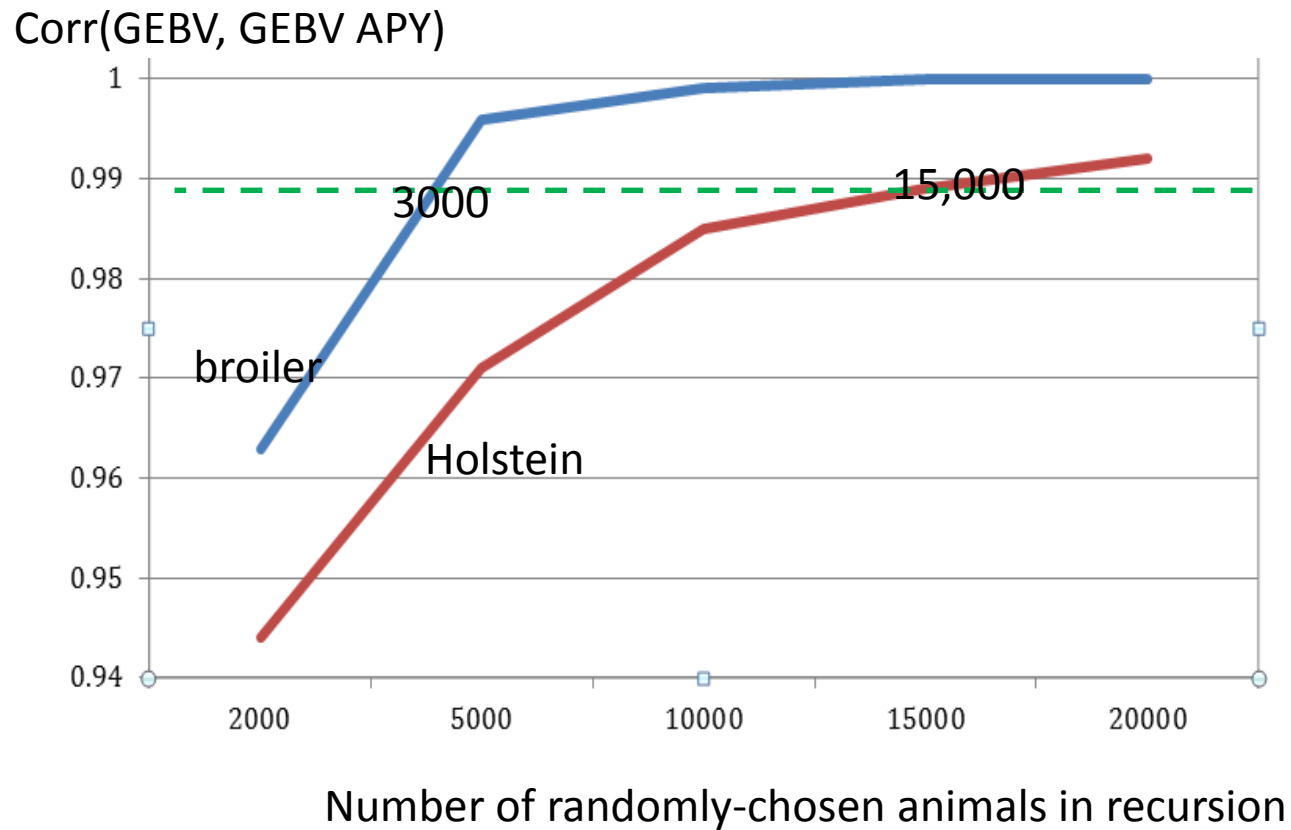
Linear cost for young animals

Tests with Holsteins (Fragomeni et al., 2015)



	G needed	G^{-1}	
Regular inverse			
APY inverse			Correlations of GEBV with regular inverse
23k bulls as core			> 0.99
17k cows as core			> 0.99
20k random animals as core			> 0.99

Impact of recursion size in Holsteins and chicken



Theory of junctions

Heterogenetic and homogenic tracts in genome (Stam, 1980)



Called independent chromosome segments Me

(Goddard et al., 2009; Daetwyler et al., 2010)

$$E(\text{Me}) = 4N_eL \text{ (Stam, 1980)}$$

N_e – effective population size

L – length of genome in Morgans

Need 12 Me SNPs to detect 90% of junctions

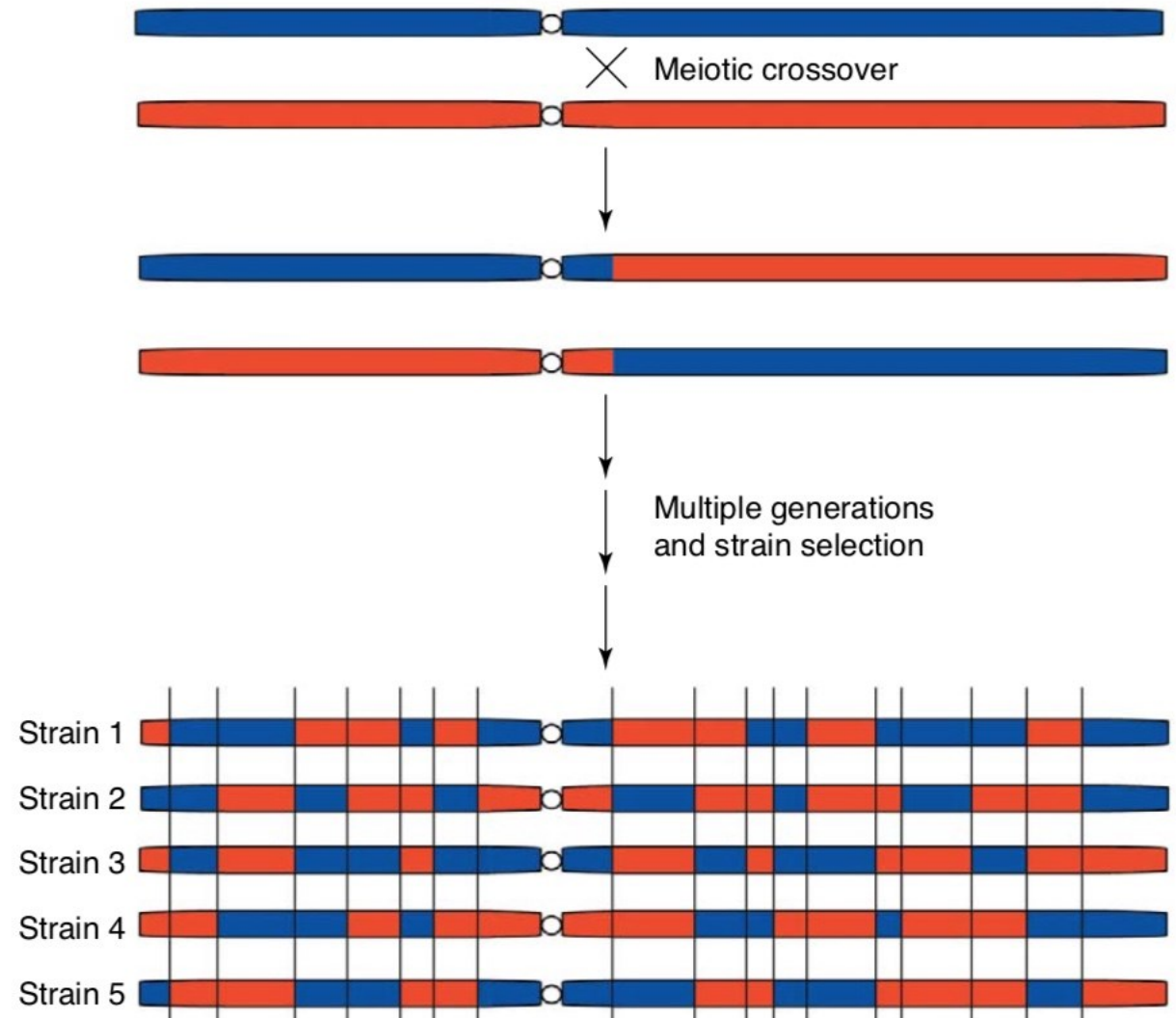
(MacLeod et al., 2005)

Haplotype blocks = Independent chromosome segments

- $E(\text{Me}) = 4N_e L$ Stam (1980)

- N_e – Effective population size
- L – Length of genome in Morgans

- $\text{Me} \begin{cases} 2N_e L & \text{Hayes } et al. (2009) \\ 2N_e L / [\log(N_e L)] & \text{Goddard } et al. (2011) \\ \text{Many more} & \text{Brard and Ricard (2015)} \end{cases}$



Theory of APY based on segments

Breeding value chromosome segments
 $\mathbf{u} = \mathbf{T}\mathbf{s}$

Choose core “**c**” and noncore “**n**” animals

$$\mathbf{s} = \mathbf{Q}\mathbf{u}_c + \boldsymbol{\varepsilon}_c$$

$$\mathbf{u}_n = \mathbf{P}_{nc}\mathbf{u}_c + \boldsymbol{\varepsilon}_n$$

small if number of core animals > number of segments

Choose core “**c**” and noncore “**n**” animals

$$\mathbf{u}_c = \mathbf{u}_c$$

BV of *noncore* animals linear function
of *core* animals

$$\mathbf{u}_n = \mathbf{P}_{nc} \mathbf{u}_c + \boldsymbol{\varepsilon}_n$$

Matrix notation

$$\begin{bmatrix} \mathbf{u}_c \\ \mathbf{u}_n \end{bmatrix} = \begin{bmatrix} \mathbf{I} & \mathbf{0} \\ \mathbf{P}_{nc} & \mathbf{I} \end{bmatrix} \begin{bmatrix} \mathbf{u}_c \\ \boldsymbol{\varepsilon}_n \end{bmatrix}$$

Var(u)

$$\mathbf{G} = \begin{bmatrix} \mathbf{I} & \mathbf{0} \\ \mathbf{P}_{nc} & \mathbf{I} \end{bmatrix} \begin{bmatrix} \mathbf{G}_{cc} & \mathbf{0} \\ \mathbf{0} & \mathbf{M}_{nn} \end{bmatrix} \begin{bmatrix} \mathbf{I} & \mathbf{P}_{cn} \\ \mathbf{0} & \mathbf{I} \end{bmatrix}$$

The inverse


$$\mathbf{G}^{-1} = \begin{bmatrix} \mathbf{I} & -\mathbf{P}_{cn} \\ \mathbf{0} & \mathbf{I} \end{bmatrix} \begin{bmatrix} \mathbf{G}_{cc}^{-1} & \mathbf{0} \\ \mathbf{0} & \mathbf{M}_{nn}^{-1} \end{bmatrix} \begin{bmatrix} \mathbf{I} & \mathbf{0} \\ -\mathbf{P}_{nc} & \mathbf{I} \end{bmatrix}$$

Misztal&Legarra&Aguilar (2014)

Unknown matrices from
conditional expectation

$$\mathbf{P}_{nc} = \mathbf{G}_{nc} \mathbf{G}_{cc}^{-1}, \quad \mathbf{M}_{nn} = \text{diag}\{g_{i,i} - \mathbf{p}_{i,1:i-1} \mathbf{g}'_{i,1:i-1}\}$$

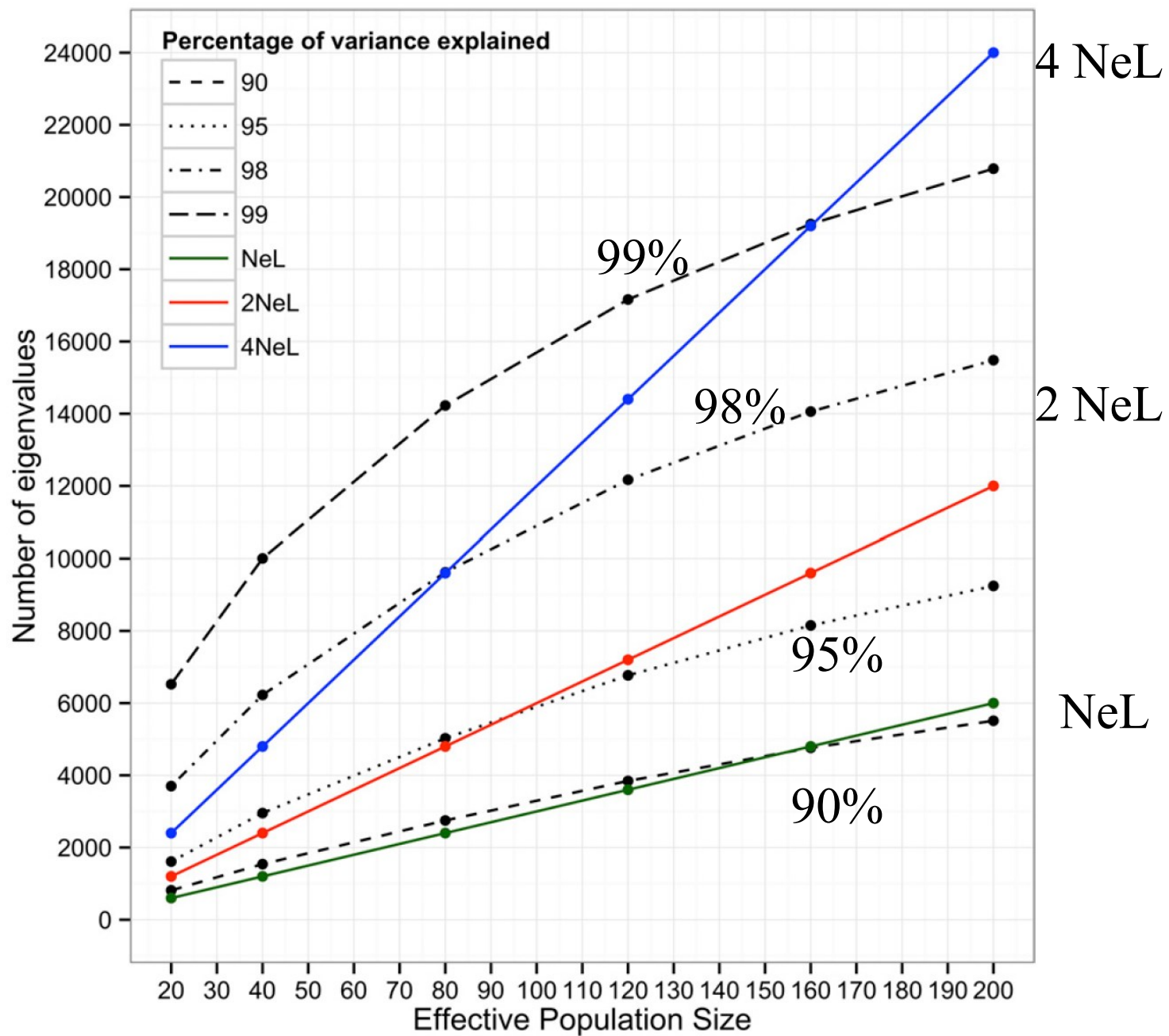
Finding dimensionalities by eigenvalues

$$\mathbf{G} = \mathbf{U} \mathbf{D} \mathbf{U}' = \mathbf{U}_s \mathbf{D}_s \mathbf{U}_s'$$


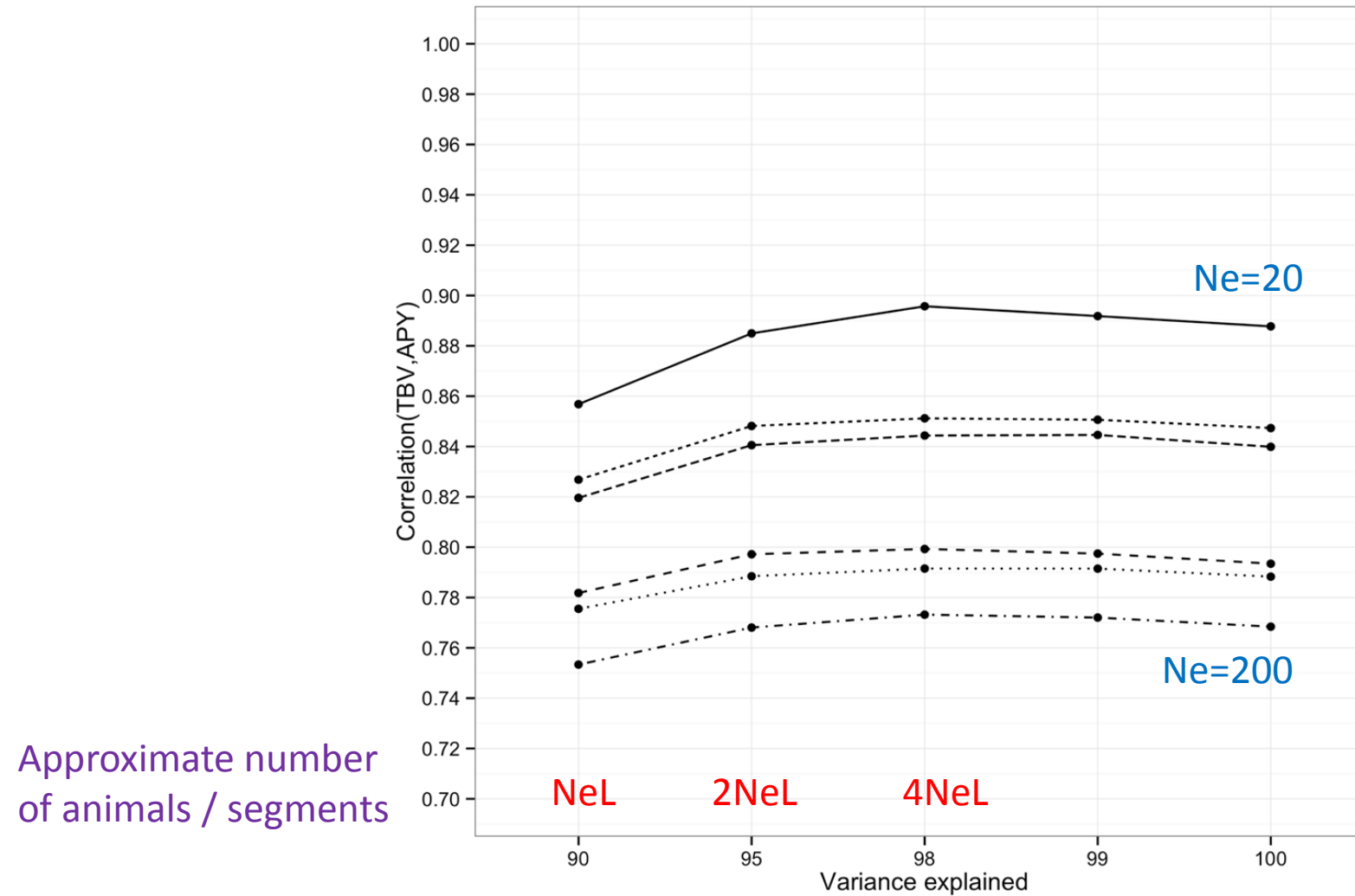
U – eigenvalues
D – eigenvectors

Eigenvalues sum to 100%

What % is useful, 95%? 98% 99%, 99.999%?



True accuracies as function of number of eigenvalues
corresponding to given explained variance in G



Accuracies maximized by 98% "information in G, 95% almost as good
Last 2% of information in G noise



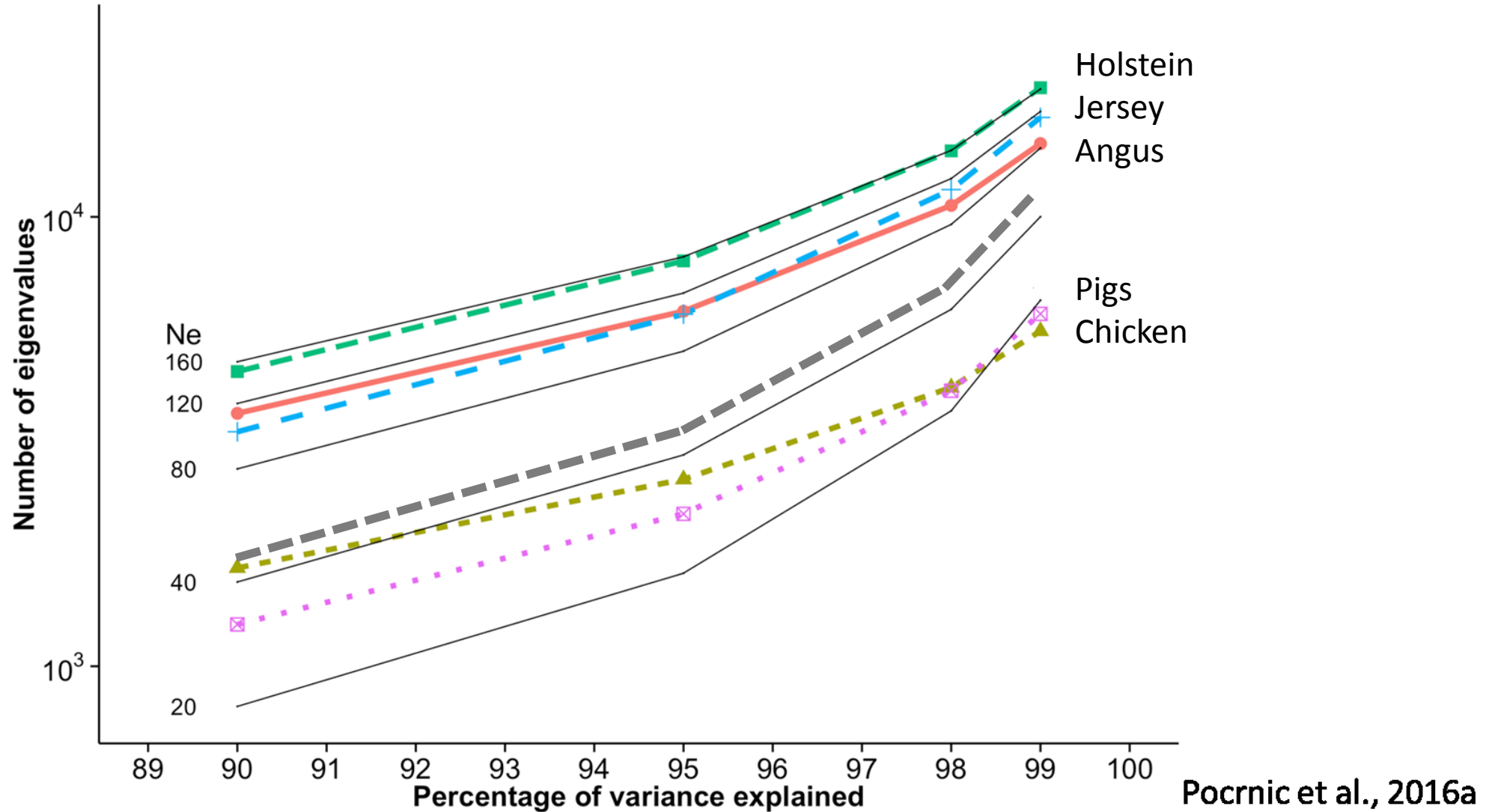
GENETICS | INVESTIGATION

The Dimensionality of Genomic Information and Its Effect on Genomic Prediction

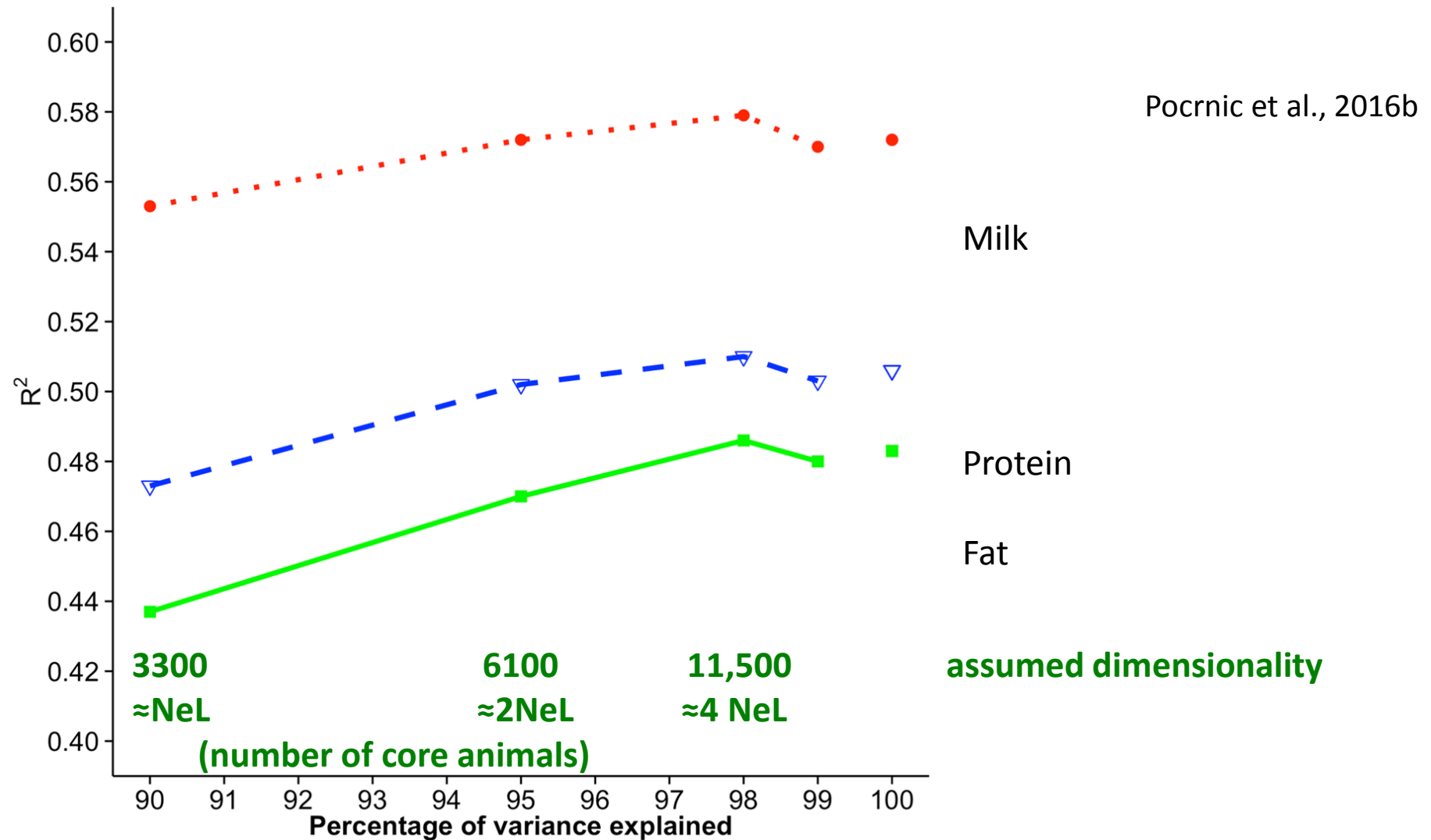
Ivan Pocrnic,^{*,1} Daniela A. L. Lourenco,^{*} Yutaka Masuda,^{*} Andres Legarra,[†] and Ignacy Misztal^{*}

^{*}Department of Animal and Dairy Science, University of Georgia, Athens, Georgia 30602, and [†]Institut National de la Recherche Agronomique, GenPhySE, F-31326 Castanet-Tolosan, France

Number of eigenvalues in G to explain given fraction of variability



Reliabilities – Jerseys (75k animals)



100% = full inverse → lower accuracy

Estimated dimensionality, effective population size and optimal number of SNP

Specie	Approx Me (98%)	Effective population size (L=30M)	Optimal number of SNP (12 x Me)
Holsteins	14k	149	170k
Jerseys	10k	101	120k
Angus	11k	113	130k
Pigs	4k	43 (L=20M)	50k
Chicken	4k	44	50k

Pocrnic et al. (2016b)

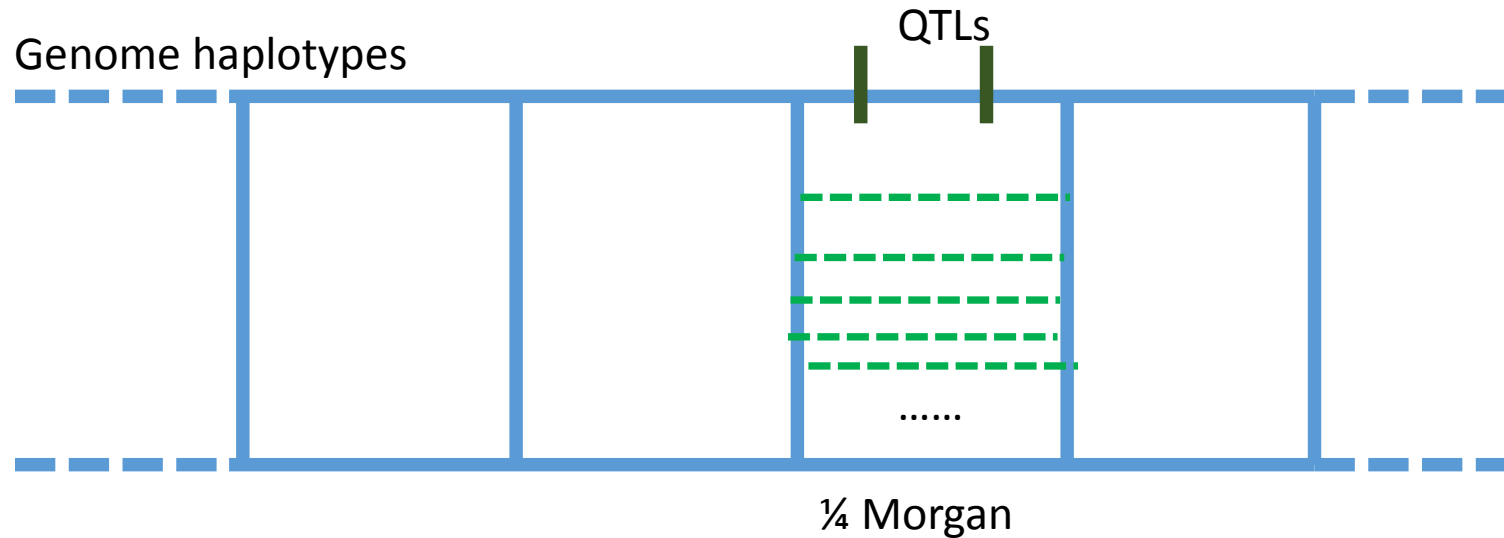
Side effects of reduced dimensionality

- Number of segments
 - 800k in humans
 - 5-15k in animals
- Impact on SNP selection and GWAS

Theory of limited dimensionality

Number of haplotypes: $4 N_e L$

N_e within each $\frac{1}{4}$ Morgan segment

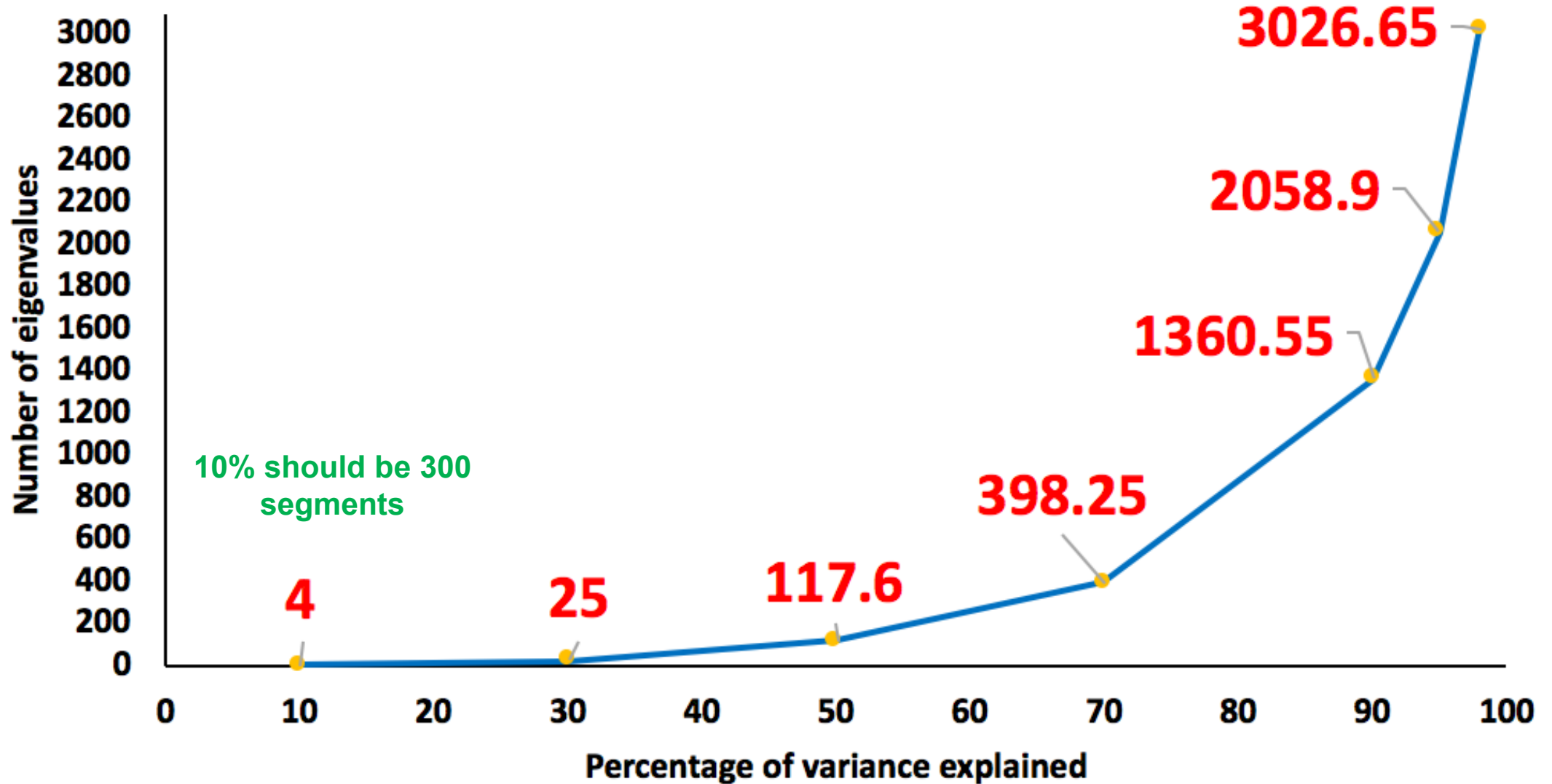


N_e haplotypes within each $\frac{1}{4}$ Morgan segment

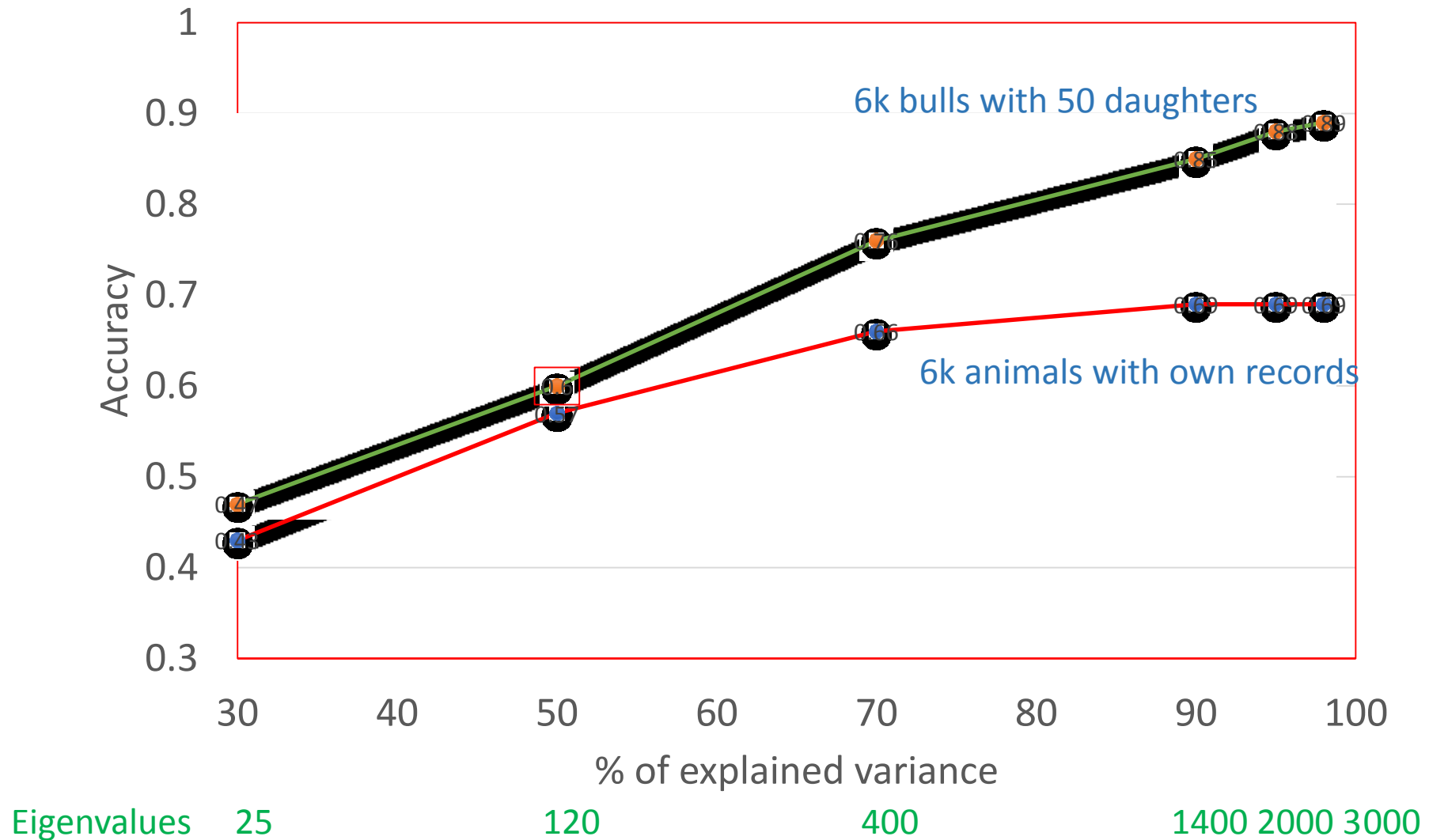
Dimensionality of $\frac{1}{4}$ Morgan case: N_e or number of identified QTLs

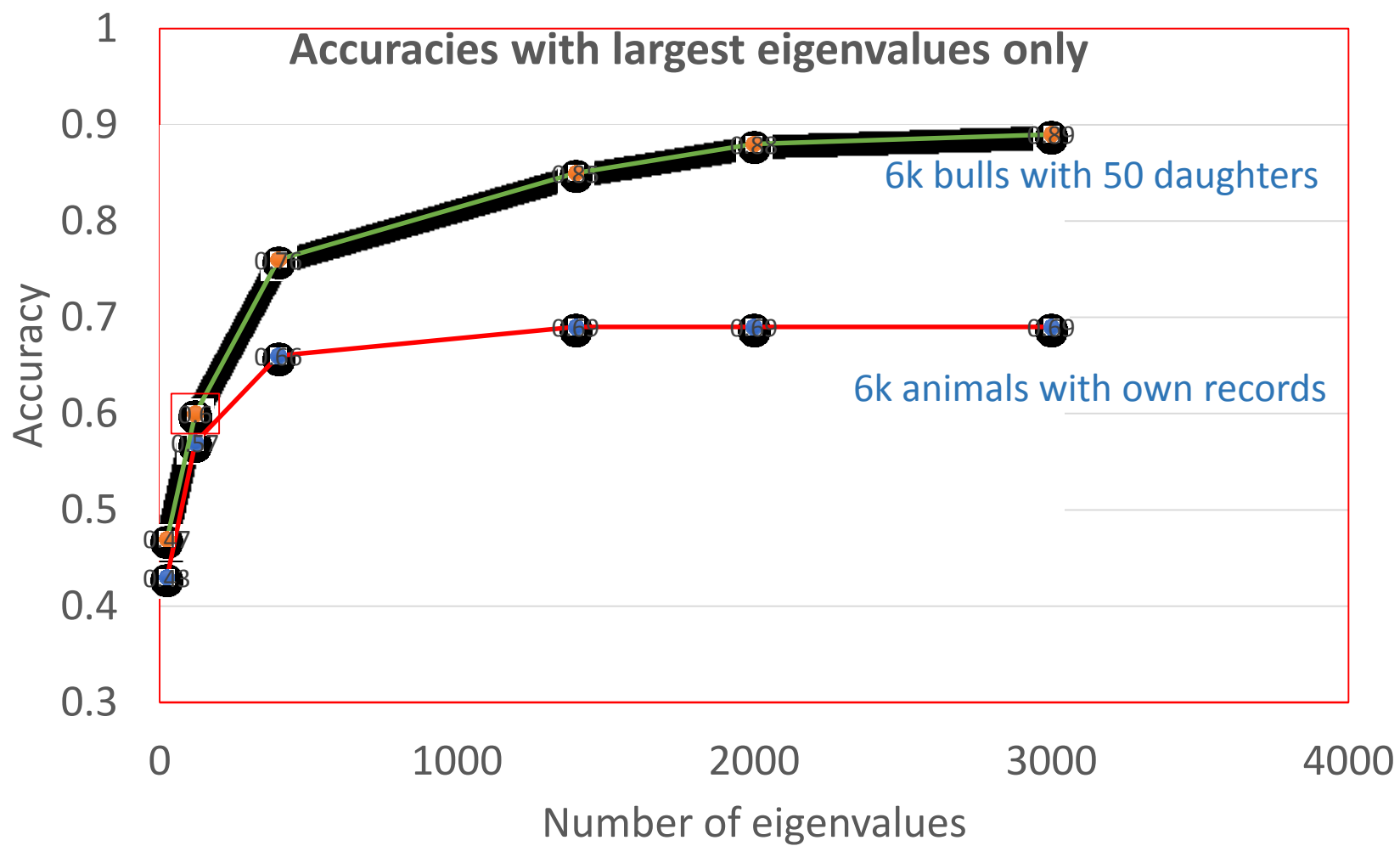
➔ Reduced dimensionality with weighted GRM

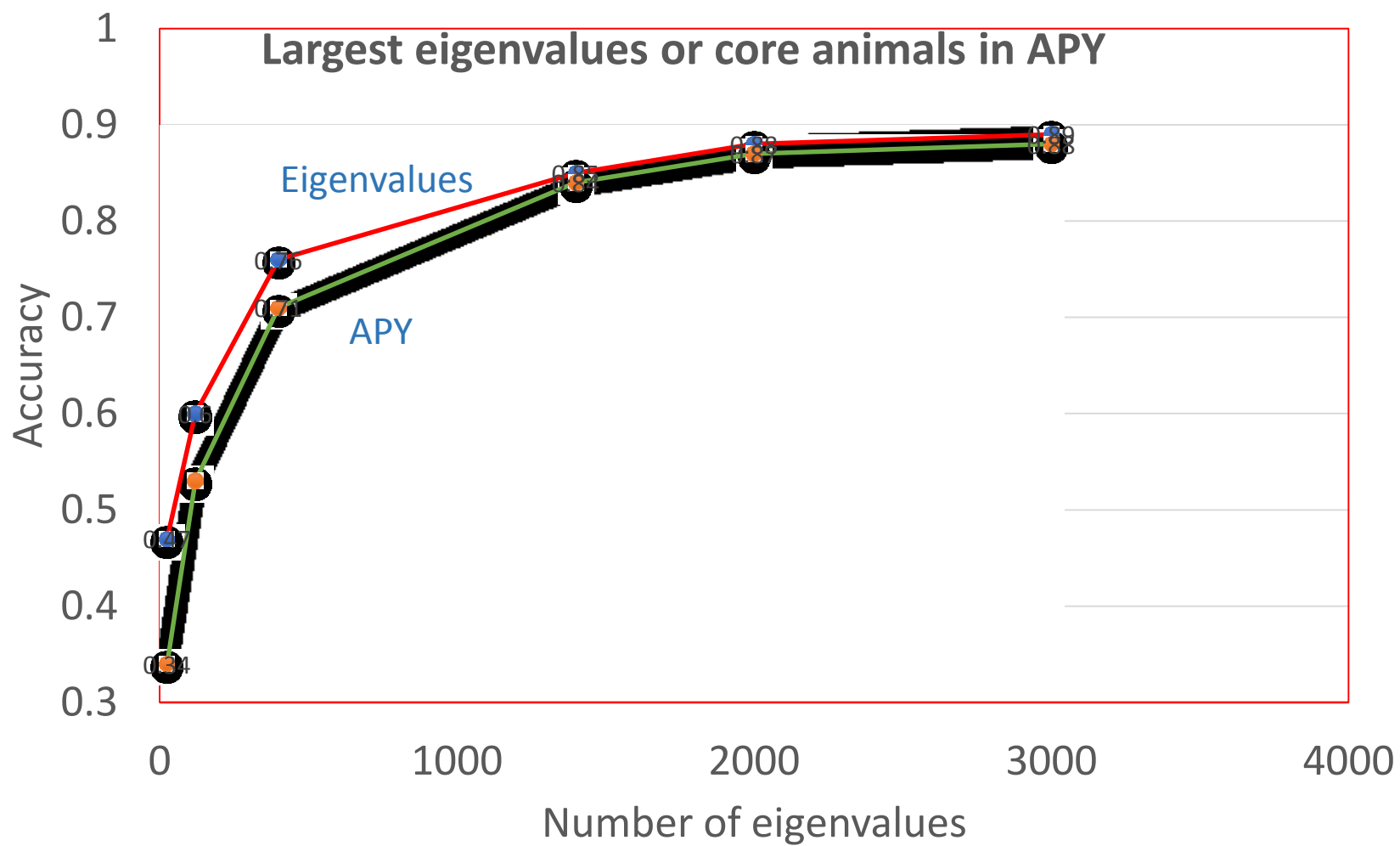
Eigenvalue profile



Accuracies with largest eigenvalues only







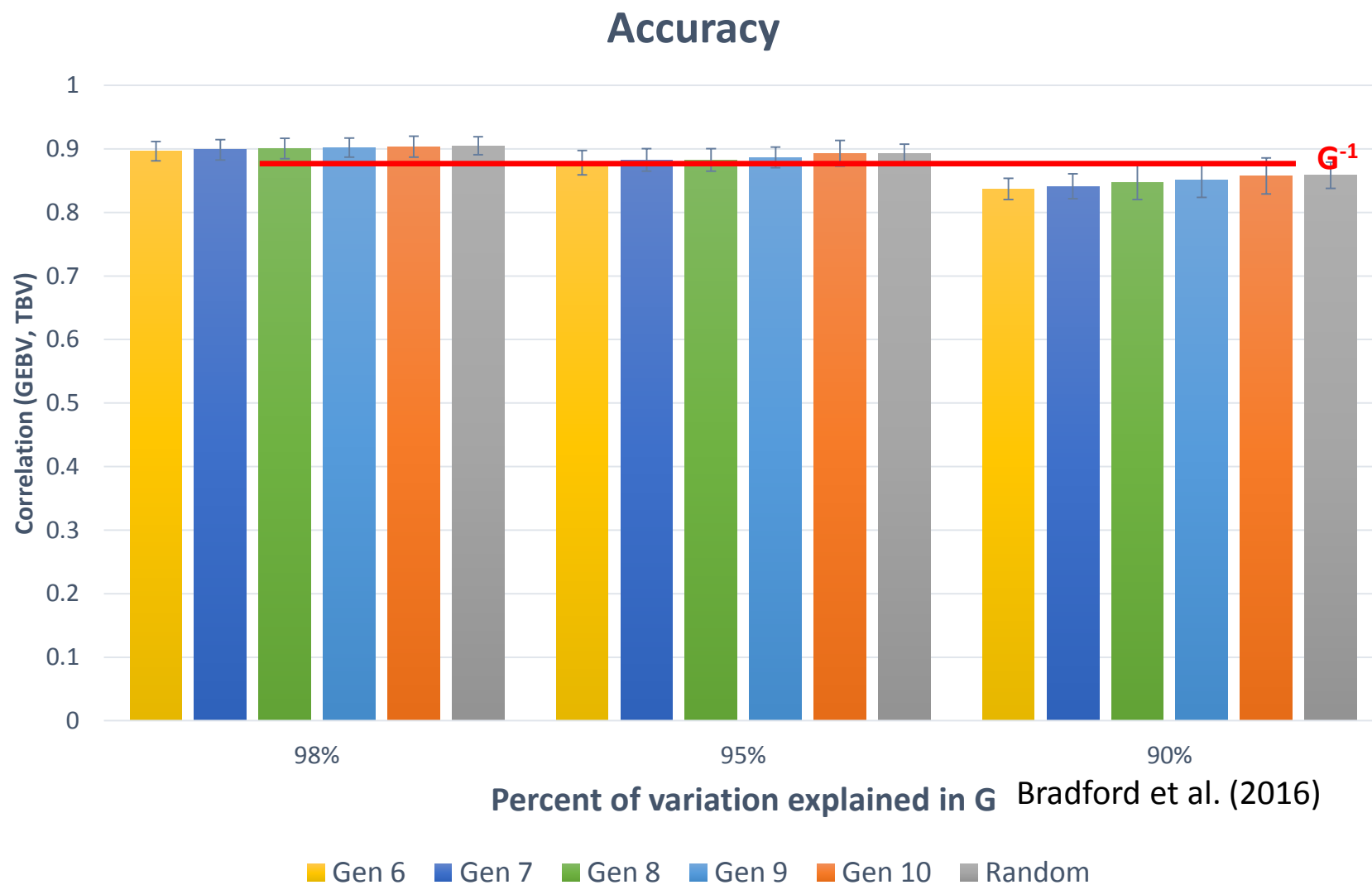


Which core animals in APY?

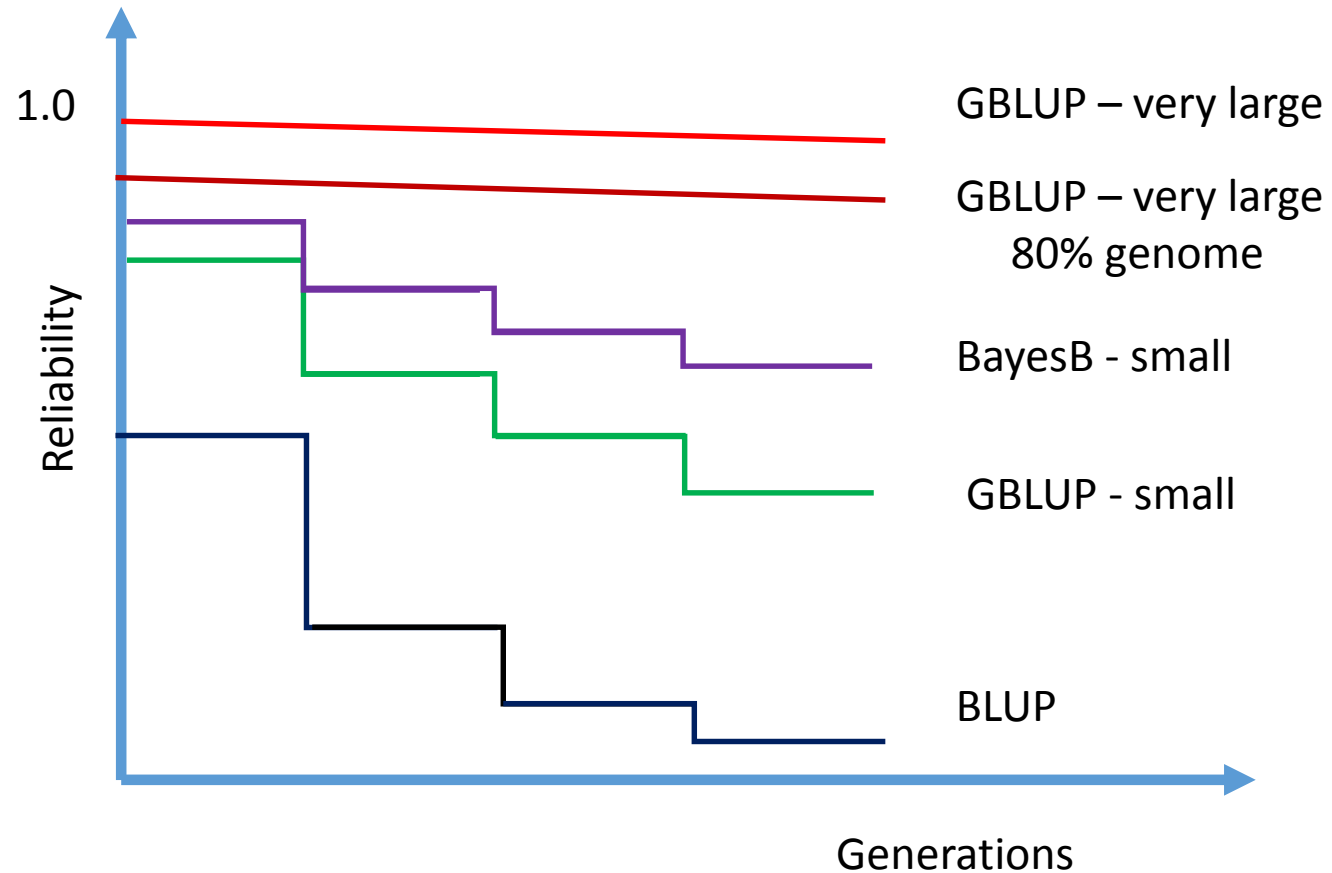
Bradford et al. (2017)

- Simulated populations (QMSim; Sargolzaei and Schenkel, 2009)
- $N_e = 40$
- #genotyped animals = 50,000
- Core animals:
 - Random gen 6 || gen 7 || gen8 || gen9 || gen 10 (y)
 - Random all generations
 - Incomplete pedigree
 - Genotypes in gen 9 and 10 imputed with 98% accuracy

Which core animals in APY?



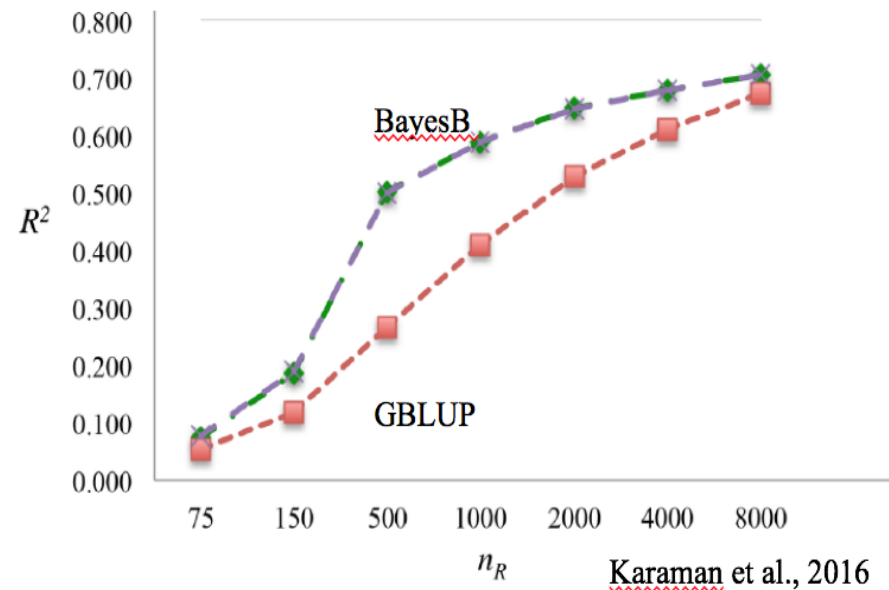
Persistence over generations



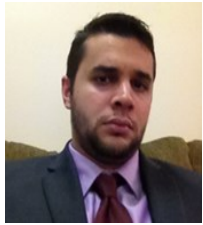
Very large – equivalent to 4NeL animals with 99% accuracy
Are SNP effects from Holstein national populations converging

Multitrait ssGBLUP: Is SNP selection important? Causative SNPs?

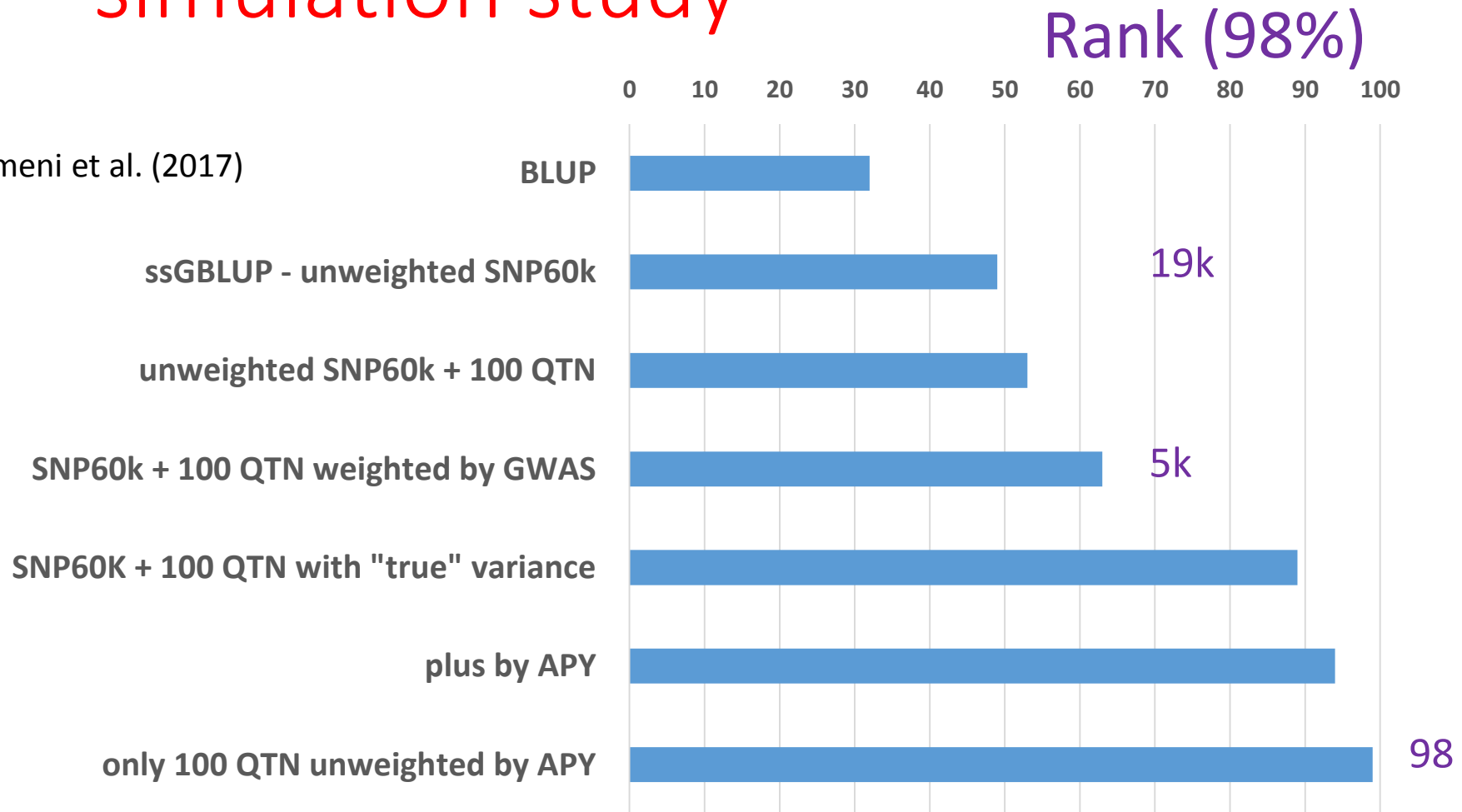
- SNP selection/weighting (BayesB, etc.)
 - Large impact with few genotypes
 - Little or no impact with many



ssGBLUP accuracies using SNP60K and 100 QTNs – simulation study

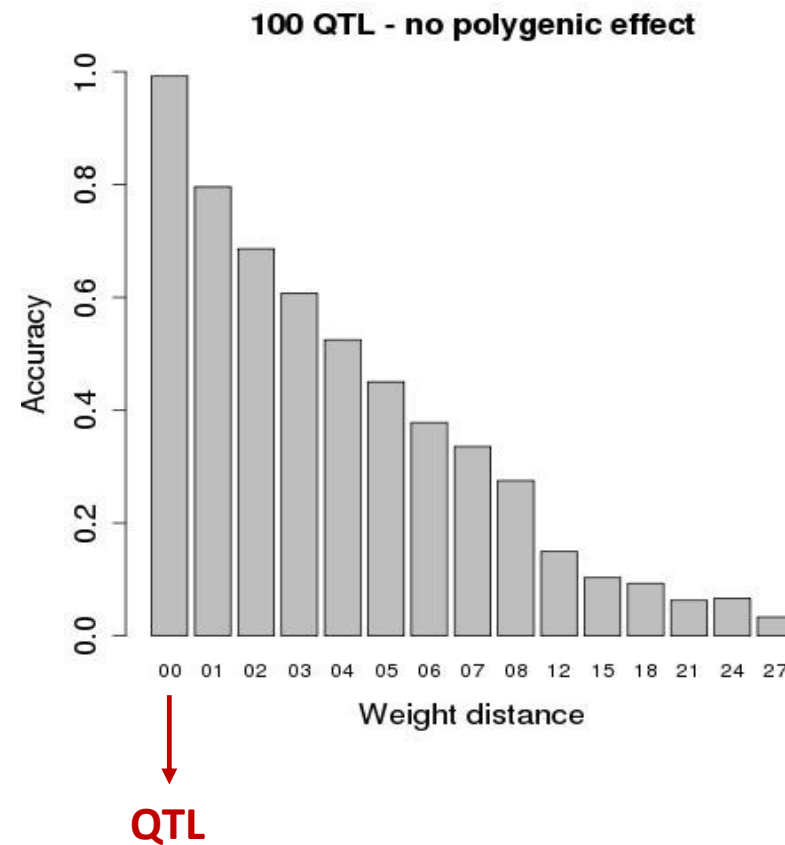


Fragomeni et al. (2017)



Accuracy and distance from markers to QTL

Fragomeni et al. (2017)



Nothing can be more fatal to progress than a too confident reliance on mathematical symbols; for the student is only too apt to take the easier course, and consider the *formula* not the *fact* as the physical reality.”

Kelvin



United States
Department of
Agriculture

National Institute
of Food and
Agriculture



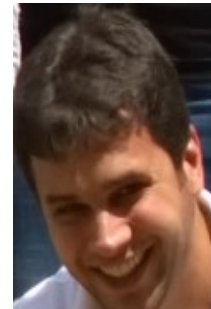
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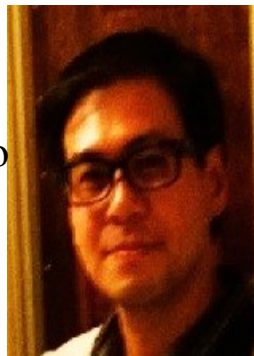
Breno
Fragomeni



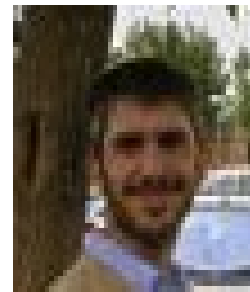
Ivan
Pocrnic



Daniela
Lourenco



Yutaka
Masuda



Andres
Legarra



Heather
Bradford

EDITORIAL

Shortage of quantitative geneticists in animal breeding

More and more I receive phone calls from various breeding companies looking to hire a PhD in quantitative genetics. They inquire if I know of a graduate versed in quantitative genetics and mixed models, with some programming skills, who can speak and write passable English, has a general understanding of markers and molecular genetics, can run and troubleshoot a genetic evaluation, and in general be a problem solver. I do not know of anyone available, I reply. There were many of them 10–15 years ago, but now they are rare. If they show up, they usually have very good offers well before graduation. My colleagues outside the USA are telling me of similar problems, although the severity of the PhD shortage is country dependent.

Why are PhDs in animal breeding with quantitative skills rare in the USA as well as in many other countries? Some 15 years ago there was a shift in governmental funding away from animal breeding and quantitative genetics to almost exclusively

Great hopes were put into finding markers for major genes (QTL) that could help solve the new challenges. Based on many association studies, there is growing consensus that few markers/QTLs can be detected, those that were detected had their estimated effects inflated, and that the benefits of using markers are limited. Of all markers found, very few were for low-heritability traits.

The new trend in animal breeding is genomic selection using SNP chips. In this methodology, one estimates effects of individual haplotypes, and genomic EBV (GEBV) is estimated as a sum of those effects. No effort is made to identify QTLs. The genomic selection is based on an assumption opposite from the previous effort in markers but the same as in 'black box' genetics: that a large number of genes are responsible for a trait.

When only a small fraction of the population is genotyped, the estimates of haplotype effects will be derived via EBV obtained through classical methods

Development of the combined matrix

Initial (Misztal et al., 2009)

$$\mathbf{H} = \mathbf{A} + \begin{bmatrix} 0 & 0 \\ 0 & \mathbf{G} - \mathbf{A}_{22} \end{bmatrix}$$

1-ungenotyped animals
2-genotyped animals

Comprehensive (Legarra, 2009)



$$\mathbf{H} = \mathbf{A} + \begin{bmatrix} \mathbf{A}_{12}\mathbf{A}_{22}^{-1} & \mathbf{0} \\ \mathbf{0} & \mathbf{I} \end{bmatrix} \begin{bmatrix} \mathbf{I} \\ \mathbf{I} \end{bmatrix} [\mathbf{G} - \mathbf{A}_{22}] \begin{bmatrix} \mathbf{I} & \mathbf{I} \end{bmatrix} \begin{bmatrix} \mathbf{A}_{22}^{-1}\mathbf{A}_{21} & \mathbf{0} \\ \mathbf{0} & \mathbf{I} \end{bmatrix}$$

Inverse of Comprehensive (Aguilar et al., 2010)

$$\mathbf{H}^{-1} = \mathbf{A}^{-1} + \begin{bmatrix} 0 & 0 \\ 0 & \mathbf{G}^{-1} - \mathbf{A}_{22}^{-1} \end{bmatrix}$$

Christensen and Lund, 2010
Boemcke et al., 2010

Implementation at UGA

- Module genomic in BLUPF90 package (Aguilar et al. 2011)
- Option SNP_File xxx in RENUMF90
- Lots of options with defaults
- Creation of \mathbf{G}^{-1} : minutes for 10k genotypes, hours for 50k genotypes



Predictions for US final scores in Holsteins (Aguilar et al., 2010)

Prediction in 2004	DD2009	
	R ² (%)	Inflation (%)
Parent Avg	24	31
Multistep (VanRaden)	+16	16
Single-step		
Regular $G^{-1}-A_{22}^{-1}$	+17	31
Refined $1.5G^{-1}-0.6A_{22}^{-1}$	+17	4



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March 2010 (Vol. 93 | No. 3 | Pages 978-987)

E. Rollin, R.D. Berghaus, P. Rapnicki, S.M. Godden, M.W. Overton

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2011

Multitrait national genomic evaluation for type (Tsuruta et al., 2010)

- US Holsteins (10 million animals)
- 18 traits
- Almost 50,000 genotypes of bulls and cows
- 2 days computing



J. Dairy Sci. 94:4198–4204

doi:10.3168/jds.2011-4256

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Multiple-trait genomic evaluation of linear type traits using genomic and phenotypic data in US Holsteins

S. Tsuruta,^{*1} I. Misztal,^{*} I. Aguilar,[†] and T. J. Lawlor[‡]

^{*}Animal and Dairy Science Department, University of Georgia, Athens 30602

[†]Instituto Nacional de Investigación Agropecuaria, Las Piedras, Canelones 90200, Uruguay

[‡]Holstein Association USA Inc., Brattleboro, VT 05301



Genomic evaluations of broiler chicken (Chen et al., 2010)

- 180k broiler chicken
- 3 k genotyped with SNP60k chip
- 3 methods
 - BLUP- full data
 - BayesA – genotyped subset
 - Single step – subset and full data set

Genome-wide marker-assisted selection combining all pedigree
phenotypic information with genotypic data in one step:
An example using broiler chickens

C. Y. Chen,^{*1,2} I. Misztal,^{*} I. Aguilar,^{*†} S. Tsuruta,^{*} T. H. E. Meuwissen,[‡]
S. E. Aggrey,[§] T. Wing,[#] and W. M. Muir^{||}

^{*}Department of Animal and Dairy Science, University of Georgia, Athens 30602-2771; [†]Instituto Nacional de Investigación Agropecuaria, Las Brujas 90200, Uruguay; [‡]Department of Animal and Aquacultural Sciences, Norwegian University of Life Sciences, NO-1432 Ås, Norway; [§]Department of Poultry Science, University of Georgia, Athens 30602-2772; [#]Cobb-Vantress Inc., PO Box 1030, Siloam Springs, AR 72761-1030; and ^{||}Department of Animal Science, Purdue University, West Lafayette, IN 47907-1151

Accuracies for broiler chickens

Trait	Accuracy*100			
	BLUP	BayesA Subset	Single-step Subset	Single-step Full
Body Weight	56	+4	+11	+12
Breast Meat	35	+1	+0	+6
Leg Score	29	-20	-23	+7

BayesA – days of
computing + errors

Single-step –
2 minutes

Next cycle of selection

Multiple trait

Body Weight	38		+13	+22	=
Breast Meat	39		+10	+26	+29
Leg Score	28		-21	+6	=

RESEARCH

Open Access

Different genomic relationship matrices for single-step analysis using phenotypic, pedigree and genomic information

Selma Forni^{1*}, Ignacio Aguilar^{2,3}, Ignacy Misztal³

Effect of different genomic relationship matrices on accuracy and scale¹

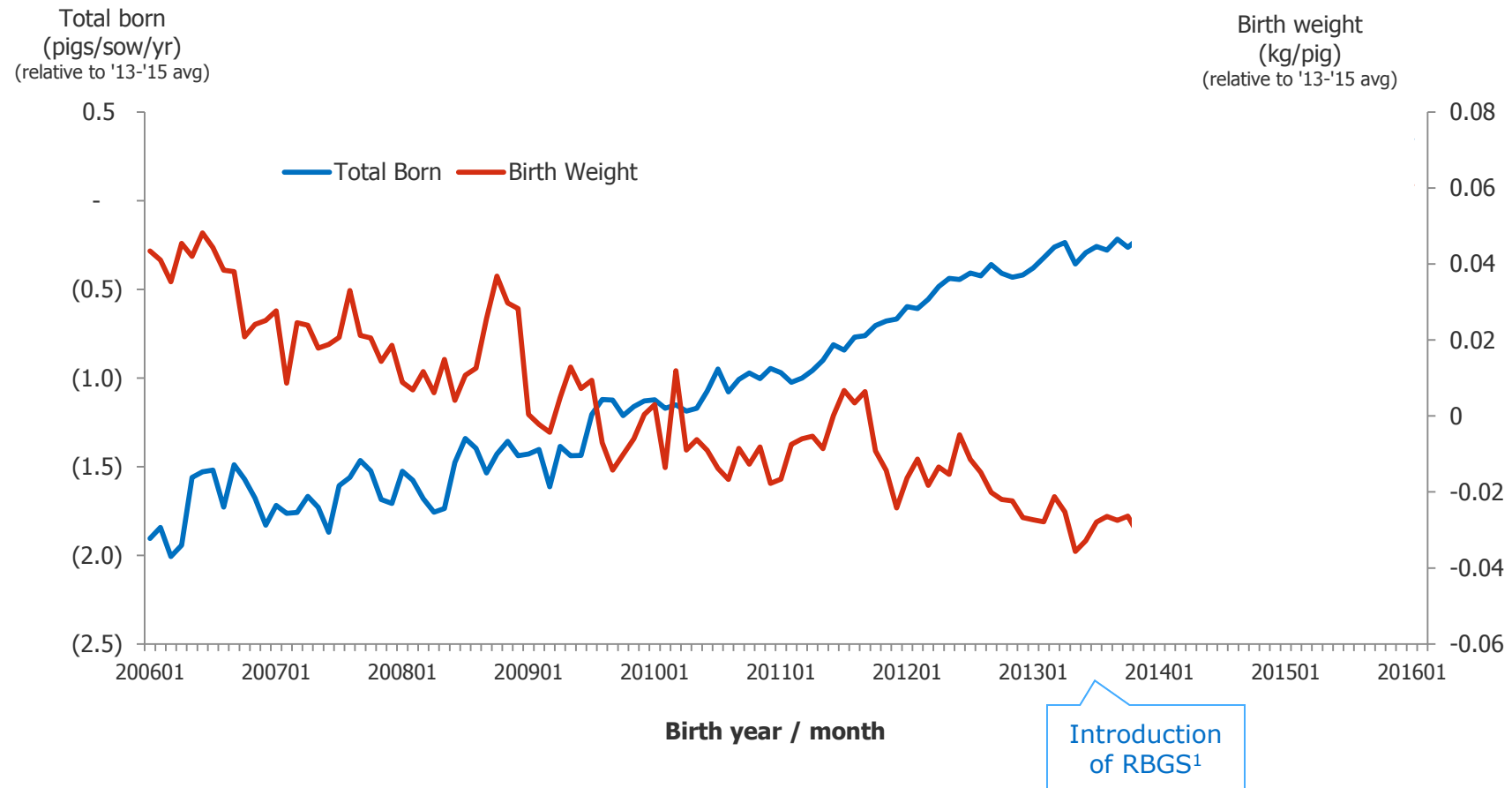
C. Y. Chen,^{*2,3} I. Misztal,^{*} I. Aguilar,^{*†} A. Legarra,[‡] and W. M. Muir[§]

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[†]Instituto Nacional de Investigación Agropecuaria, Las Brujas 90200, Uruguay;

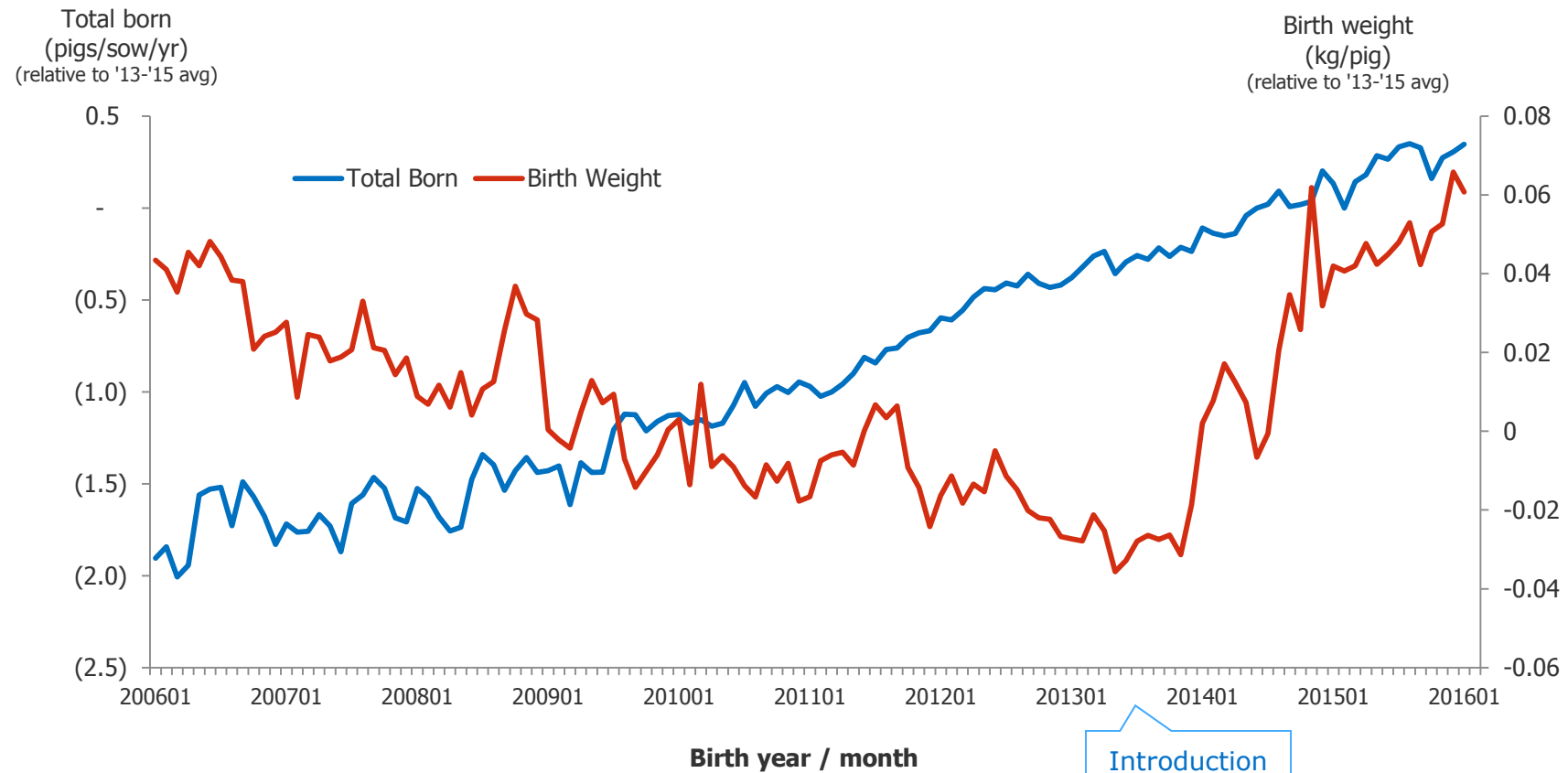
[‡]INRA, UR631 Station d'Amélioration Génétique des Animaux (SAGA), BP 52627, 32326 Castanet-Tolosan, France; and [§]Department of Animal Science, Purdue University, West Lafayette, IN 47907-1151

Trend: genetic improvement in birth weight and total born (PIC Genetic Nucleus)



1. Relationship based genomic selection
Source: PIC L02, L03 pure lines (Camborough)

Trend: genetic improvement in birth weight and total born (PIC Genetic Nucleus)



1. Relationship based genomic selection
Source: PIC L02, L03 pure lines (Camborough)



EDITORIAL

FAQ for genomic selection

Genomic selection has been practiced in many species and in many organizations. In some cases, the results have been spectacular, and in some not. When the results fall short of expectations, questions remain as to whether they were because of inadequate statistics, too small chip size, problems with quality control or basic issues. In the end, one wonders what the limits of genomic selection are, and what will follow it. Based on published and unpublished results on genomic selection, one can prepare a FAQ sheet. Here it is. While looking at it, remember that FAQs change over time.

I have heard that with 1000 animals genotyped and phenotyped I will have accurate predictions for many generations. Is this true? *Not really. One needs more genotypes and the genomic associa-*

number of recent ancestors in the reference population. If that number is high and the populations are strongly linked, the accuracy may be decent. If that number is low, the accuracy will be close to 0. In the extreme, the genomic prediction for a different population, while ignoring the parent average, may be less accurate than the regular EBV.

Are prediction equations developed with one breed useful for other breeds? *They are not. They would be if SNP effects were gene effects that are similar across breeds. However, SNP effects point mostly to common haplotypes of recent ancestors, or in other words, we are getting 'better' additive relationships.*

If this is the case, what fraction of the additive variability is explained by genes or closely

ssGBLUP for Genome Wide Association Studies

- Large research interest in GWAS
- Limitations if Bayesian methods
 - Simple models
 - Single trait
 - Complicated if not all animals genotyped



Can ssGBLUP be used for GWAS?

Genet. Res., Camb. (2012), **94**, pp. 73–83. © Cambridge University Press 2012
doi:10.1017/S0016672312000274

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Genome-wide association mapping including phenotypes
from relatives without genotypes

H. WANG¹*, I. MISZTAL¹, I. AGUILAR², A. LEGARRA³ AND W. M. MUIR⁴

¹Department of Animal and Dairy Science, University of Georgia, Athens, GA 30602-2771, USA

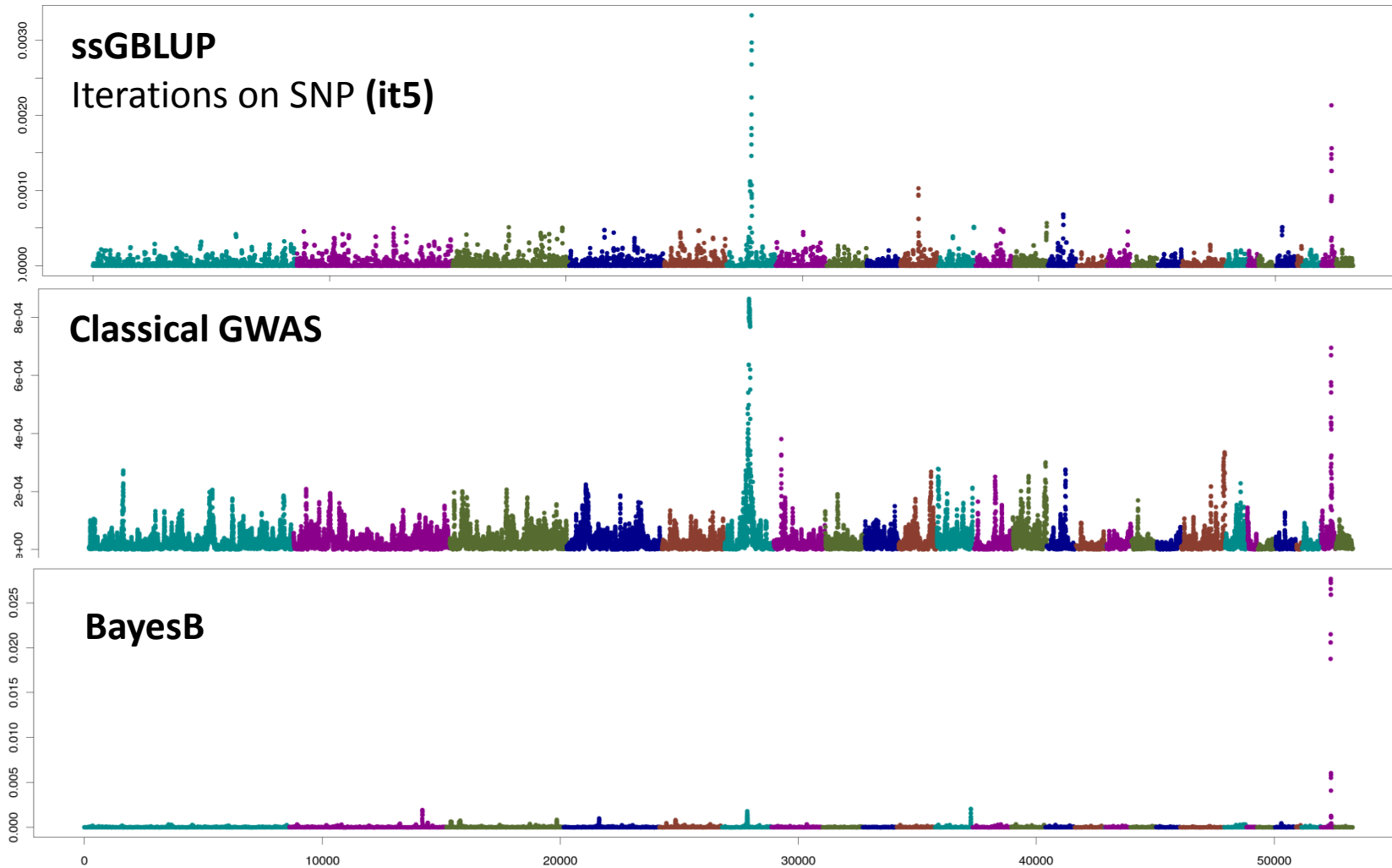
²Instituto Nacional de Investigación Agropecuaria, INIA Las Brujas, 90200 Canelones, Uruguay

³INRA, UR631 Station d'Amélioration Génétique des Animaux (SAGA), BP 52627, 32326 Castanet-Tolosan, France

⁴Department of Animal Science, Purdue University, West Lafayette, IN 47907-1151, USA

(Received 19 September 2011; revised 8 December 2011, and 9 March 2012; accepted 13 March 2012)

Three Methods for GWAS – chicken

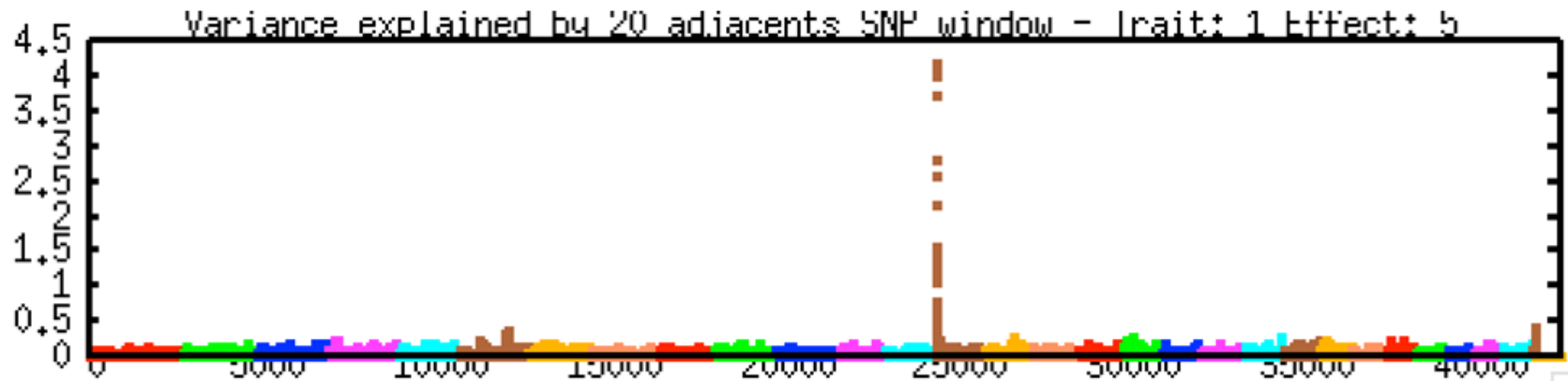


Can large QTL exist despite selection?

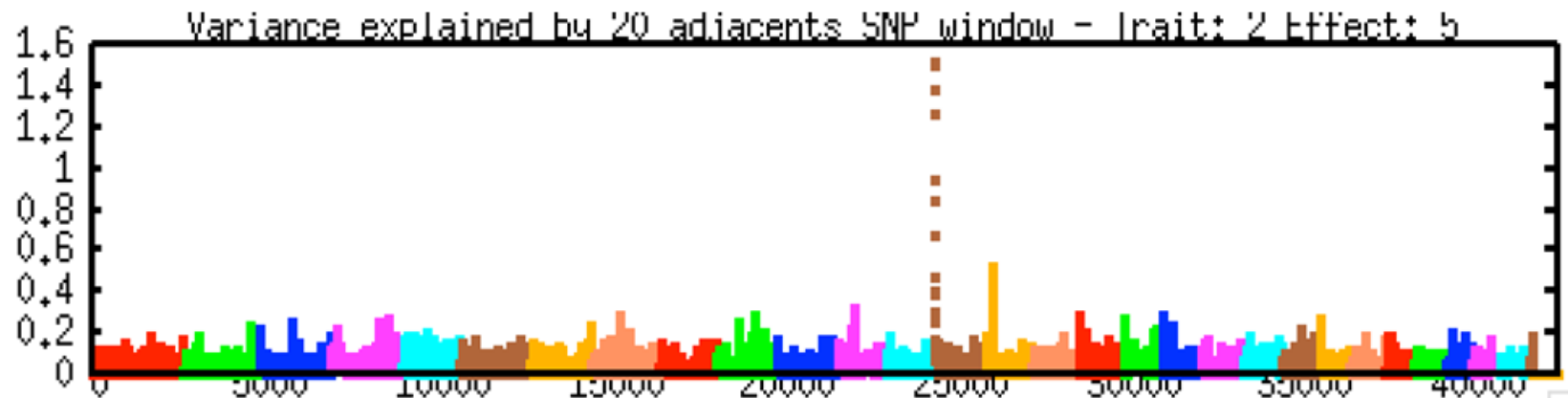


- Genetics and genomics of mortality in US Holsteins
- (Tokuhisa et al, 2014; Tsuruta et al., 2014)
- 6M records, SNP50k genotypes of 35k bulls

Milk – first parity

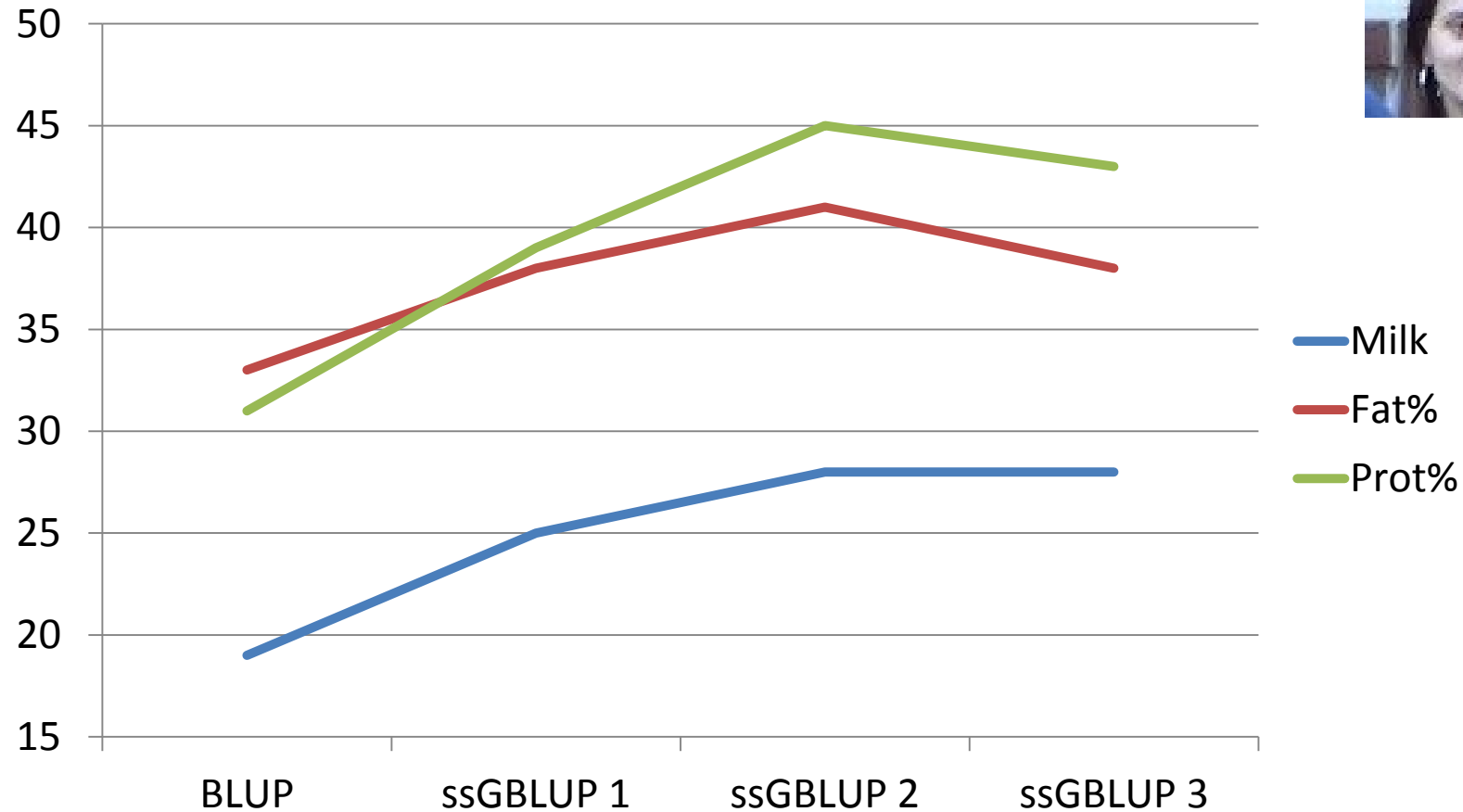
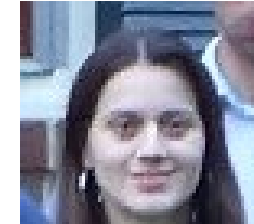


Mortality – first parity



R^2 in Israeli dairy – 1400 genotypes

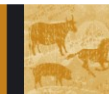
(Lino et al., 2012)



Why unknown parent groups

- Different lines or breeds (Harris and Johnson, 2012)
- Unrecorded parents across generations

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ORIGINAL ARTICLE

Unknown-parent groups in single-step genomic evaluation

I. Misztal¹, Z.G. Vitezica², A. Legarra³, I. Aguilar⁴ & A.A. Swan⁵

¹ Department of Animal and Dairy Science, University of Georgia, Athens, GA, USA

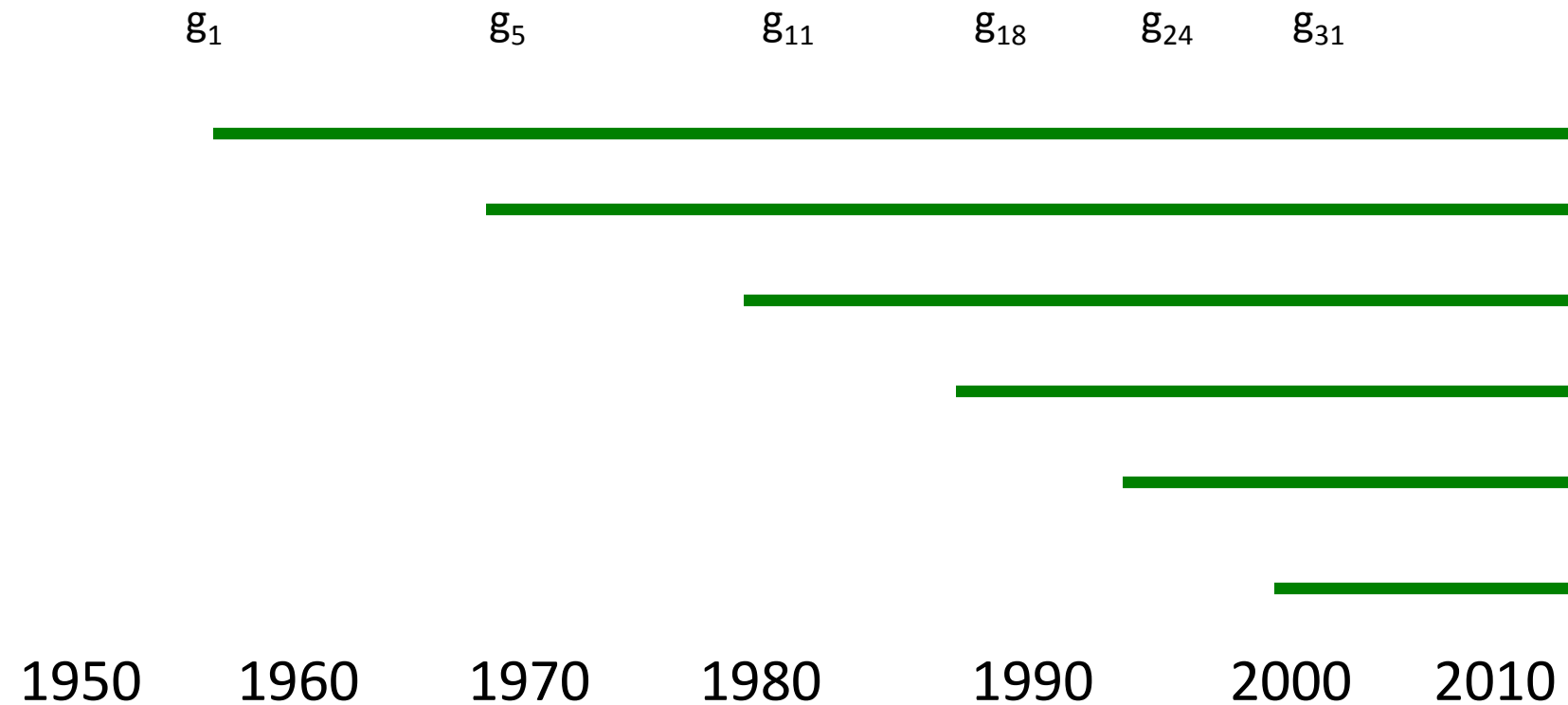
² Université de Toulouse, UMR 1289 TANDEM, INRA/INPT-ENSAT/ENVIT F-31326, Castanet-Tolosan, France

³ INRA, Station d'Amélioration Génétique des Animaux, Castanet-Tolosan, France

⁴ Instituto Nacional de Investigación Agropecuaria,, Las Brujas, Uruguay

⁵ Animal Breeding and Genetics Unit, University of New England, Armidale, NSW, Australia

Pedigree depth for young animals



Pedigree length and convergence

$$\mathbf{H}^{-1} = \mathbf{A}^{-1} + \begin{bmatrix} \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{G}^{-1} - \mathbf{A}_{22}^{-1} \end{bmatrix}$$

Big \mathbf{A}_{22} makes \mathbf{H} less PD,
Reduces convergence rate

$$\mathbf{G}^{-1} - \mathbf{A}_{22}^{-1}$$

Good convergence and genotyped animals biased down

$$\mathbf{G}^{-1} - \mathbf{A}_{22}^{-1}$$

Bad convergence and genotyped animals biased up

$$\mathbf{G}^{-1} - \mathbf{A}_{22,1}^{-1} - \mathbf{A}_{22,2}^{-1} - \mathbf{A}_{22,3}^{-1}$$

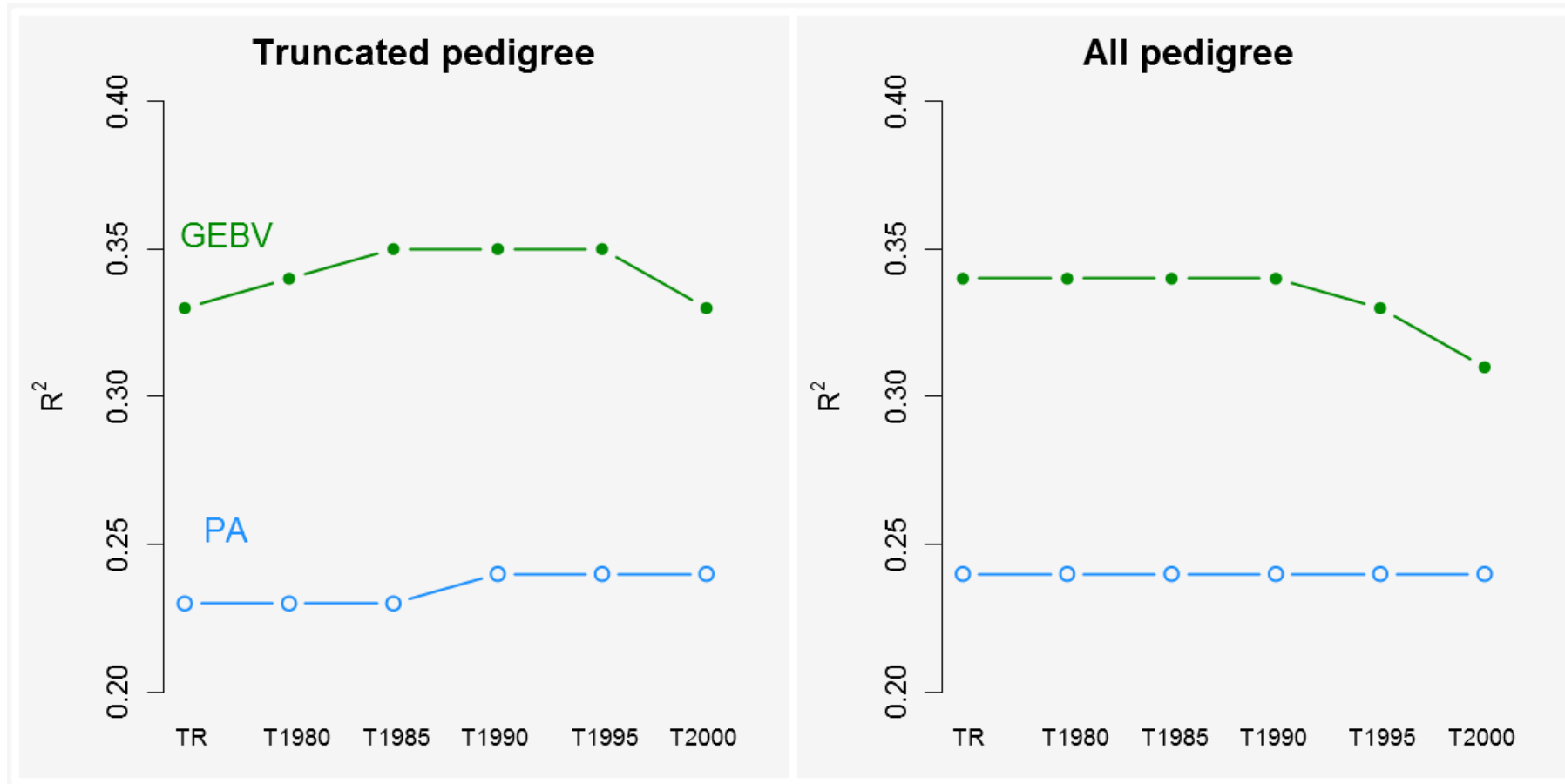
Long medium short
pedigrees

Bad convergence and genotyped
animals biased down and up

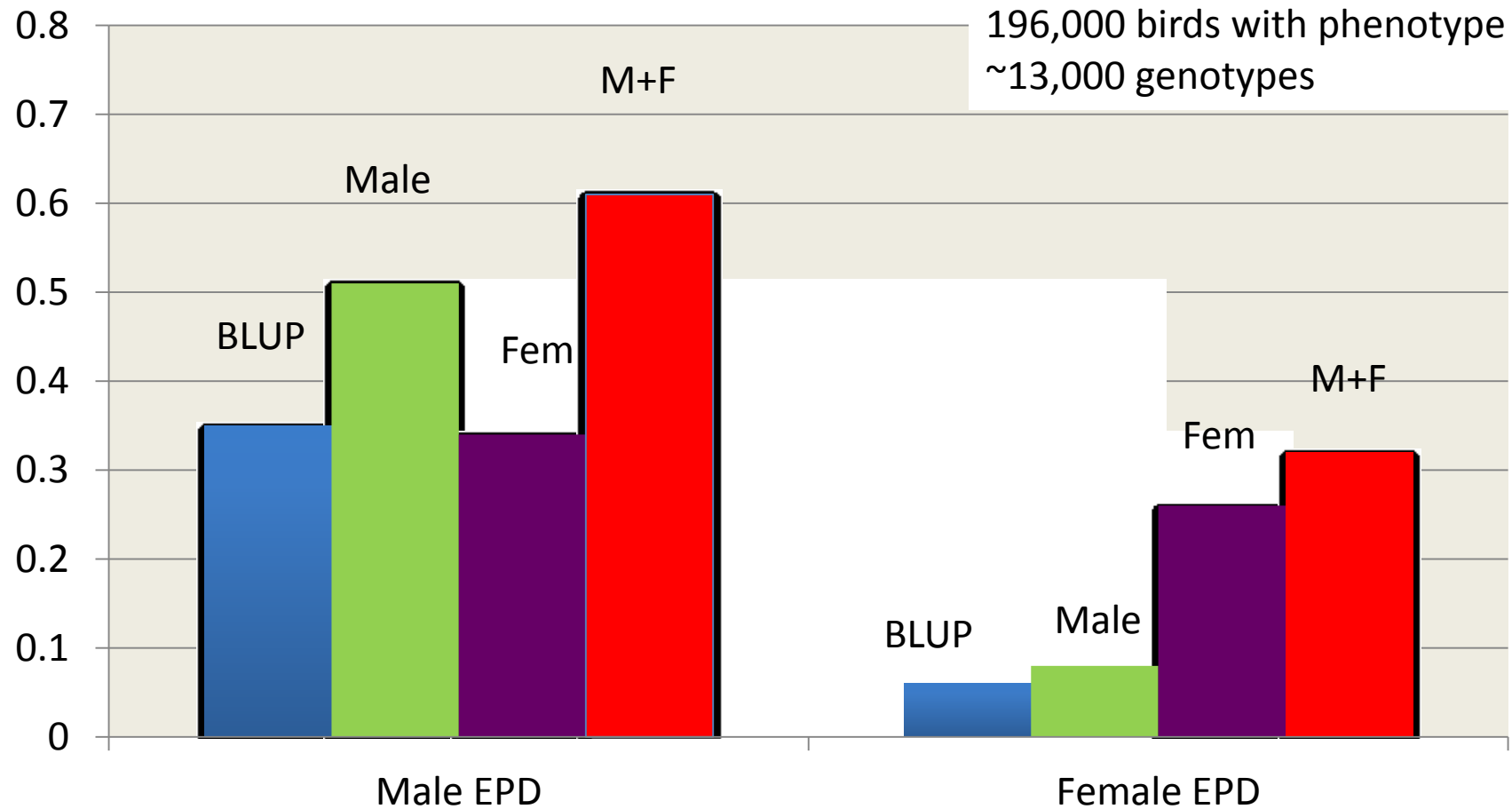
Cut pedigree and data?



US Holsteins – final scores

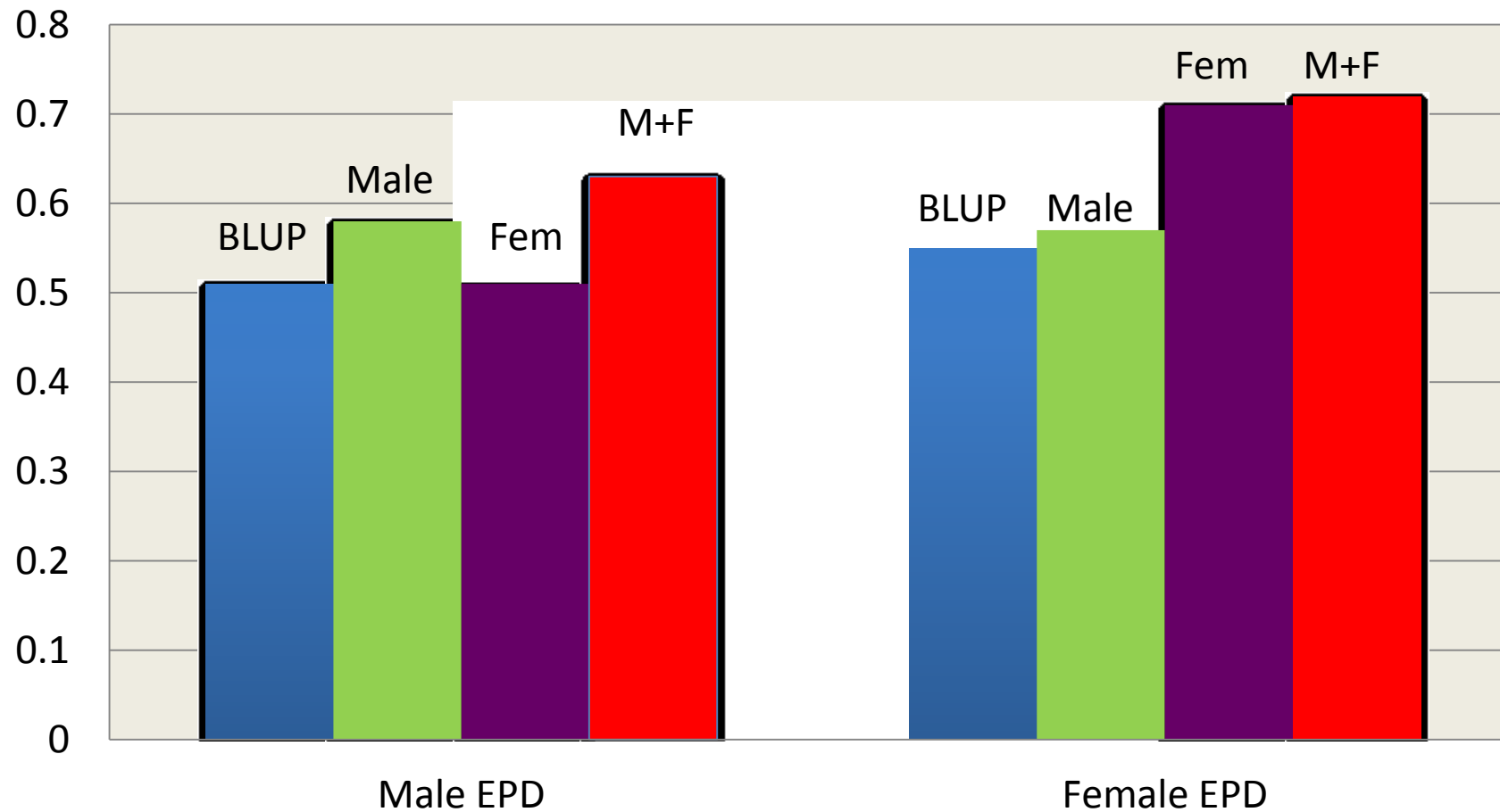


Realized broiler accuracies with male, female or both genotypes – Trait A



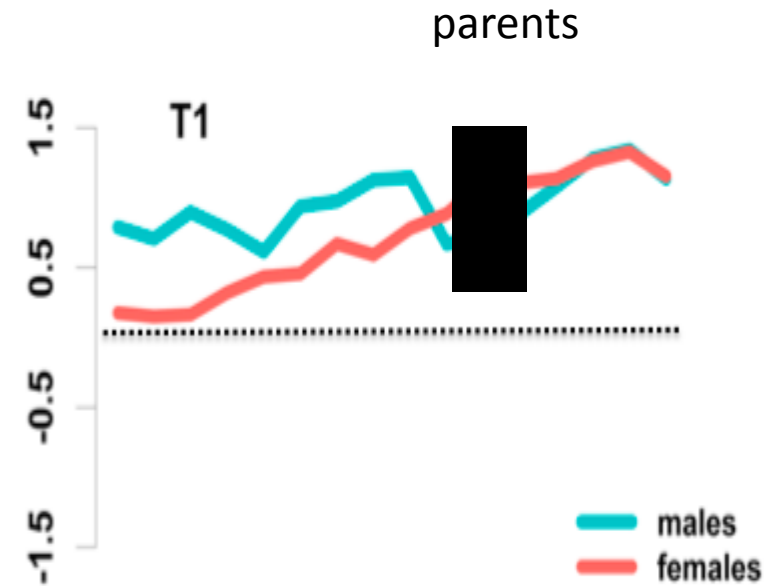
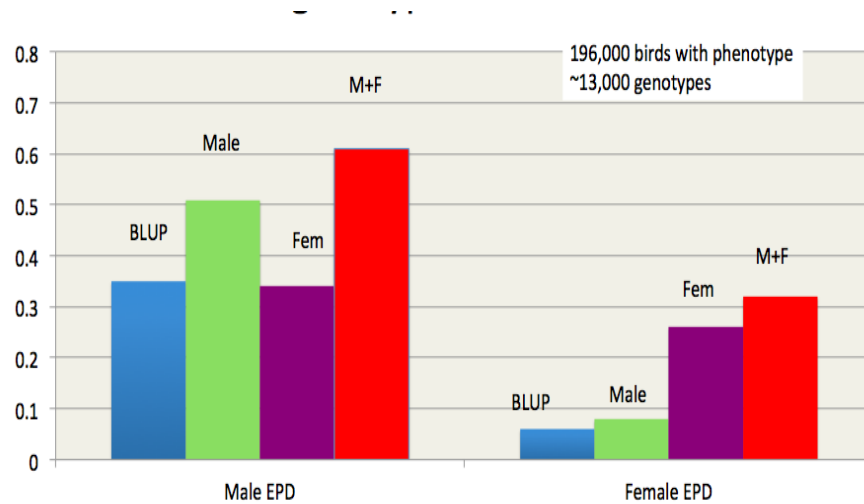
(Lourenco et al., submitted)

Realized accuracies with male, female or both genotypes – Trait D



(Lourenco et al., in prep)

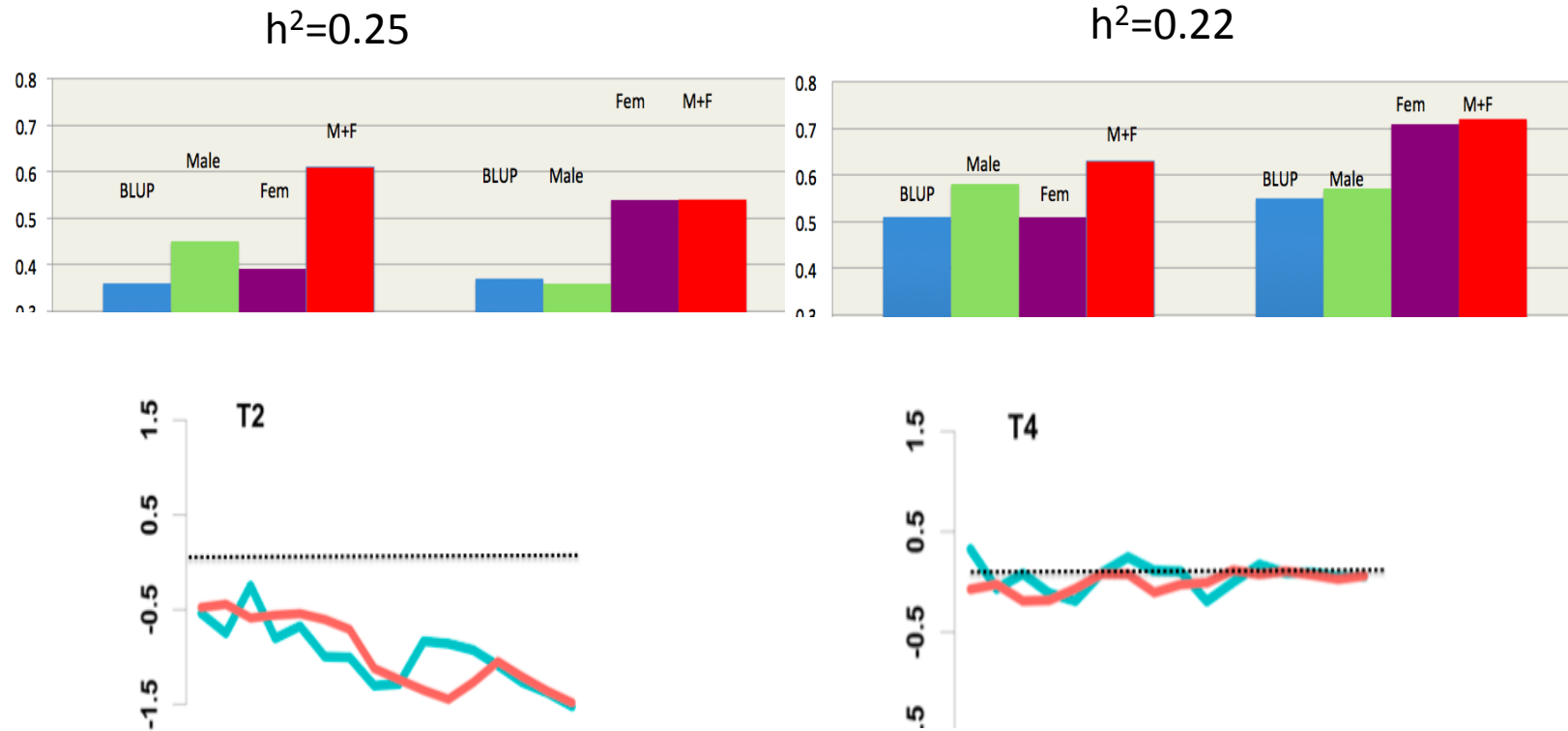
Why realized accuracies differ by sex?



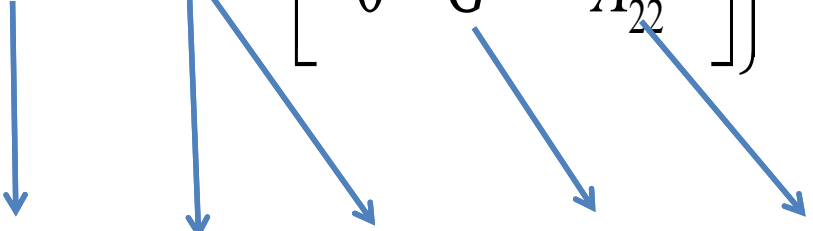
Bigger selection pressure on females

Selection graph for GEBV; possibly more differential selection EBV from BLUP

Why realized accuracies differ by traits for similar h^2



Decomposition of GEBV in Single-step

$$\left\{ Z'MZ + \alpha A^{-1} + \begin{bmatrix} 0 & 0 \\ 0 & G^{-1} - A_{22}^{-1} \end{bmatrix} \right\} \hat{u} = Z'My$$


$$GEBV = w_1 CD + w_2 PA + w_3 PC + w_4 DGV + w_5 PI$$

$$\square w_1 = 1$$

CD – contemporary
deviation
PA – Parent average
PC – Progeny
Contribution

DGV – direct genomic
value
PI – Parental Index

No genotype, no extra accuracy

GEBV for young animals

Complete $GEBV = w_2 PA + w_4 DGV + w_5 PI$

If genotype via SNP only $GEBV = DGV$

If no genotype $GEBV = PA$

Little improvement with genomics if animal not genotyped

EDITORIAL

Is genomic selection now a mature technology?

A couple of years ago, I wrote 'FAQ for genomic selection' in JABG (Volume 8, 245–246), and statements there are still intact IMHO. With many new studies, many murky points became clear and new puzzles appeared.

The genetic evaluation by BLUP became mature technology after the discovery of inexpensive inverse of the numerator relationship matrix (Henderson) and computing methodologies by iteration on data (Schaeffer). Then, the largest evaluations could be conducted by BLUP. Refinements continued, but the main steps were done. One can wonder whether now the genomic selection is also a mature technology.

validation continues. Properties of a particular validation are clearer by looking at the decomposition of GEBV into five components: parent average, yield deviation, progeny contribution, direct genomic value and pedigree index [e.g. Lourenco *et al.*, (2015) *Genet. Sel. Evol.*, **47**:56]. One big plus of a genomic validation is that it usually includes BLUP validation, often exposing problems in BLUP models such as excessive complexity. Good BLUP models are important as bad EBVs usually mean bad GEBVs. Realized accuracies may be very low due to strong selection [Bijma (2012) *J Anim Breed Genet.*, **129**:345–358].

Single-step GBLUP (ssGBLUP) became a universally

New studies

- Unbiased evaluations of US Holstein with > 2 M genotypes of varying quality
- Helping Interbull survive
 - Unbiased pseudo-observations for bulls
 - GBLUP MACE
- Crossbreeding evaluation without reduction of accuracy
- Resilience and genomic selection

Programming/methodology

- Better approximations of accuracy
- Better GWAS
- GUI?

Applied studies

- Pigs
 - Mortality, survival, changing correlations
- Chickens
 - Sexual dimorphism,...
- Dairy
- Beef
 - Altitude, GxE
- Fish

- Heat stress
- GxE
- Resilience
- Theory

Trends

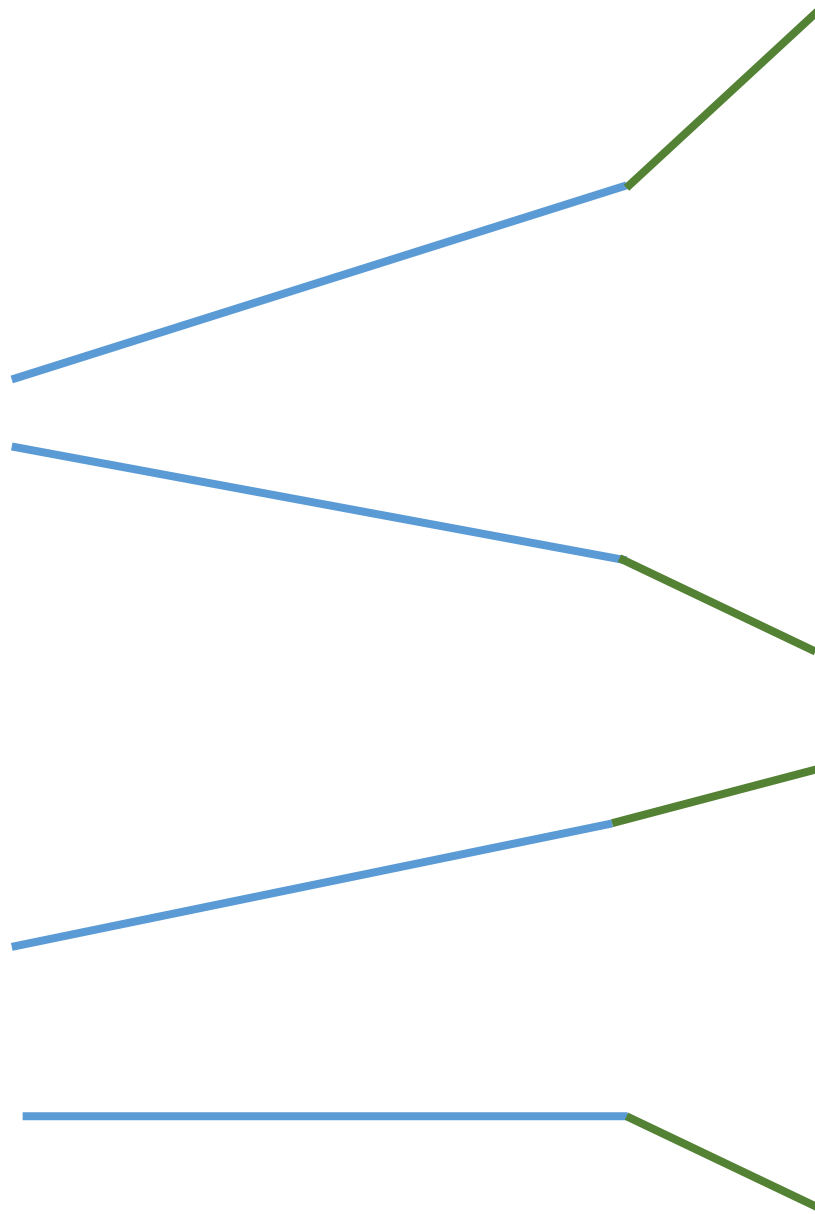
Genomic selection

Production (high h^2)

Raw fitness (low h^2)

Management

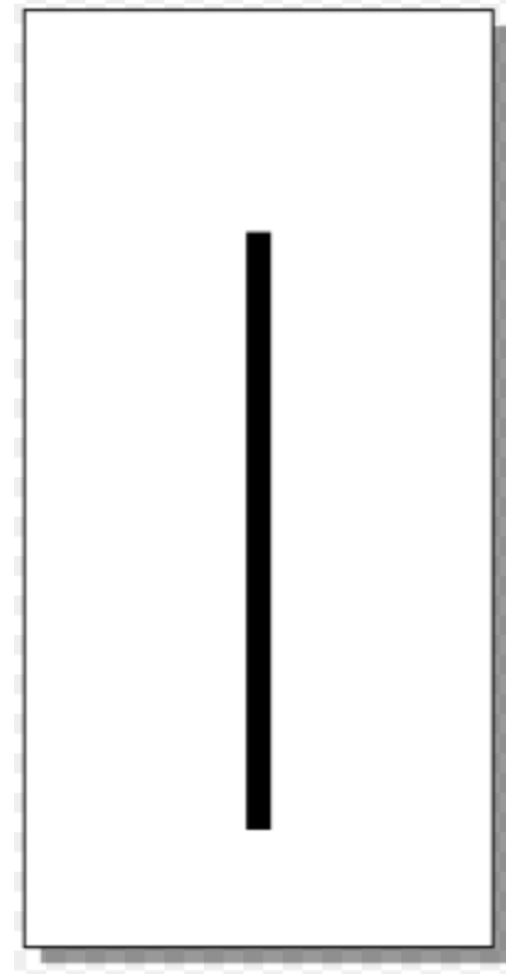
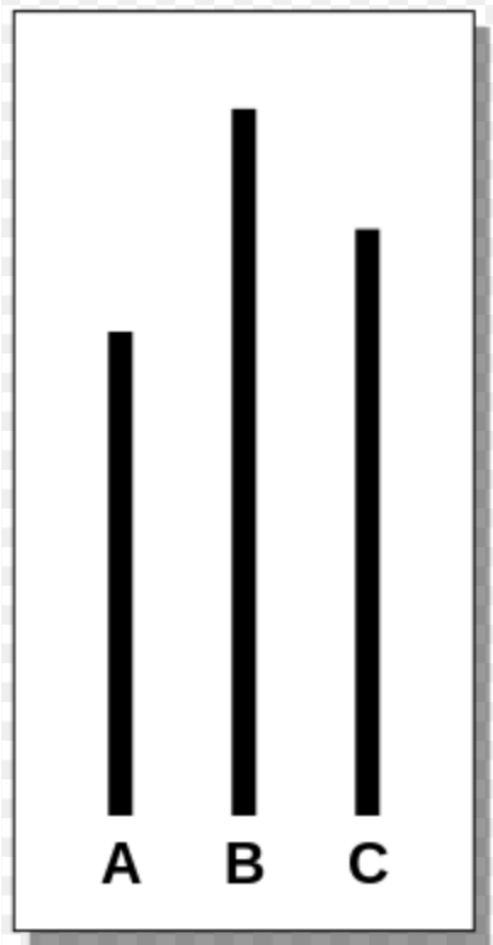
Realized fitness



Is UGA a good place to come?

- Good place for Science
- Improving South
- Politics small at universities
- Funding available
- Interesting projects
- Data from biggest animal institutions across species

Asch (1951) experiments



A, B or C?