

LIVESTOCK INBREEDING IN THE GENOMIC ERA

ANAFIBJ WORKSHOP - Managing genetic diversity in dairy

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Cremona, Italy – July 14, 2022

Inbreeding and Genomic Information

Landscape Change



Genomics to predict breeding values is now standard in animal breeding

- ▶ Adopted in pretty much all species
- ▶ Mature and effective machinery for the prediction of GEBV

In dairy > 6 million individuals have genotype information.

- ▶ Their genotypes not fully integrated or exploited

Opportunity to incorporate population/herd management at the genomic level.

- ▶ Purebred:
 - ▶ Management of Lethal and Sub-Lethal Mutations.
 - ▶ Functional Inbreeding Depression.
 - ▶ Genetic Diversity.
 - ▶ Breed/Population divergence.
 - ▶ Optimal Matching of Genomes.



The accumulation of inbreeding is unavoidable:

- ▶ Intense directional selection
- ▶ High variance of reproductive success
- ▶ Use of BLUP and truncation selection

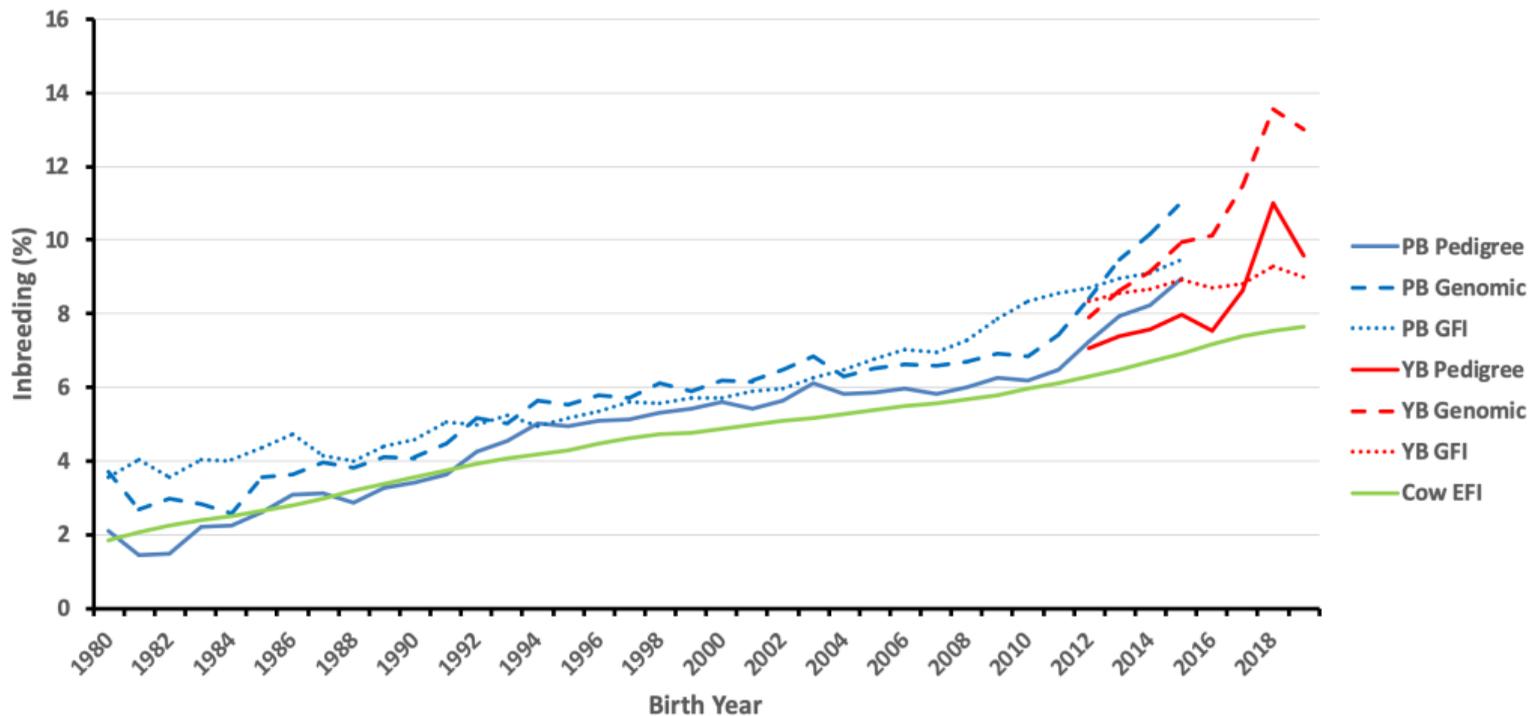
Inbreeding "**can**" reduce the mean value of a trait



- ▶ The rate of inbreeding per year increases due to shortening of generation interval
- ▶ The rate of inbreeding per generation decreases because MS is better assessed
- ▶ The rate of inbreeding per generation decreases because a larger pool of genotypes can potentially be sampled

All of these are true but the "**net**" effect is a faster accumulation of homozygosity in the population

How genomic selection influences inbreeding



Source: CDCB (April 2019) USDA

What does Inbreeding Measures

And why do we care

Inbreeding



The probability of 2 random alleles at the same locus from 2 gametes which unite to be IBD from a common ancestor Crow and Kimura, 1970

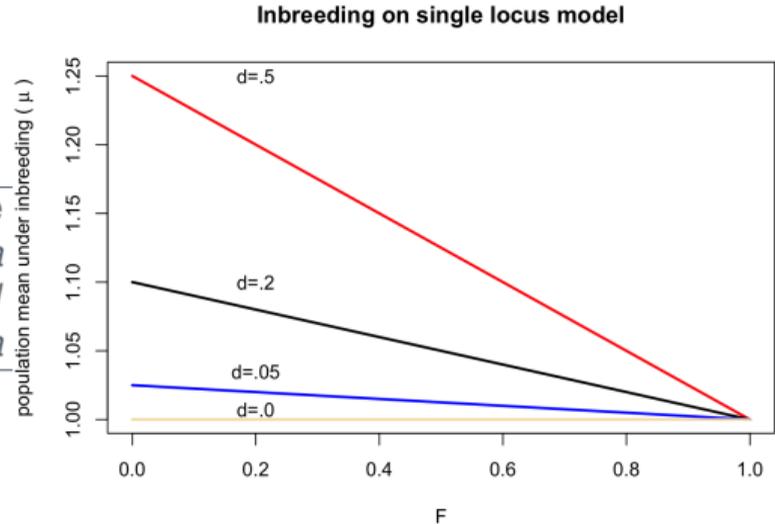
genotype	Frequency	Genotypic Value
A_1A_1	$R_{11} = p^2(1 - F) + pF$	a
A_1A_2	$2R_{12} = 2pq(1 - F)$	d
A_2A_2	$R_{22} = q^2(1 - F) + qF$	$-a$

The mean of the inbred population will therefore be:

$$\mu F = a(p - q) + 2d(1 - F)pq$$

The reduction in the population mean due to inbreeding $-2pqFd$:

<https://www.overleaf.com/project/5d09064c0cb8bb7af1c4c8e8>



Inbreeding Depression



Model	Parent genotypes	F ₁ hybrid genotypes and their fitness (or quality) relative to the parent genotypes
Recessive deleterious mutations Dominance hypothesis		
Single locus	$A/A \times a/a$	A/a Intermediate fitness but above the parental average (homozygote shows inbreeding depression)
Multiple loci (effects of different mutant alleles marked in hybrids)	$A/A \times b/b$ $a/a \times B/B$	$A/a \quad B/b$ High fitness (heterosis and inbreeding depression)
Recessive deleterious mutations at closely linked loci Pseudo-overdominance	$A \quad b$ — $A \quad b$ × $a \quad B$ — $a \quad B$	$A \quad b$ — $a \quad B$ Higher fitness than the parent genotypes
Single loci with heterozygous advantage True overdominance	A_1/A_1 × A_2/A_2	A_1/A_2 High fitness (heterosis and inbreeding depression in homozygote)

Genetic Variance Under Inbreeding



The total genetic variance in the population following inbreeding is (Weir and Cockerham, 1977)

$$V_{GF} = (1 + F)V_A + (1 - F)V_D + 4FC_{AD} + FV_H - F^2D_H$$

where V_A and V_D are the additive genetic and dominance variances in the base population ($F = 0$).

$$C_{AD} = \sum_i P_i \alpha_i \delta_{ii}, V_H = \sum_i P_i \delta_{ii}^2, D_H = \left(\sum_i P_i \delta_{ii} \right)^2$$

When dominance variance is zero,

$$V_{A_F} = (1 + F)V_A$$

Under correct conditions inbreeding may have advantages for selection because the variance of breeding values is increased.

OK then. How Much Dominance is there then?



Genetics Selection Evolution

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- Conclusions
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- References

Research | Open Access

Genomic analysis of dominance effects on milk production and conformation traits in Fleckvieh cattle

Johann Grill , Andris Legarra, Zilina G Vitvicka, Luis Yáñez, Christian Edel, Beate Ermerling and Kay-Uwe Götts

Genetics Selection Evolution 2014, 46:40

<https://doi.org/10.1186/s12771-014-0040-0> © Grill et al.; licensee BioMed Central Ltd. 2014

Received: 11 October 2013 | Accepted: 6 May 2014 | Published: 24 June 2014

Estimating Additive and Non-Additive Genetic Variances and Predicting Genetic Merits Using Genome-Wide Dense Single Nucleotide Polymorphism Markers

Guosheng Su , Ole F. Christensen, Tage Odensek, Mark Herington, Mogens S. Lund

Published: September 13, 2012 • <https://doi.org/10.1371/journal.pone.0049209>



Journal of Dairy Science
Volume 96, Issue 12, December 2013, Pages 4814-4821



Mating programs including genomic relationships and dominance effects¹

C. Su , R. K. Fox, Vanabalan J. J., O'Connell J. K., Nisbet J. D., Gnanou J.

<https://doi.org/10.3168/jds.2013-4095>

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Research article | Open Access

Dissection of additive, dominance, and imprinting effects for production and reproduction traits in Holstein cattle

Ziwei Jiang, Botang Shen, Jeffrey R. O'Connell, Paul H. Vanabalan, John B. Cole and Li Ma 

BMC Genomics 2017, 18:425

<https://doi.org/10.1186/s12864-017-3801-8> © The Author(s) 2017

Received: 7 April 2017 | Accepted: 20 May 2017 | Published: 30 May 2017

Genetics Selection Evolution

Many

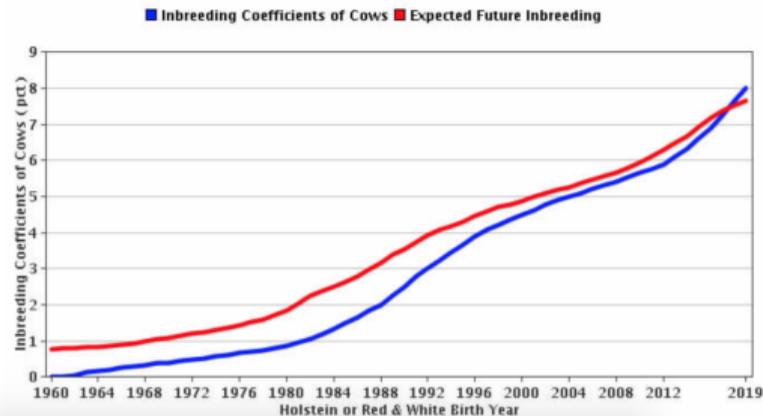
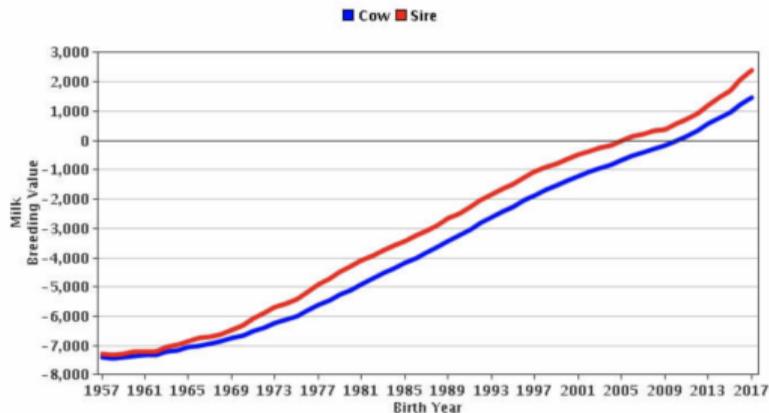
Research Article | Open Access

Accounting for dominance to improve genomic evaluations of dairy cows for fertility and milk production traits

Hansen Nilas , Jennie E. Pryce, Oscar González Recio, Benjamin G. Coakley and Ben J. Hayes

Genetics Selection Evolution 2016, 48:8

OK then. How Much Dominance is there then?



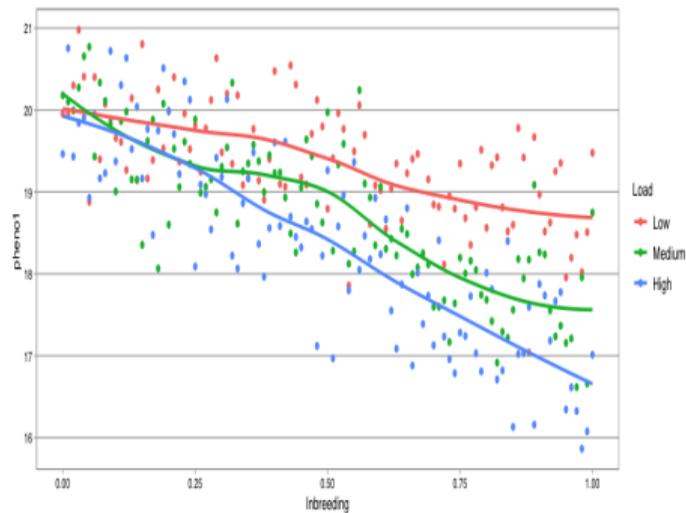
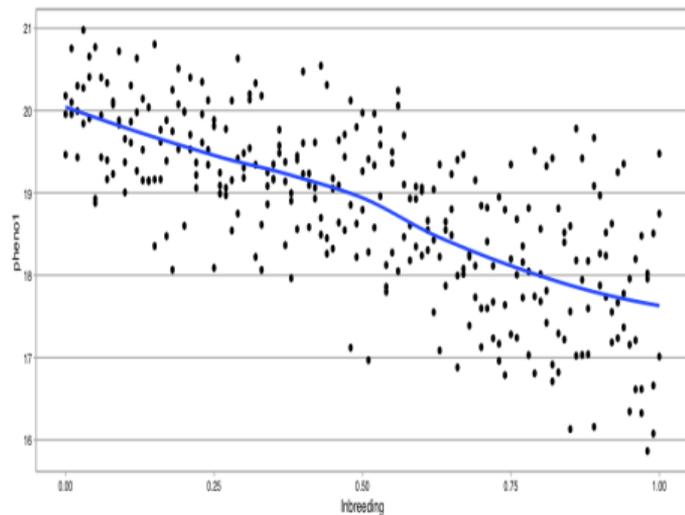
3

$$V_{GF} = (1 + F)V_A + (1 - F)V_D$$



- ▶ How can two individuals with similar breeding value be further discriminated on the basis of genomic diversity and fitness
- ▶ How should we do breeding balancing short and long term gains as well as fitness and overall variability?

Primary Question



Johnsson et al. *Genet Sel Evol* (2019) 51:14
<https://doi.org/10.1186/s12711-019-0456-8>

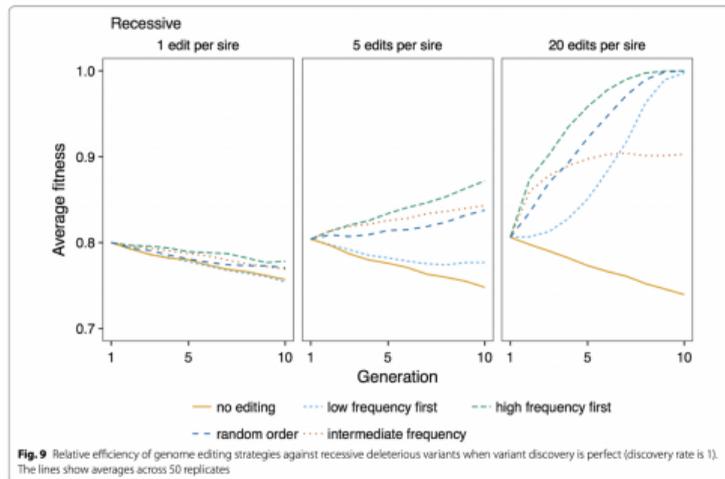
GSE Genetics
Selection
Evolution

RESEARCH ARTICLE

Open Access

Removal of alleles by genome editing (RAGE) against deleterious load

Martin Johnsson^{1,2}, R. Chris Gaynor¹, Janez Jenko¹, Gregor Gorjanc¹, Dirk-Jan de Koning² and John M. Hickey^{1*}



Determining Inbreeding Depression Based on Dominance Estimates



Finding Dominance is not easy:

- ▶ The proportion of the genetic variance at a causal variant that is captured by markers is ρ^2 (correlation between SNP and causal variant) for additive variance and ρ^4 for dominance variance ⁴
- ▶ Independence between additive and dominance effects does not hold in reality ⁵
- ▶ Given the directionality of dominance, the a priori dominance effect of a gene should be positive so we account for it with inbreeding ⁶

⁴Zhu et al 2015

⁵Huang and Mackay 2016

⁶Xiang et al. 2016

ORIGINAL RESEARCH ARTICLE

Front. Genet., 14 May 2019 | <https://doi.org/10.3389/fgene.2019.00412>



A Large-Scale Genome-Wide Association Study in U.S. Holstein Cattle

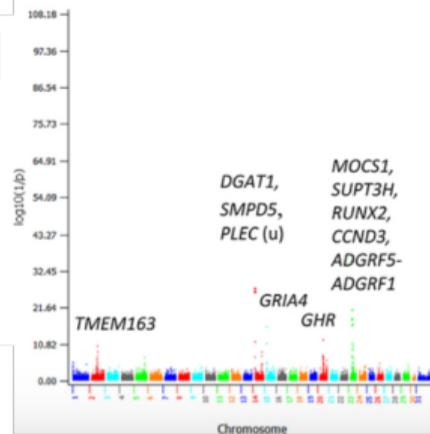
Jical Jiang¹, Li Ma¹, Dzianis Prakapenka², Paul M. VanRaden³, John B. Cole³ and Yang Da^{2*}

¹Department of Animal and Avian Sciences, University of Maryland, College Park, MD, United States

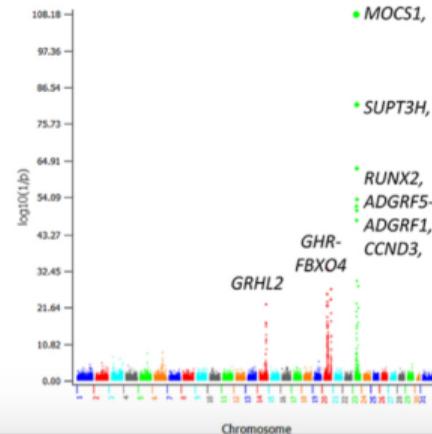
²Department of Animal Science, University of Minnesota, Saint Paul, MN, United States

³Animal Genomics and Improvement Laboratory, USDA-ARS, Beltsville, MD, United States

C Manhattan Plot: FPC, dominance



D Manhattan Plot: PPC, dominance



Is Inbreeding still a useful Measure?

Yes it is

▶ Pedigree Based Inbreeding

- ▶ Expected probability of IBD
- ▶ Underestimate true inbreeding coefficient

▶ Genomic Based Inbreeding

- ▶ Realized proportion of genome IBS
- ▶ Approximate IBD probability

▶ ROH Based Inbreeding

- ▶ Estimate local (recent) autozygosity
- ▶ Approximate IBD probability

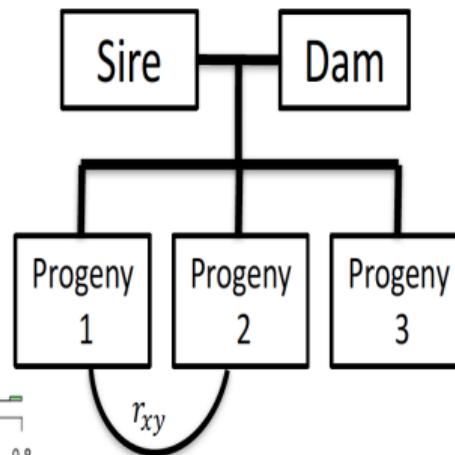
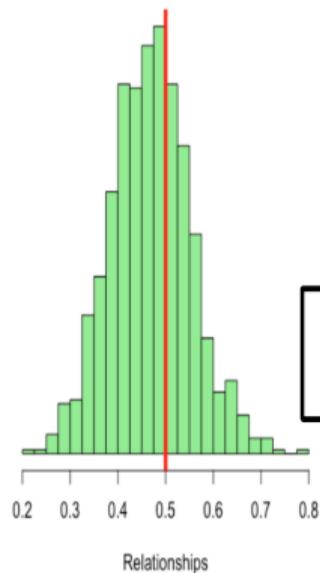
▶ HBD Based Inbreeding

- ▶ Estimate local autozygosity
- ▶ Models IBD probability

Pedigree vs. Genomic Inbreeding

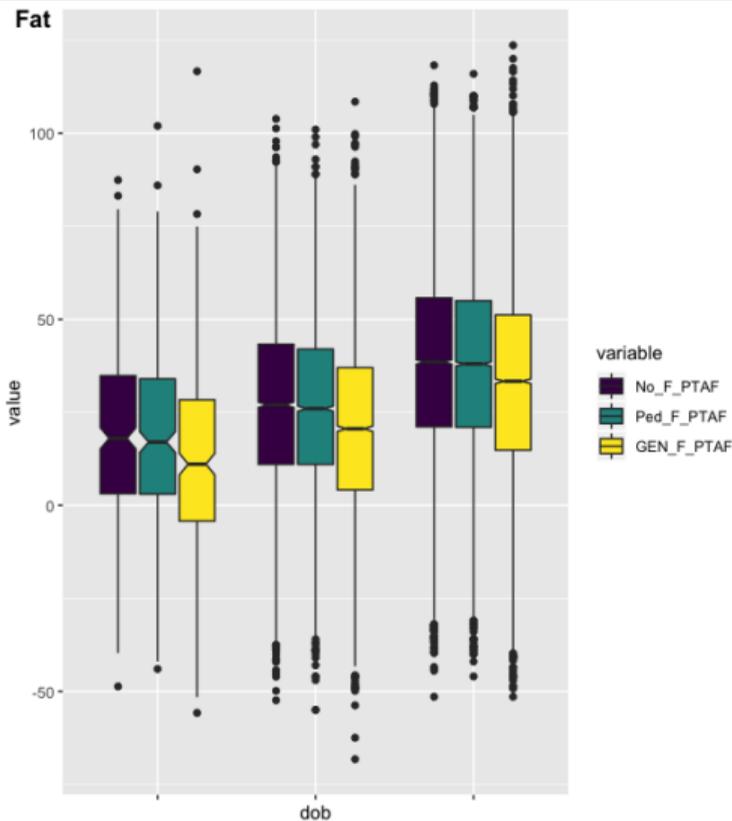
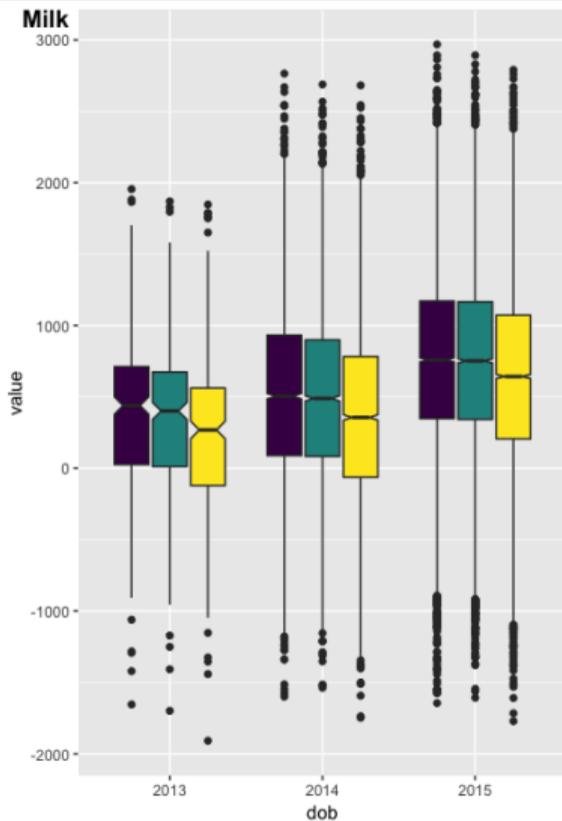
Visualizing Genomic Relationships

Full-Sib Relationships



Not all Inbreeding is Created Equal

Inbreeding Load



Not all Inbreeding is Created Equal

Inbreeding Load

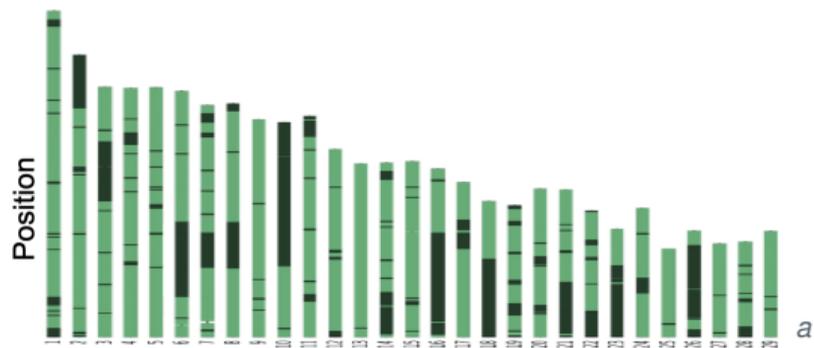
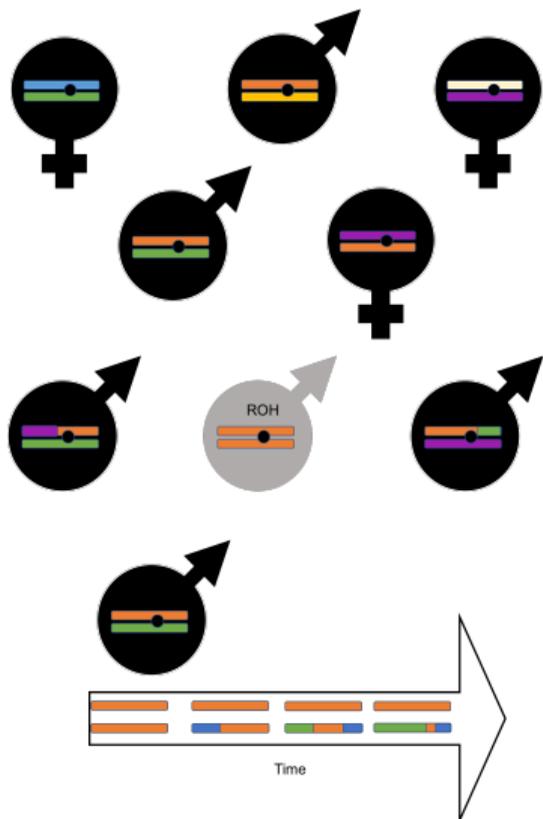


Trait	-10logp Pedigree	-10logp Genomic
Milk	4.95	18.06
Fat	4.67	9.96
Pro	2.18	13.47
PL	0.33	1.5
DPR	0.57	0.08
SCS	0.11	0.14

Characterizing Local Inbreeding

ROH

Definition and advantages



^aBaes, 2018

Identifying and managing inbreeding at the global and local level with the use of genomic information

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Investigation of regions impacting inbreeding depression and their association with the additive genetic effect for United States and Australia Jersey dairy cattle

Jeremy T. Howard, Mekonnen Haile-Mariam, Jennie E. Pryce and Christian Maltecca

- Abstract
- Background
- Results
- Discussion
- Conclusion
- Methods
- Declarations
- References

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A simple strategy for managing many recessive disorders in a dairy cattle breeding program

John B. Cole

- Abstract
- Background
- Methods
- Results and discussion
- Conclusions

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Identification of genomic regions associated with inbreeding depression in Holstein and Jersey dairy cattle

Jennie E Pryce, Mekonnen Haile-Mariam, Michael E Goddard and Ben J Hayes

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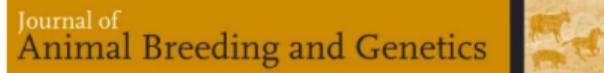
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Characterizing homozygosity across United States, New Zealand and Australian Jersey cow and bull populations

Jeremy T Howard, Christian Maltecca, Mekonnen Haile-Mariam, Ben J Hayes and Jennie E Pryce

- Abstract
- Background
- Results
- Discussion
- Conclusions
- Methods
- Declarations



ORIGINAL ARTICLE

Geno-Diver: A combined coalescence and forward-in-time simulator for populations undergoing selection for complex traits

A heuristic method to identify runs of homozygosity associated with reduced performance in livestock

J. T. Howard, F. Tiezzi, Y. Huang, K. A. Gray, C. Maltecca

Journal of Animal Science, Volume 95, Issue 10, October 2017, Pages 4318–4332,
<https://doi.org/10.2527/jas2017.1664>

Published: 01 October 2017 Article history



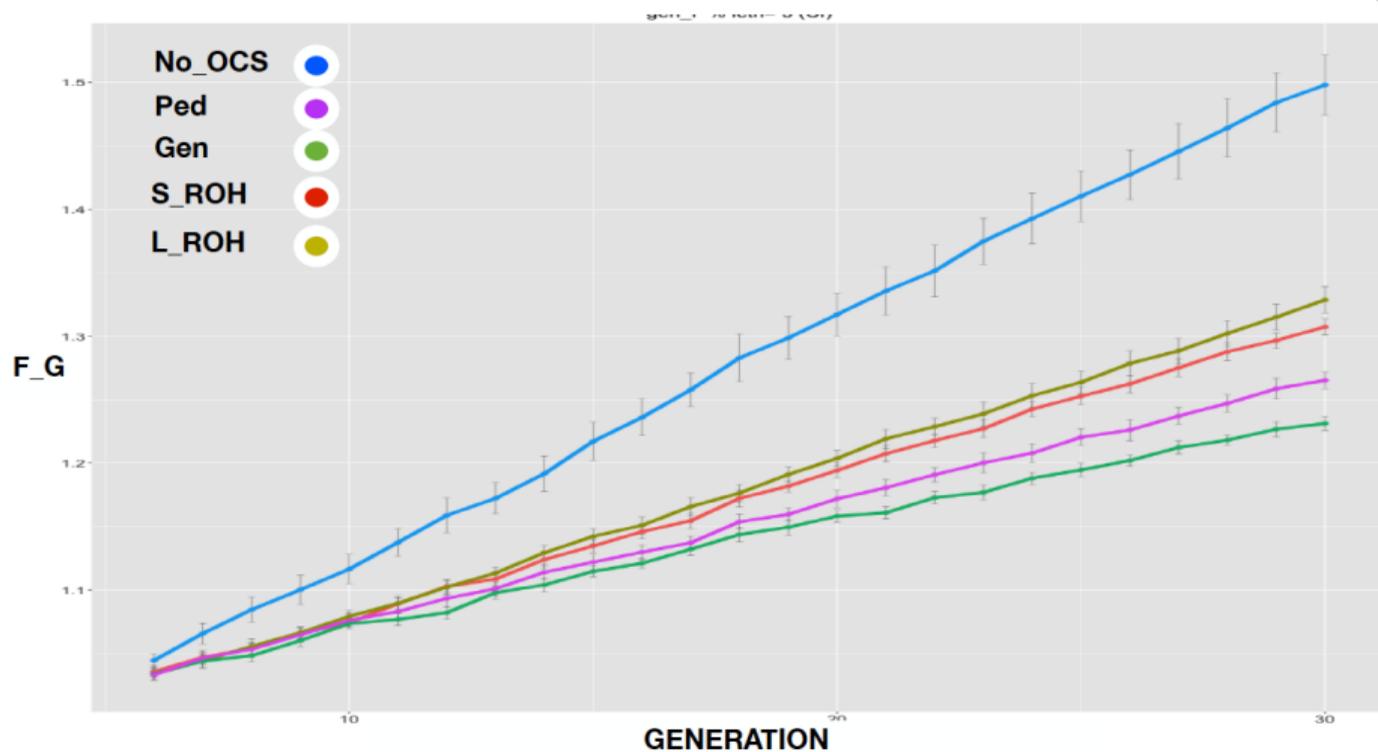
GenoDiver

A Coalescent Forward in Time Simulation Toolkit

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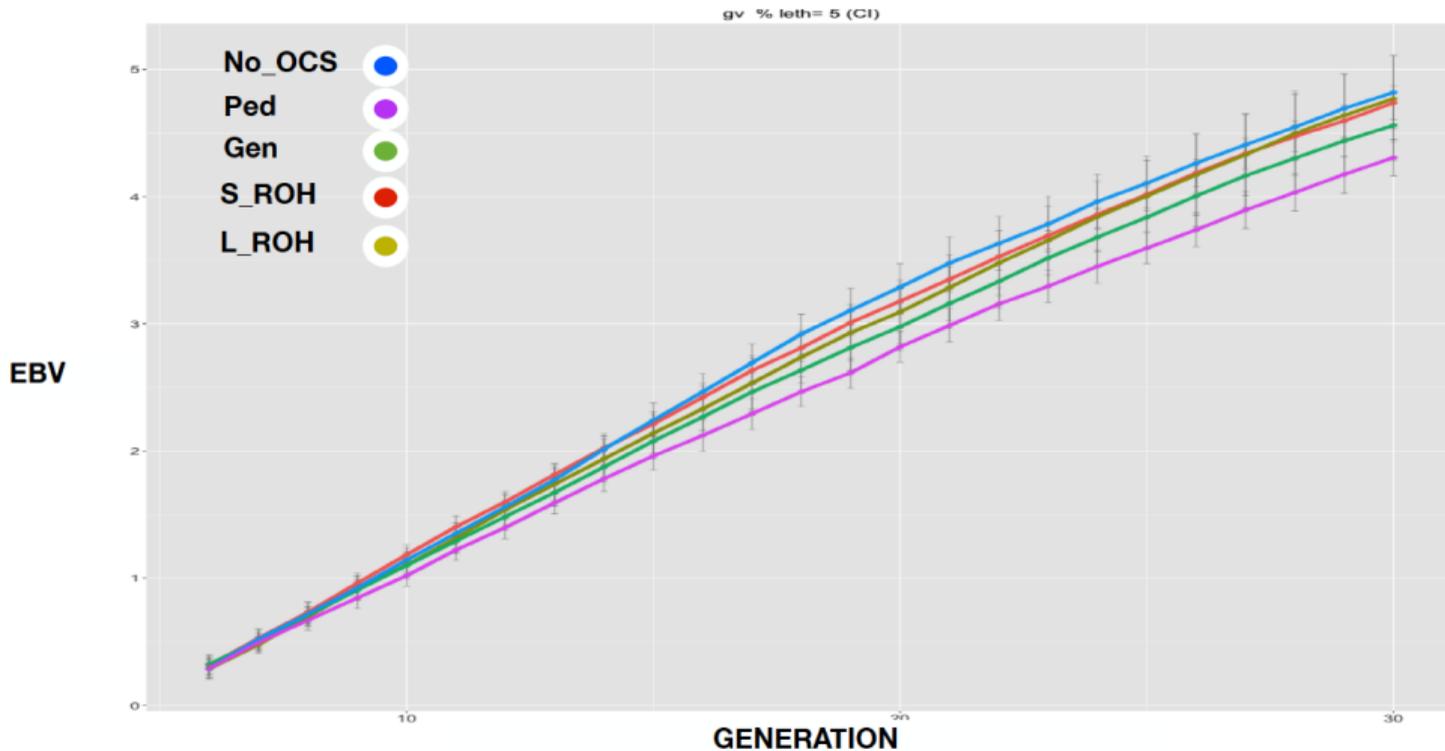
Optimal Contribution Selection

ROH



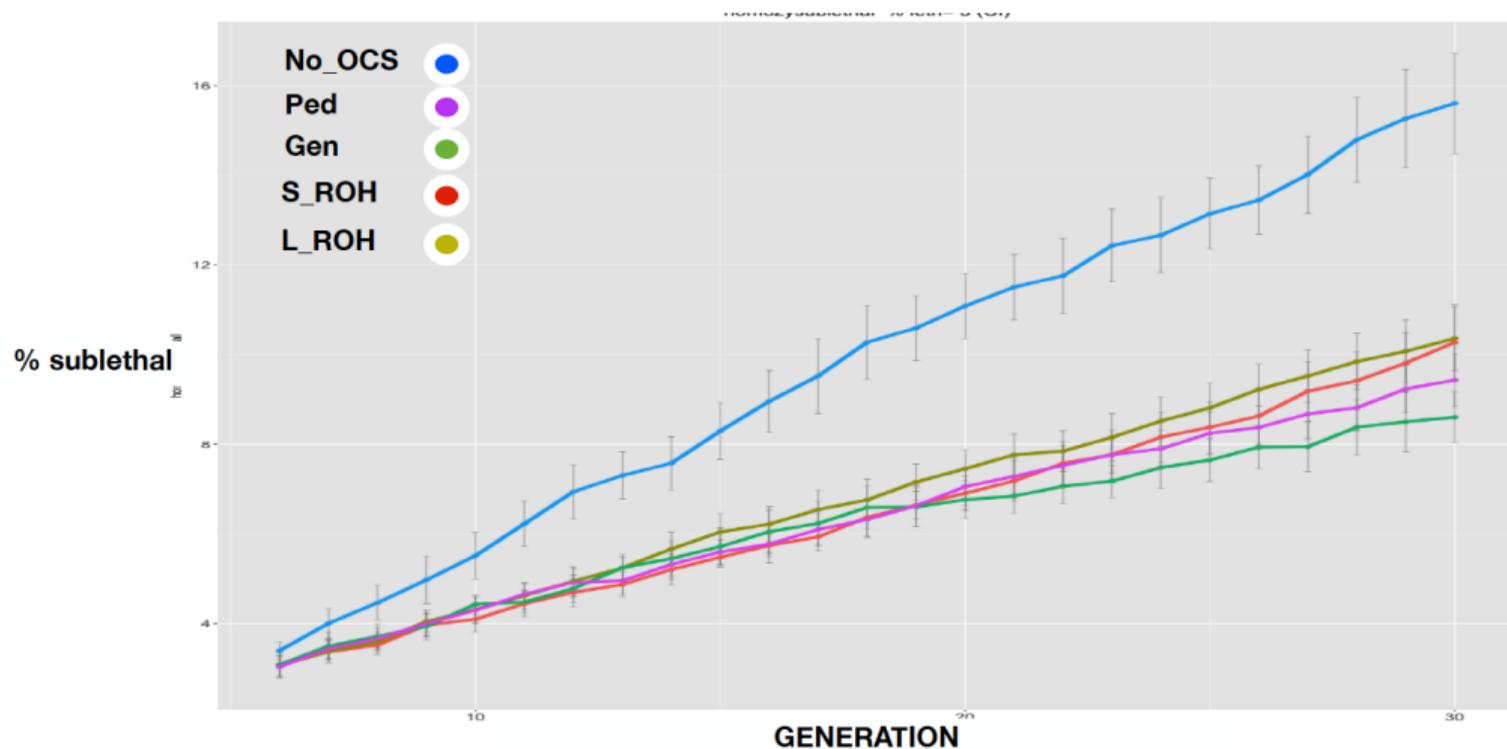
Optimal Contribution Selection

ROH



Optimal Contribution Selection

ROH





There are many theoretically satisfying ideas...

- **...but nobody uses them**
- **Geneticists don't breed cows, farmers do**
- **Many cows now mated at random to a portfolio of bulls**
- **Everyone thinks their neighbor should use different bulls**

Some methods for avoiding inbreeding

Optimal contribution theory

Minimization of progeny inbreeding

Linear programming

Look-ahead mate selection

Selection against lethal alleles

Index selection including Mendelian sampling variance

Genomic selection including dominance

A simple strategy for managing many recessive disorders in a dairy cattle breeding program

John B. Cole 

Haplotype	Functional/ <i>Gene name</i>	Chromosome	Location (Mbp)	Haplotype frequency (%)	Timing ¹
HBR	Black/red coat color/ <i>MC1R (MSHR)</i>	18	14.71	0.75	—
HCD	Cholesterol deficiency/ <i>APOB</i>	11	77.87	2.28	W
HDR	Dominant red color/ <i>MC1R (MSHR)</i>	3	9.36	0.03	—
HH0	Brachyspina/ <i>FANCI</i>	21	20.77	1.65	E,B
HH1	<i>APAF1</i>	5	62.81	1.28	E
HH2	—	1	93.50-95.58	1.21	E
HH3	<i>SMC2</i>	8	93.75	2.64	E
HH4	<i>GART</i>	1	1.99	0.23	E
HH5	<i>TFB1M</i>	9	91.85-91.94	2.39	E
HH6	<i>SDE2</i>	16	29.01-29.05	0.44	Old age
HHB	<i>BLAD/ITGB2</i>	1	144.77	0.21	W
HHC	<i>CVM/SLC35A3</i>	3	43.26	1.10	E,B
HHD	<i>DUMPS/UMPS</i>	1	69.15	0.01	E
HHM	Mulefoot/ <i>LRP4</i>	15	76.81	0.05	B
HHP	Polledness (dominant)/ <i>POLLED</i>	1	2.57	0.88	—
HHR	Red coat color/ <i>MC1R (MSHR)</i>	18	14.71	3.29	—

¹Timing of embryonic loss/calf death for homozygous animals: B = calf death at/shortly after birth, E = embryonic loss/abortion, W = calf death weeks/months after birth (Cole et al., 2016; Cole et al., 2018).

- Large amount of research has been conducted on finding lethal haplotypes (VanRaden et al., 2011; Sahana et al., 2013; Hoff et al. 2017).
- Within livestock populations undergoing selection lethals mutations are effectively removed from the population, while sub-lethal mutations are difficult to remove.
- What about sub-lethal mutations (i.e. affected animal **doesn't die**, but instead has **reduced performance**)?

Mate Two Carriers

	D	d
D	DD	Dd
d	Dd	dd

Appears in genotype data as an ROH



Inbreeding Load Matrix (ILM)

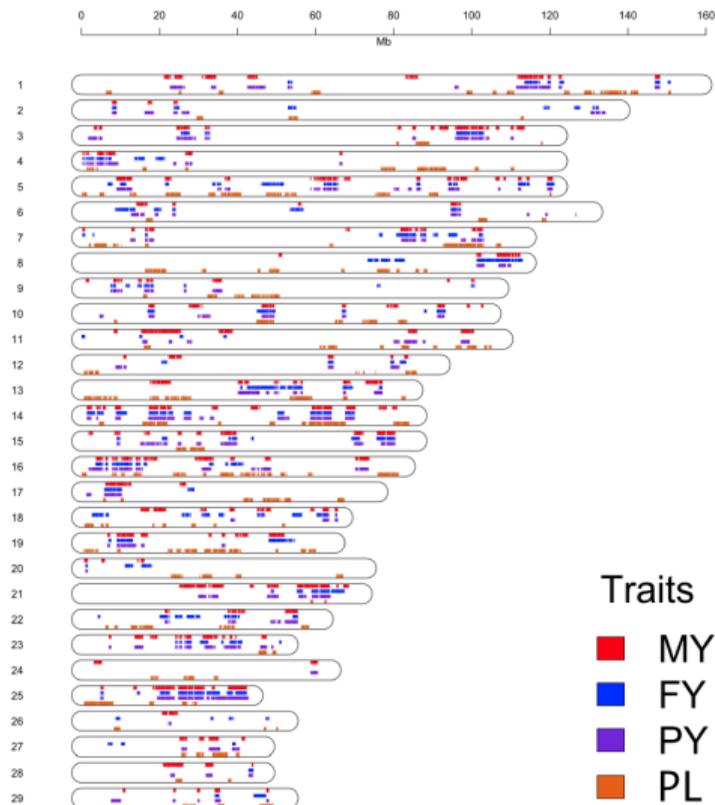
- Summarize effects of unfavorable haplotypes identified.
- Across two individuals:

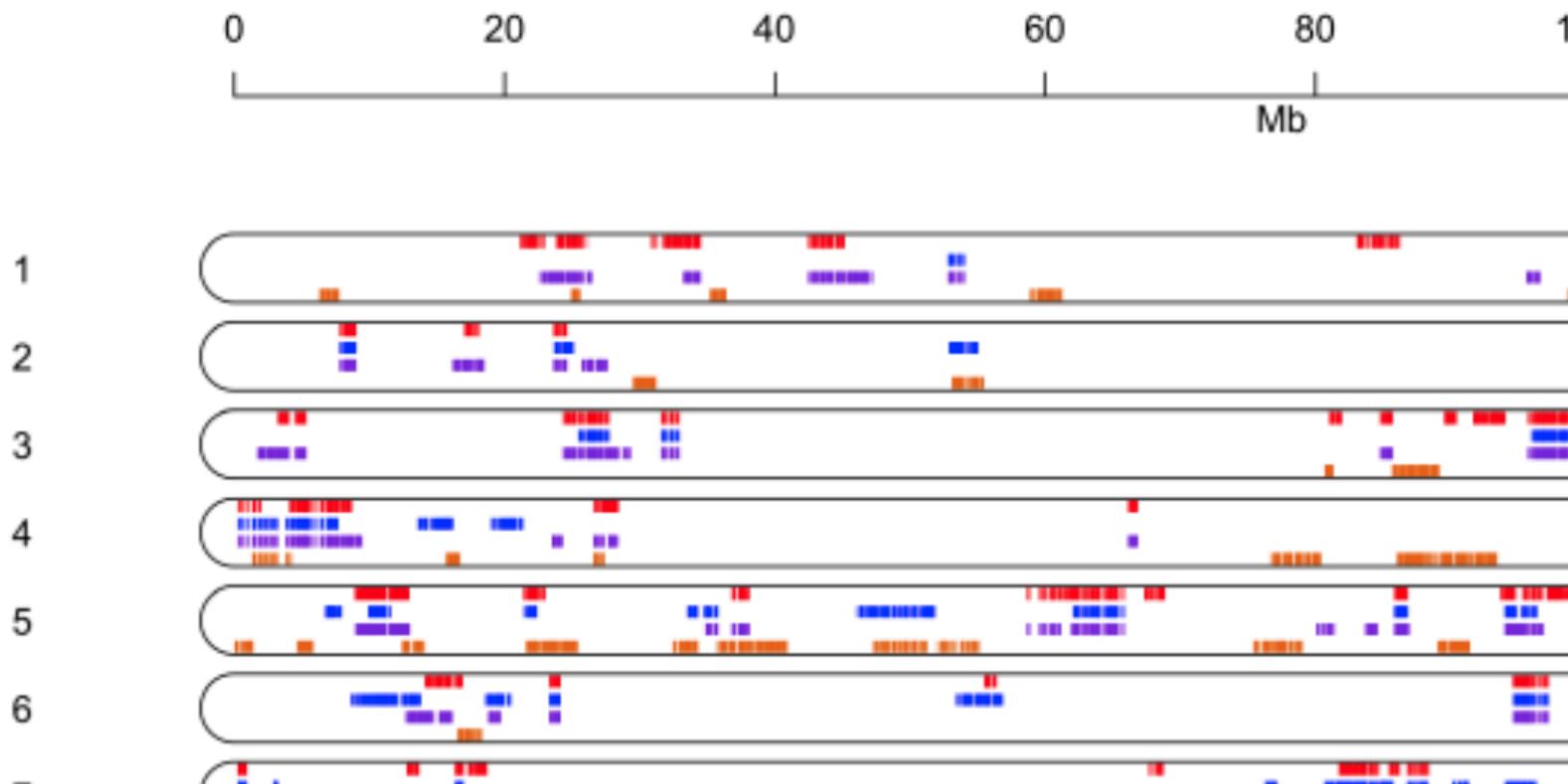


- Within an individual:



$$\left(\begin{array}{cc} \sum_{i=0}^{i=\text{Haplotypes}} \left(\frac{1}{4} * (X_1X_1 + X_1X_2 + X_2X_1 + X_2X_2) * \beta_i & \sum_{i=0}^{i=\text{Haplotypes}} \left(\frac{1}{4} * (X_1Y_1 + X_1Y_2 + X_2Y_1 + X_2Y_2) * \beta_i \right) \vdots \\ \vdots & \vdots \\ \vdots & \vdots \end{array} \right)$$



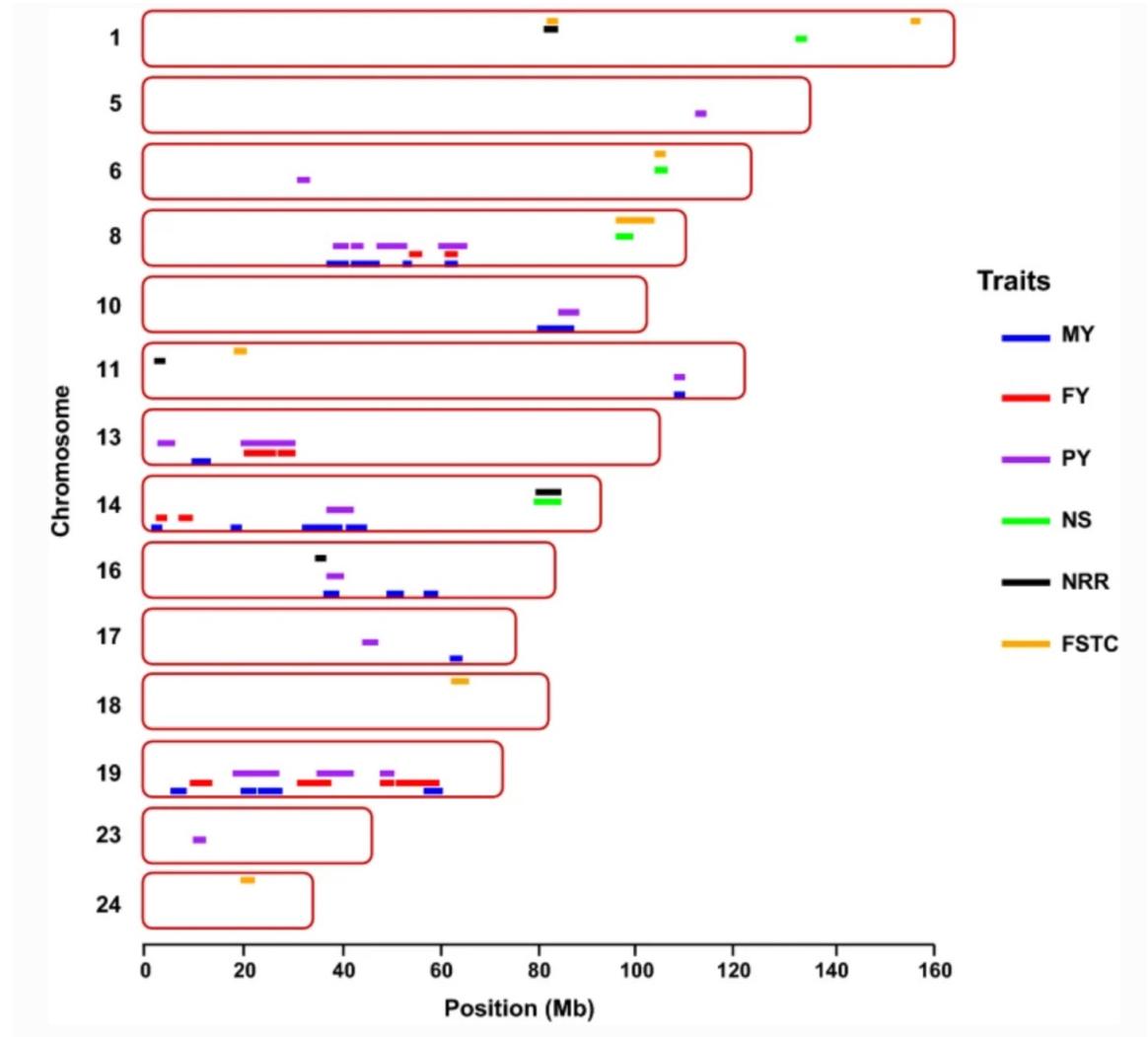


Research Article | [Open Access](#) | [Published: 30 August 2021](#)

Identification of unique ROH regions with unfavorable effects on production and fertility traits in Canadian Holsteins

[Bayode O. Makanjuola](#) , [Christian Maltecca](#), [Filippo Miglior](#), [Gabriele Marras](#), [Emhimad A. Abdalla](#), [Flavio S. Schenkel](#) & [Christine F. Baes](#)

[Genetics Selection Evolution](#) **53**, Article number: 68 (2021) | [Cite this article](#)



Inbreeding offset

Inbreeding Load



Trait	-10logp Pedigree	-10logp Genomic	-10logp Diag. ILM
Milk	4.95	18.06	27.45
Fat	4.67	9.96	16.56
Pro	2.18	13.47	21.43
PL	0.33	1.5	4.75
DPR	0.57	0.08	1.21
SCS	0.11	0.14	0.58

- A mate allocation matrix (B ; Pryce et al. 2012) constructed:

$$B_{ij} = \lambda_1 * EBV_{ij} - \lambda_2 * F_{ij} - \lambda_3 * ILM_{ij},$$

- Can be constructed based on lethal and unfavorable haplotypes/mutations.
- Penalize breeding value based on inbreeding metric and functional inbreeding.

	Dam1	Dam2	Dam3	Dam4	Dam5
Sire 1	$B_{\text{Sire 1, Dam 1}}$	$B_{\text{Sire 1, Dam 2}}$	$B_{\text{Sire 1, Dam 3}}$	$B_{\text{Sire 1, Dam 4}}$	$B_{\text{Sire 1, Dam 5}}$
Sire 2	$B_{\text{Sire 2, Dam 1}}$	$B_{\text{Sire 2, Dam 2}}$	$B_{\text{Sire 2, Dam 3}}$	$B_{\text{Sire 2, Dam 4}}$	$B_{\text{Sire 2, Dam 5}}$
Sire 3	$B_{\text{Sire 3, Dam 1}}$	$B_{\text{Sire 3, Dam 2}}$	$B_{\text{Sire 3, Dam 3}}$	$B_{\text{Sire 3, Dam 4}}$	$B_{\text{Sire 3, Dam 5}}$
Sire 4	$B_{\text{Sire 4, Dam 1}}$	$B_{\text{Sire 4, Dam 2}}$	$B_{\text{Sire 4, Dam 3}}$	$B_{\text{Sire 4, Dam 4}}$	$B_{\text{Sire 4, Dam 5}}$
Sire 5	$B_{\text{Sire 5, Dam 1}}$	$B_{\text{Sire 5, Dam 2}}$	$B_{\text{Sire 5, Dam 3}}$	$B_{\text{Sire 5, Dam 4}}$	$B_{\text{Sire 5, Dam 5}}$

Characterizing Age of Inbreeding

Identify Homozygous by descent

Characterizing HBD segments and age related autozygosity

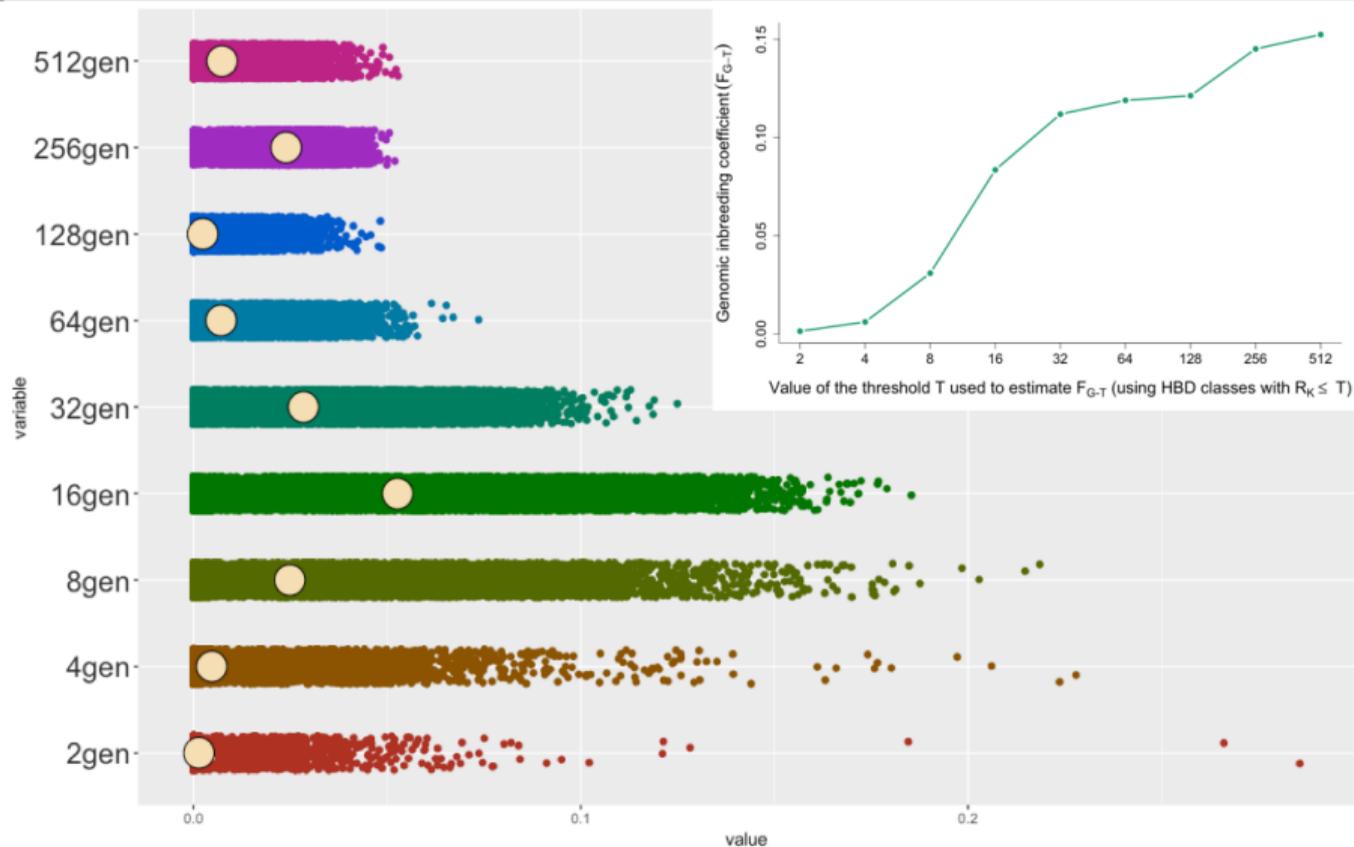


- ▶ HBD happens when individuals inherit copies of ancestral chromosome
- ▶ Copies are inherited through different patterns
- ▶ The length of HBD depend on the number of generations and the population structure
- ▶ Inbreeding can then be divided into different age classes and these related to the overall depression load based on their age⁸

⁸Druet, et al. 2017

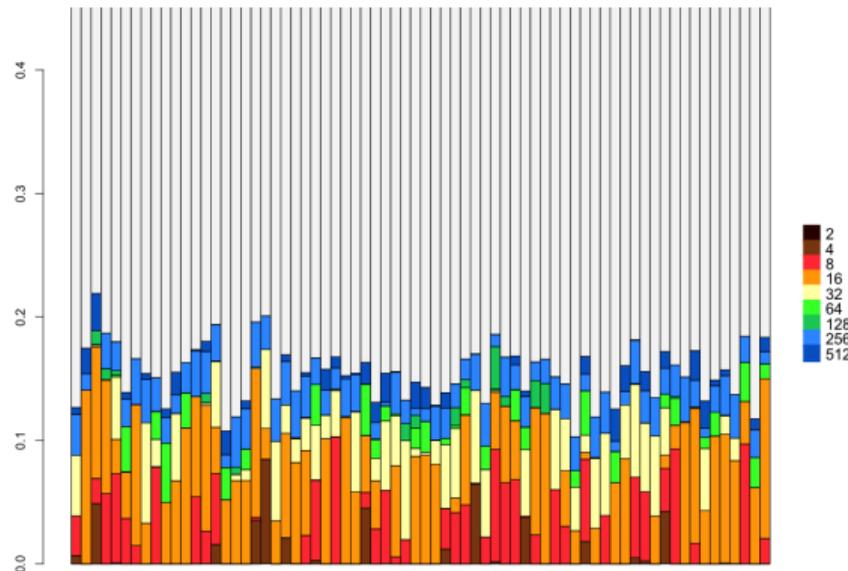
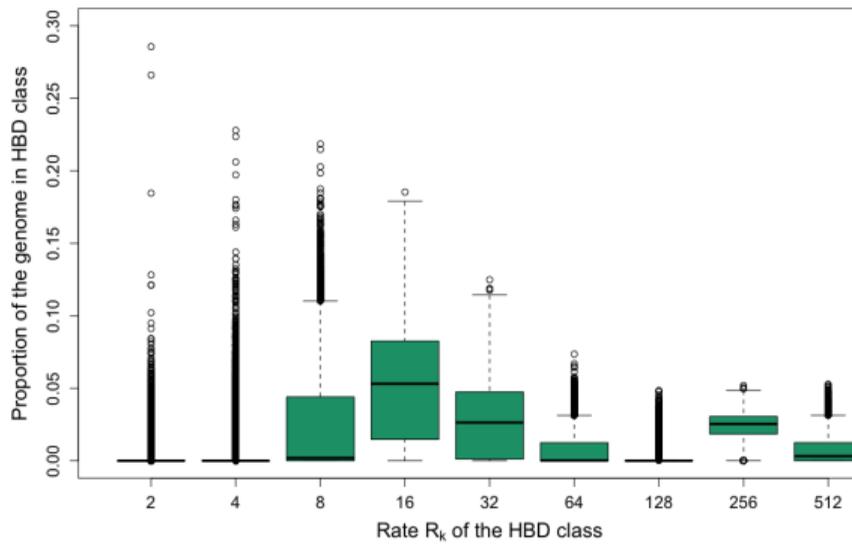
HBD

Characterizing the population through HBD



HBD

Characterizing the population through HBD



HBD

Characterizing the population through HBD



Trait	Pedigree Regression	Genomic Regression
Milk	-91.1	-108.2
Fat	-3.63	-3.58
Pro	-1.81	-2.86
PL	-0.56	-0.85
DPR	-0.12	-0.02
SCS	-0.08	~0

HBD	Trait	Regression
2-8 Gen	Milk	-138.1
18-128 Gen		-88.3
>128 Gen		-185.3
2-8 Gen	Fat	-4.44
18-128 Gen		-3.82
>128 Gen		-5.12
2-8 Gen	Pro	-3.38
18-128 Gen		-2.60
>128 Gen		-4.43
2-8 Gen	PL	-0.83
18-128 Gen		-0.32
>128 Gen		0.08
2-8 Gen	DPR	-0.14
18-128 Gen		-0.04
>128 Gen		0.02

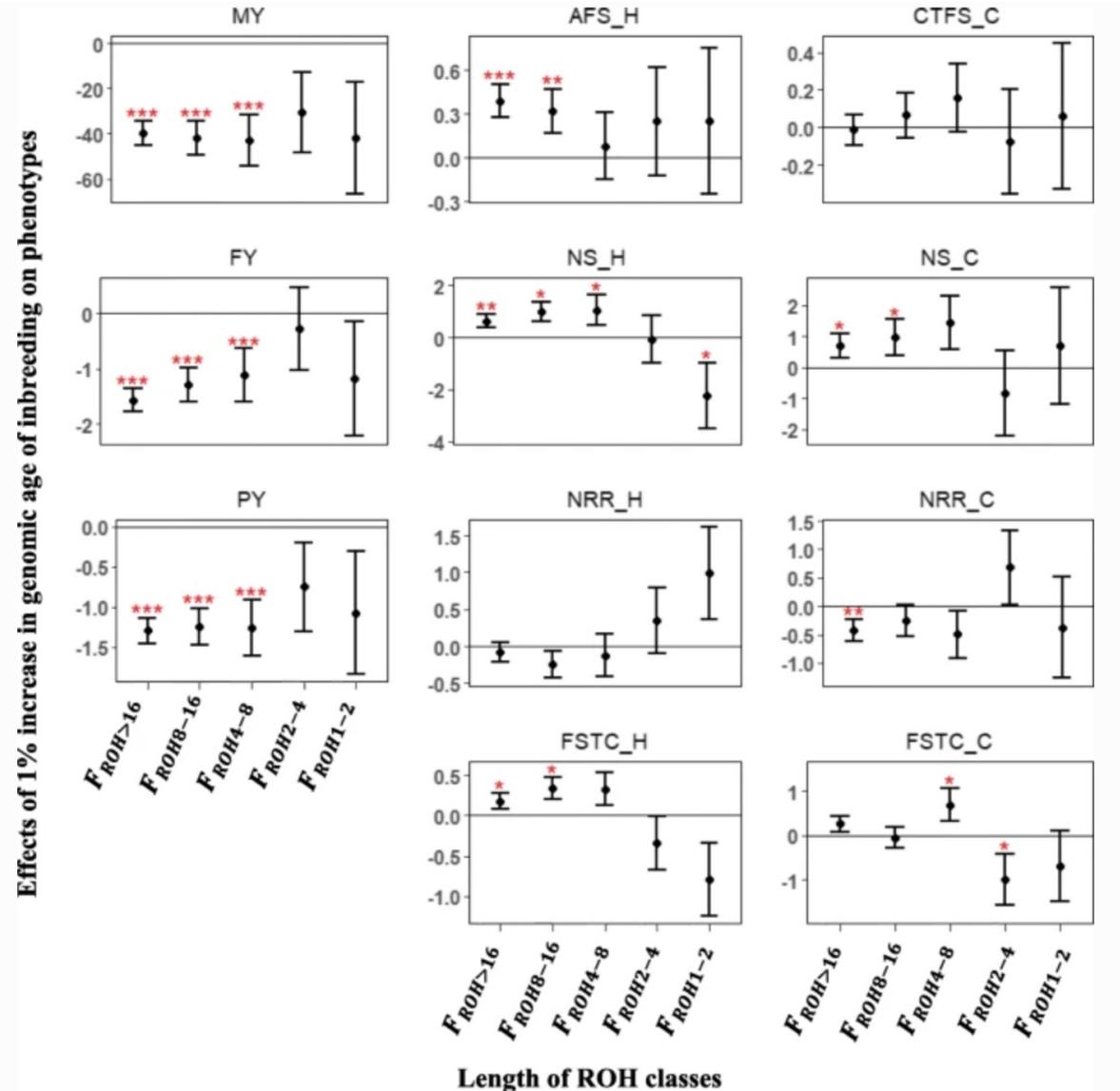
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Effect of recent and ancient inbreeding on production and fertility traits in Canadian Holsteins

[Bayode O. Makanjuola](#) , [Christian Maltecca](#), [Filippo Miglior](#), [Flavio S. Schenkel](#) & [Christine F. Baes](#)

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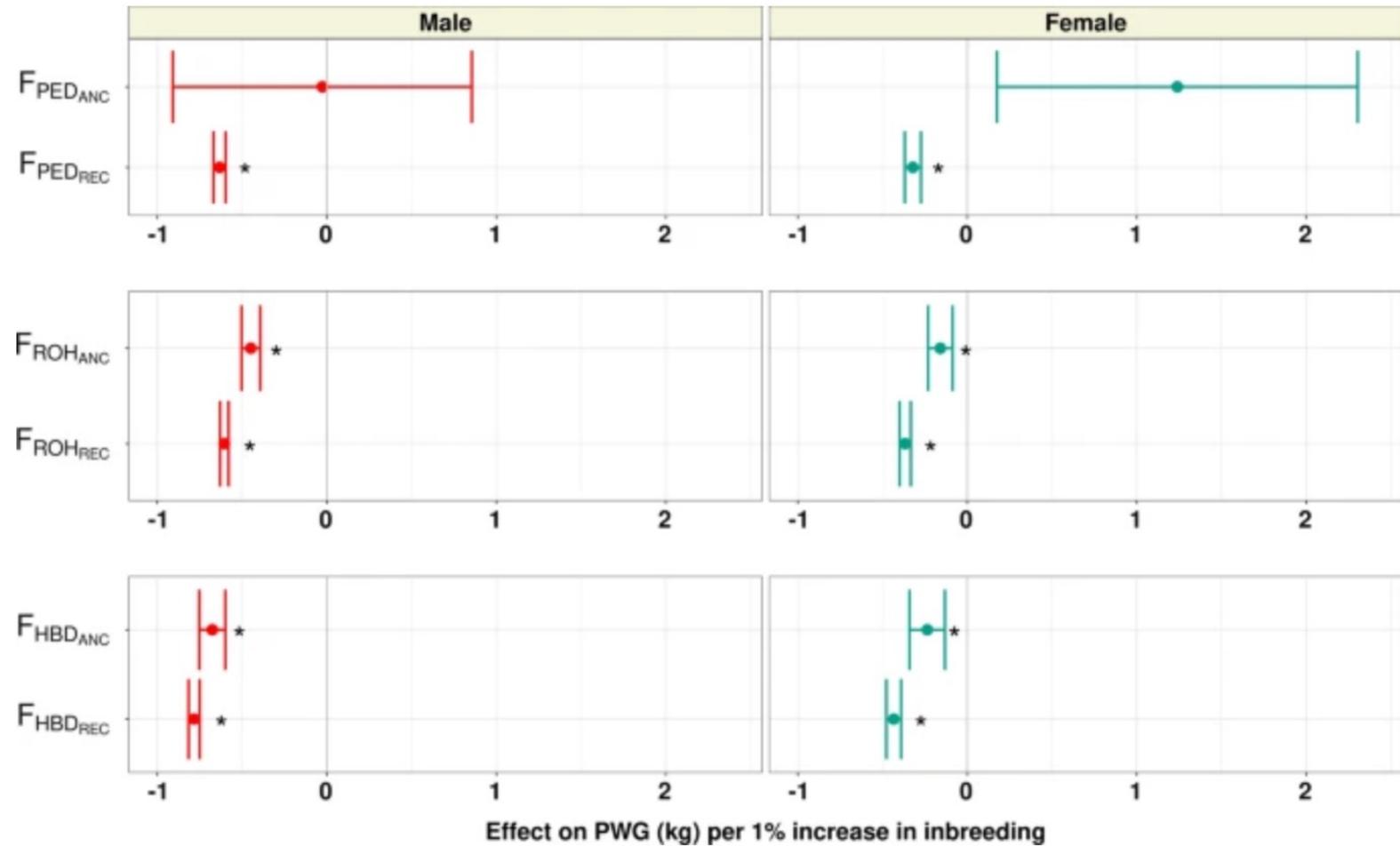
Research Article | [Open Access](#) | [Published: 16 June 2021](#)

Trends in genetic diversity and the effect of inbreeding in American Angus cattle under genomic selection

[Emmanuel A. Lozada-Soto](#) [✉](#), [Christian Maltecca](#), [Duc Lu](#), [Stephen Miller](#), [John B. Cole](#) & [Francesco Tiezzi](#)

Genetics Selection Evolution **53**, Article number: 50 (2021) | [Cite this article](#)

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Near future

- ▶ Characterization annotation of haplotypes
- ▶ Refining HBD structure

Mid future

- ▶ Validation of haplotypes in larger populations (across breeds)
- ▶ Implement ILM for validated haplotypes

$$EBV_{c0} = EBV - \lambda_0 F_P$$

$$EBV_{c1} = EBV - \lambda_1 F_G$$

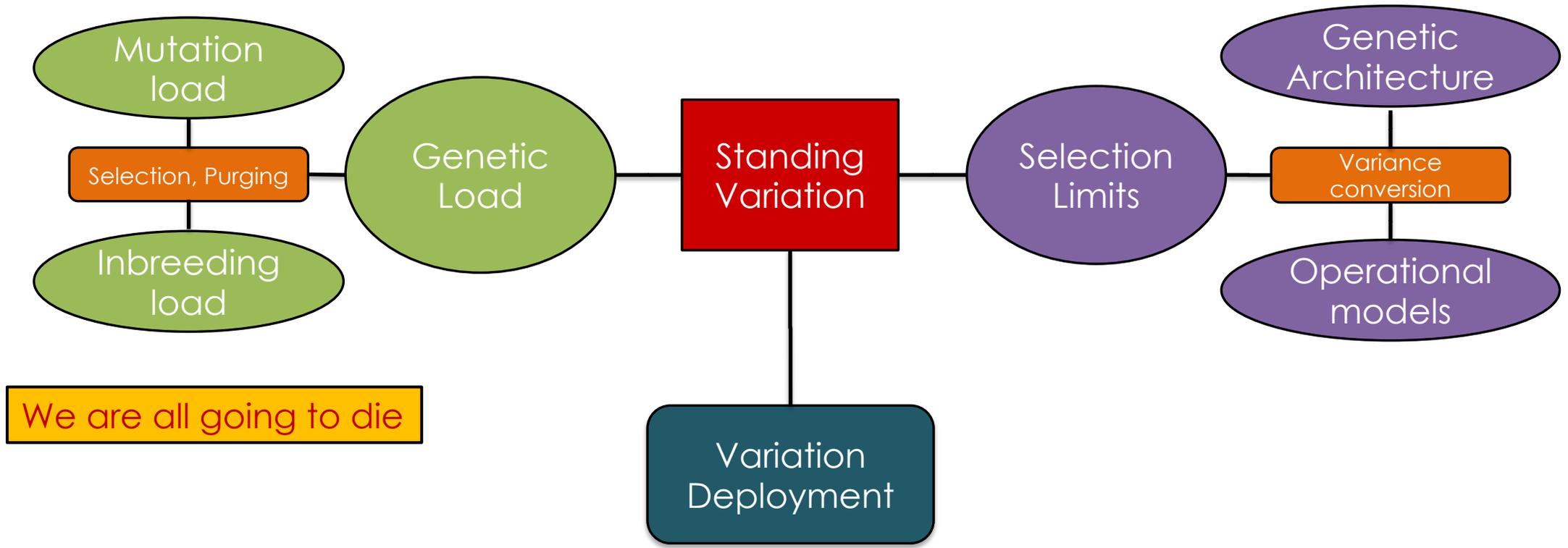
$$EBV_{c2} = EBV - \lambda_1 F_{G_{hbd_1}} \dots - \lambda_n F_{G_{hbd_n}}$$

$$EBV_{c3} = EBV - \lambda_1 F_{G_{hbd_1}} \dots - \lambda_n F_{G_{hbd_n}} - \lambda_{n+1} F_{ILM}$$

It's Complicated

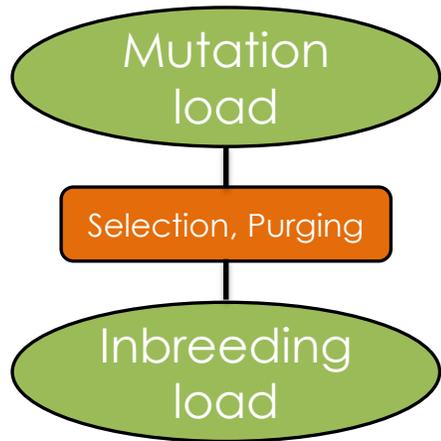
Managing Diversity (minus the logistics)

There's nothing left to select



We are all going to die

Genetic Load



Genome wide homozygosity measures are bad indicators of genetic load

- We use them because we struggle to identify (sublethal) deleterious variants
- Genetic architecture is a direct function of the selection process
 - How much directional dominance there is in dairy cattle is still an open question

We often assume that purging is not happening or not fast enough

- Dairy populations are under strong indirect and direct selection for “functional fitness”
- Fitness it’s hard to define and quantify on the field

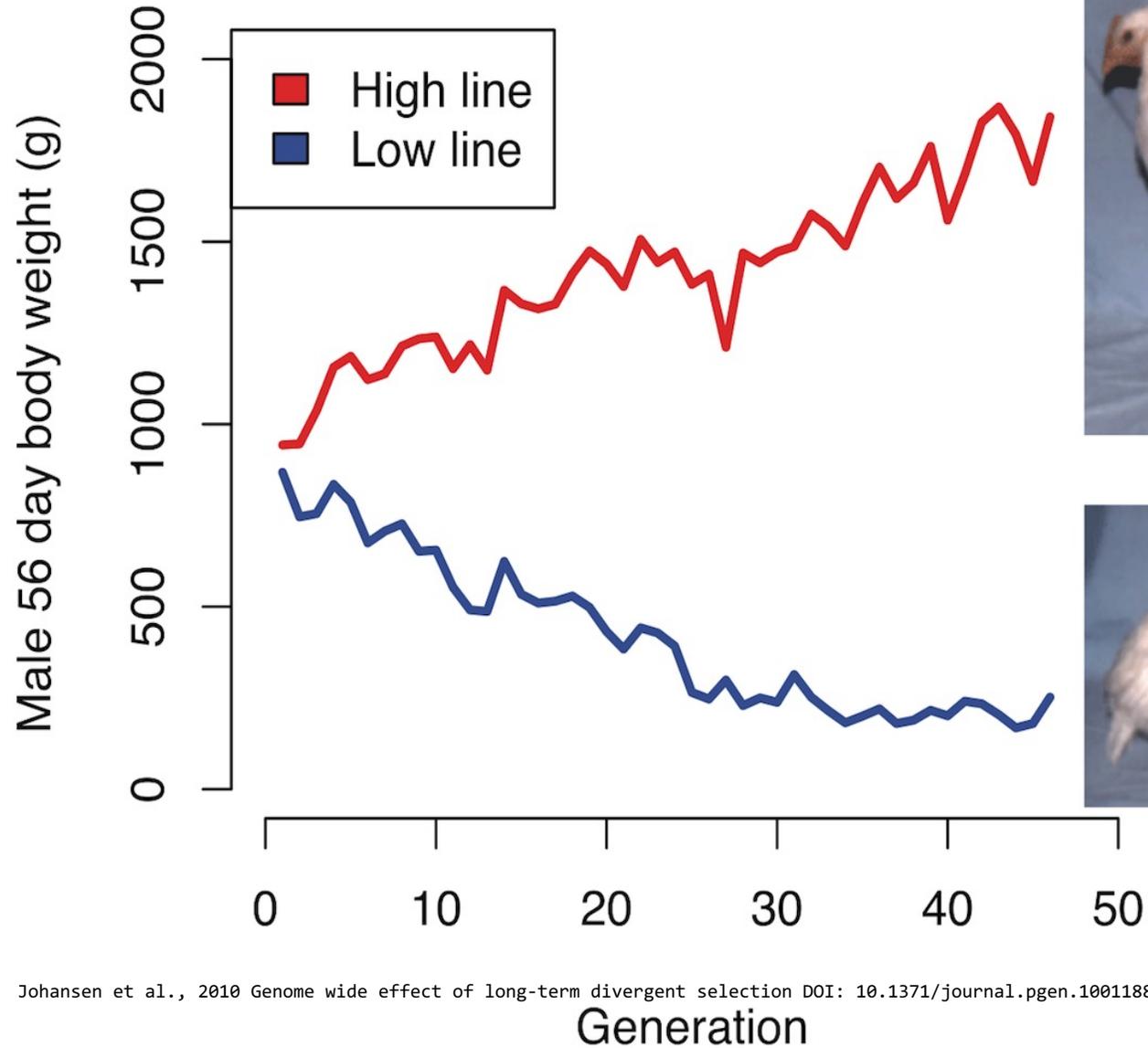
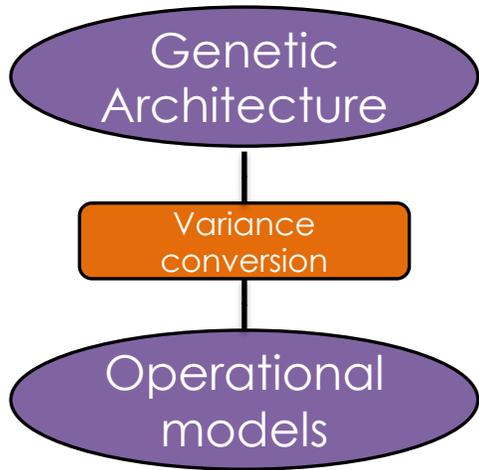
Inferring genomic architecture of inbreeding from breeding populations is more complicated than for additive variation

- It is not economically feasible to conduct selection experiments in dairy
- Some of these questions cannot truly be answered retrospectively

- Increase focus on deep phenotyping
- Increase integration of functional annotation
- Increase numbers of genotyped individuals
- Refine analysis tools
- Integrating of model organism approaches
- Investigating the potential advanced technologies
- Data sharing

On the short-term homozygosity will remain an issue best managed through logistic structuring of the breeding process

Genetic Diversity



Review > [J Anim Breed Genet.](#) 2017 Jun;134(3):196-201. doi: 10.1111/jbg.12270.

"Conversion" of epistatic into additive genetic variance in finite populations and possible impact on long-term selection response

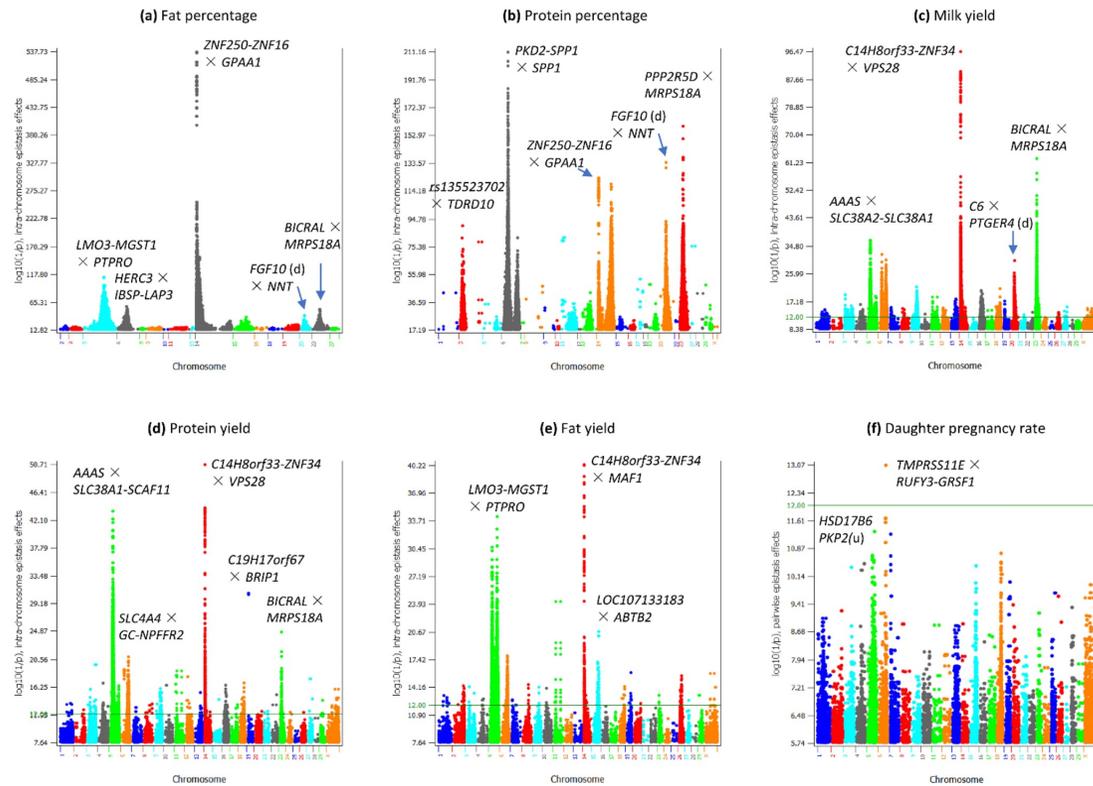
W G Hill ¹

Johansen et al., 2010 Genome wide effect of long-term divergent selection DOI: 10.1371/journal.pgen.1001188

Open Access Article

A Large-Scale Genome-Wide Association Study of Epistasis Effects of Production Traits and Daughter Pregnancy Rate in U.S. Holstein Cattle

by [Dzianis Prakapenka](#)¹, [Zuoxiang Liang](#)¹, [Jicai Jiang](#)², [Li Ma](#)³ and [Yang Da](#)^{1,*}

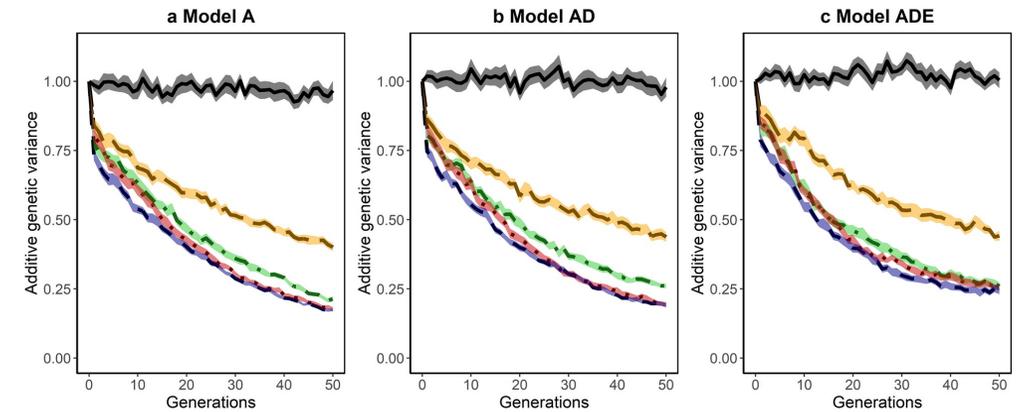


> Genet Sel Evol. 2022 Mar 7;54(1):19. doi: 10.1186/s12711-022-00709-7.

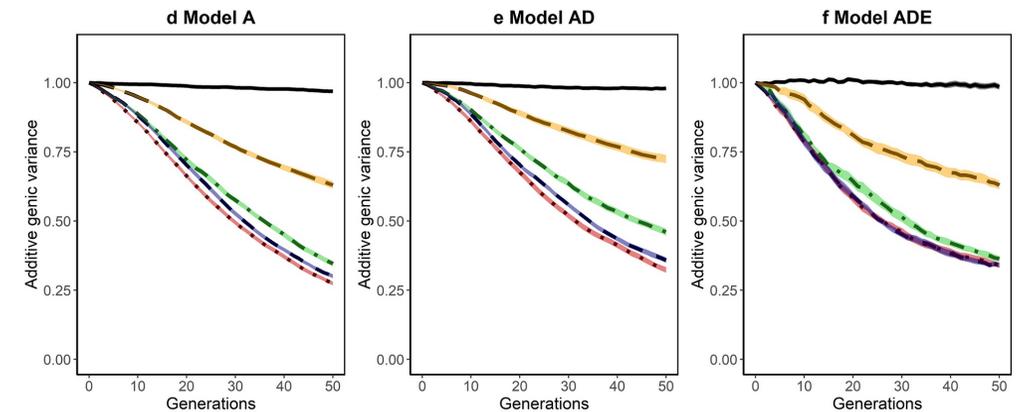
The long-term effects of genomic selection: 1. Response to selection, additive genetic variance, and genetic architecture

[Yvonne C J Wientjes](#)¹, [Piter Bijma](#)², [Mario P L Calus](#)², [Bas J Zwaan](#)³, [Zulma G Vitezica](#)⁴, [Joost van den Heuvel](#)³

Additive genetic variance



Additive genic variance



Method: RANDOM (black), MASS (orange), PBLUP_OP (green), GBLUP_NoOP (red), GBLUP_OP (blue)

Research article | [Open Access](#) | [Published: 27 April 2018](#)

Characterization of recombination features and the genetic basis in multiple cattle breeds

[Botong Shen](#), [Jicai Jiang](#), [Eyal Seroussi](#), [George E. Liu](#) & [Li Ma](#) ✉

BMC Genomics **19**, Article number: 304 (2018) | [Cite this article](#)



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Research

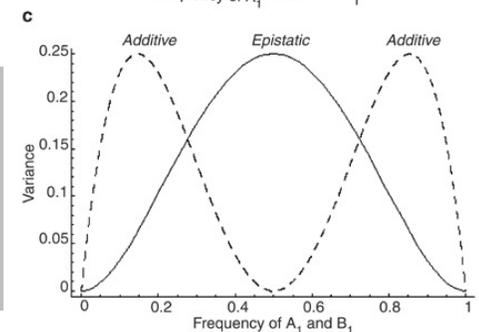
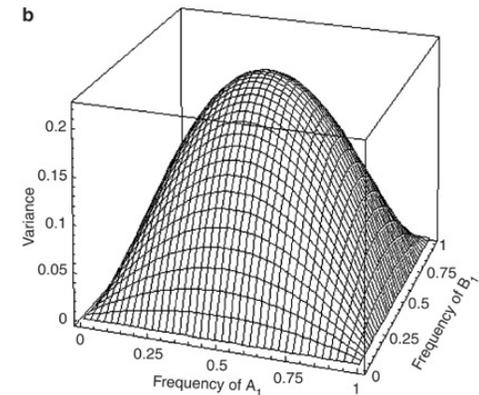
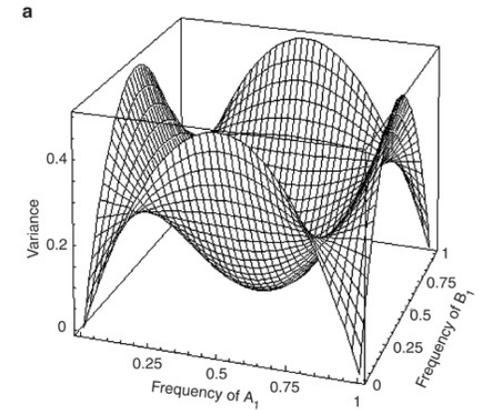
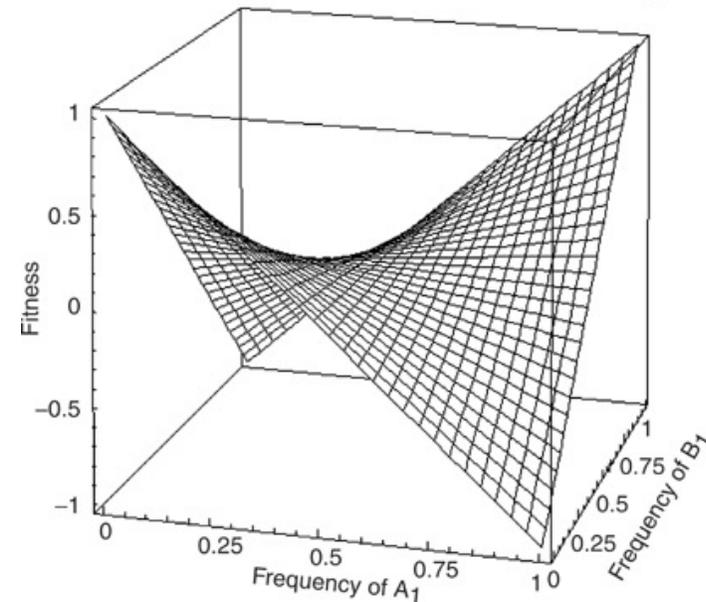
Variance of gametic diversity and its application in selection programs

[D.J.A. Santos](#)^{1,2} ✉, [J.B. Cole](#)³, [T.J. Lawlor Jr.](#)⁴, [P.M. VanRaden](#)³, [H. Tonhati](#)², [L. Ma](#)¹ ✉

The conversion of variance and the evolutionary potential of restricted recombination

[M Neiman](#) ✉ & [T.A Linksvayer](#)

Heredity **96**, 111–121 (2006) | [Cite this article](#)



Genetic recombination is usually considered to facilitate adaptive evolution. However, recombination prevents the reliable cotransmission of interacting gene combinations and can disrupt complexes of coadapted genes. If interactions between genes have important fitness effects, restricted recombination may lead to evolutionary responses that are different from those predicted from a purely additive model and could even aid adaptation.

Future Direction

- Optimal contribution 
- Minimization of progeny inbreeding 
- Selection against lethal alleles 
- Index selection including Mendelian sampling variance 
- Genomic selection including dominance 

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Jicai Jiang NCSU