¹ *Title:* SNP Genotype Effects Model as an ² Alternative to Animal Models

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6 Running Title: Genotype Effects Model

7 Summary

The animal model in dairy cattle has become obsolete due to the pre-8 selection of bull calves based on genomic EBVs that is occurring in many countries. The bias caused by intense pre-selection permeates EBVs of all 10 animals via the additive relationship matrix and/or the genomics relationship 11 matrix, and is getting more severe the longer that pre-selection is employed. 12 There is little that can be done (in a statistical sense) to remove the pre-13 selection bias. Goddard (2011) and Schaeffer (2011) both proposed changing 14 from animal models to models that estimate unbiased SNP genotype effects in 15 order to avoid the pre-selection biases. The details of such a model and the 16 procedures around it are presented using a small example. 17

- ¹⁸ Keywords: Animal model
- ¹⁹ Genotype effects model
- 20 Markers
- 21

22 Introduction

The individual cow model was described in Henderson's course notes as 23 early as 1967. Quaas and Pollak (1980) changed the name to animal model. 24 which has persisted. Animal models were first adopted in dairy cattle around 25 1987 (Wiggans and Misztal, 1987) for milk production in Ayrshire dairy cattle, 26 and 1988 for dairy conformation (Jamrozik and Schaeffer, 1988). Within five 27 years many countries were calculating animal model genetic evaluations for 28 dairy cattle traits. Kennedy et al. (1988) showed that the animal model, 29 using the additive genetic relationship matrix, could account for non-random 30 matings of bulls to cows, but the model still required that progeny groups of 31 each mating were a random sample of all genetically possible offspring. This 32 assumption is now violated due to preselection of male progeny on the basis of 33 particular marker genotypes and associated genomic estimated breeding values 34 (GEBV). Today, the progeny of each mating being grown and measured are 35 no longer a random sample of all potential progeny, but rather an intensely 36 selected set of progeny. Consequently, inclusion of selected offspring in an 37 animal model biases the evaluations of the sire and dam. Bias also affects 38 the EBVs of contemporaries of the selected progeny. From there the bias is 39 spread to the EBVs of all animals in the pedigree. The fact that the bias is 40 spread to every animal, means its effects are slightly muted over all. However, 41 rankings of animals can be affected, genetic trends can be overestimated, and 42 therefore, gains expected from using genomics could be lost due to bias caused 43 by pre-selection. The animal model, in this situation, has become obsolete, 44 and should be replaced. 45

Schaeffer (2011) and Goddard (2011) proposed replacing the animal model 46 with a SNP genotype effects model (SGEM). SGEM have been published by 47 various authors since 2001, but now there is a pressing need to use them in 48 place of animal models. In a SGEM attention is on the unbiased estimation 49 of SNP genotype effects rather than on animal breeding values. The SGEM is 50 the same as an animal model, except the many hundreds of thousands animal 51 additive genetic values are dropped and replaced by 50,000 (or fewer) SNP 52 genotype additive effects, where the SNP genotypes (coded as 1, 0, or -1) are 53 used as covariates. A problem is that not all animals with records (data) have 54 been genotyped, and thus, SNP genotypes have to be predicted for all animals 55 in the pedigree, using a model like that of Gengler (2007,2008) or Mulder et 56 al.(2010). 57

The purpose of this paper is to illustrate all of the calculations through a small example that would be needed to apply a SGEM. Unbiased GEBV can be obtained for each animal after unbiased SNP genotype effects have been estimated. They can also be used to estimate genetic variances and covariances among traits.

63 Material and Methods

64 Data

Example data are given in Table 1. There are 28 animals, of which 20 have observations and 14 have been genotyped for 7 SNPs. Normally, there would be hundreds of thousands of animals with observations, and perhaps 30,000 would be genotyped for 50,000 SNPs. In this example, the 7 SNPs are assumed to account for all of the genetic effects in the trait (which is how the example was constructed). Four animals are inbred. Two traits have been observed, but each trait will be processed separately.

⁷² Table 1 goes here.

73 Prediction of Marker Genotypes

The first step in the procedure is predict SNP genotypes for animals that have not, or could not, be genotyped.

Gengler et al. (2007, 2008) and Mulder et al. (2010) have used an animal model applied to the genotypes (-1, 0, or 1) of genotyped animals with an overall mean, and an animal additive effect. The additive genetic relationship matrix, **A** amongst all animals with phenotypes and ancestors, is used, and a very high heritability is assumed. The model for one marker at a time is

$$s_{ji} = \mu + g_i + e_i,$$
 (1)

81 where

- $s_2 = s_{ji}$ is marker j genotype, either -1, 0, or 1, for animal i,
- μ is an overall mean,
- g_i is an animal's breeding value for the marker genotype, and

 e_i is a residual error.

In terms of the example, **g** is a vector of 28 by 1 for all of the animals in Table 1. The observation vector is **s** of 14 by 1 because only 14 animals were genotyped, namely, 3, 7, 10, 11, 12, 15, 16, 17, 21, 22, 23, 25, 26, and 27, and represents a column in Table 1 corresponding to one of the SNP markers. Each marker is analyzed separately.

⁹¹ In matrix notation, for marker 1

$$\mathbf{s}_{1} = \begin{pmatrix} 1\\ 0\\ 0\\ 0\\ -1\\ -1\\ 1\\ 1\\ 0\\ 0\\ 0\\ 1\\ 0\\ 0\\ 0 \end{pmatrix},$$
$$= \mathbf{1}\mu + \mathbf{Zg} + \mathbf{e}$$

92 where

\mathbf{Z} =) 0) 0) 0) 0) 0) 0) 0	0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0	0 0 0 0 0 0 0 0 0	0 (0 0 (2 0 (0 0 (0 0 (0 0 (0)) 0) 0) 1) 0 	0 0 1 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
) 0) 0) 0) 0	0 0 0 0 0	0 0 0 0	$\begin{array}{ccc} 0 & 0 \\ 0 & 0 \\ 0 & 0 \\ 0 & 0 \\ 0 & 0 \\ 0 & 0 \\ 0 & 0 \end{array}$	0	0 0 0 0 0 0	0 (0 0 (0 0 (0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
=	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0		$egin{array}{c} 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 1 \\ 0 \\ 0 \\ 0 \\$	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0		0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 ((0 () 0 () 0 () 0 () 0 () 0 () 0 () 1 () 0 ()) 0) 0) 0) 0) 0) 0) 0) 0) 0) 0	$egin{array}{c} 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 1 \\ 0 \end{array}$	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	$ \begin{array}{c} 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \\$

The A matrix is needed for all 28 animals, and this can be calculated using the tabular method. Knowing that

$\mathbf{A} = \mathbf{T}\mathbf{B}\mathbf{T}'$

where \mathbf{T} is lower triangular and \mathbf{B} is diagonal, the diagonals of \mathbf{B} are 1 for animals 1 through 6, and 0.5 for all other animals, except animals 22 and 23 which were 15/32 for each. These allow for the easy creation of A^{-1} following Henderson's rules (1976).

$$E(\mathbf{g}) = \mathbf{0}$$

$$E(\mathbf{e}) = \mathbf{0}$$

$$Var(\mathbf{g}) = Var\begin{pmatrix} \mathbf{g}_w \\ \mathbf{g}_o \end{pmatrix} = \begin{pmatrix} \mathbf{A}_{ww} & \mathbf{A}_{wo} \\ \mathbf{A}_{ow} & \mathbf{A}_{oo} \end{pmatrix} \sigma_g^2$$

$$Var(\mathbf{e}) = \mathbf{I}\sigma_e^2$$

⁹⁹ where **g** is partitioned into animals with genotypes, \mathbf{g}_w , and animals without ¹⁰⁰ genotypes, \mathbf{g}_o . Let

$$\sigma_e^2/\sigma_g^2 = 0.05 = \lambda$$

which corresponds to a heritability of 0.9523. A heritability of 1 might cause computational problems.

¹⁰³ The mixed model equations are

$$\begin{pmatrix} N & \mathbf{1}' & \mathbf{0}' \\ \mathbf{1} & \mathbf{I} + \mathbf{A}^{ww}\lambda & \mathbf{A}^{wo}\lambda \\ \mathbf{0} & \mathbf{A}^{ow}\lambda & \mathbf{A}^{oo}\lambda \end{pmatrix} \begin{pmatrix} \widehat{\boldsymbol{\mu}} \\ \widehat{\mathbf{g}_w} \\ \widehat{\mathbf{g}_o} \end{pmatrix} = \begin{pmatrix} \mathbf{1}'\mathbf{s} \\ \mathbf{s} \\ \mathbf{0} \end{pmatrix}.$$
 (2)

104

The solutions for animals plus the overall mean gives a prediction of each 105 animal's genotype. The predicted genotypes can be used directly in \mathbf{X} , as con-106 tinuous covariates, in Equation 3. Mulder et al. (2010) found a .69 correlation 107 between predicted genotypes and actual genotypes in a simulation study. The 108 result depends on how many animals were genotyped versus the number to 109 be predicted. Each SNP marker would be analyzed separately. The predicted 110 SNP genotypes can be used to analyze any trait, and only need to be calculated 111 once. The results for animals in the example, $(\hat{\mu} + \hat{\mathbf{g}})$, are in Table 2. 112

113 Table 2 goes here.

The predicted genotypes should be re-calculated whenever new animals are added to the pedigree, or whenever new animals have been genotyped. The predicted genotypes can be used in analyses of any trait. In some cases animals might be genotyped with different SNP chips. The SNP genotype effects should be on a set of SNPs that are common to each chip, or which can be imputed from the various different SNP chips. Imputation should be accomplished prior to predicting SNP genotypes for all animals. This would allow all genotyped animals to participate in subsequent analyses.

One might choose to use a subset of SNPs, for example, only SNPs with minor allele frequencies between 0.3 to 0.5, or SNPs that are distributed evenly within and across chromosomes. Probably 5,000 to 50,000 SNP markers would be sufficient. Studies are needed to determine an optimum number of markers. However, the number of animals with records, N_r , and the number of genotyped animals, N_g , should be greater than the number of SNP markers, m. $(N_r > N_g > m)$

¹²⁹ SNP Genotype Effects Model

If animals have both phenotypic records and genotypes for markers, thenan appropriate linear model would be

$$\mathbf{y} = \mathbf{W}\mathbf{c} + \mathbf{X}\mathbf{m} + \mathbf{e} \tag{3}$$

132 where

- $_{133}$ y is a vector of observations,
- $_{134}$ **c** is a vector of 4 contemporary group effects,
- ¹³⁵ **m** is a fixed vector of 7 marker additive effects,
- \mathbf{e} is a random vector of residuals,
- W is the design matrix relating contemporary group effects to the observa tions, and
- X is a matrix containing marker genotypes (i.e. the results in Table 2),
 corresponding to each observation.
- ¹⁴¹ The expectations of the random vectors and the variances are given below.

$$E(\mathbf{e}) = \mathbf{0},$$

$$Var(\mathbf{e}) = \mathbf{I}\sigma_e^2.$$

¹⁴² The equations to solve are

$$\left(\begin{array}{cc} \mathbf{W}'\mathbf{W} & \mathbf{W}'\mathbf{X} \\ \mathbf{X}'\mathbf{W} & \mathbf{X}'\mathbf{X} \end{array}\right) \left(\begin{array}{c} \widehat{\mathbf{c}} \\ \widehat{\mathbf{m}} \end{array}\right) = \left(\begin{array}{c} \mathbf{W}'\mathbf{y} \\ \mathbf{X}'\mathbf{y} \end{array}\right).$$

Contemporary groups could have been a random factor, and the model, in real life, needs a factor to account for time trends. The number of markers, *m*, should be greatly less than the number of animals, and therefore, should be solvable more quickly than an animal model.

This model is not biased by using animals that have been pre-selected because no animal additive genetic relationships have been utilized. Also, **m** is a vector of fixed effects in the model. The emphasis is on the unbiased estimation of fixed marker genotype effects through regressions on predicted marker genotypes.

Each trait is analyzed separately. This simplifies the software that is needed to do the analysis, and reduces the amount of computer time for the analyses. That is, the contemporary group effects can be absorbed into the matrix of marker genotype effects, then the resulting matrix can be directly inverted and solved. No iteration procedure is necessary. The results for the two traits are given in Table 3.

158 Table 3 goes here.

The correlation between the SNP estimates for trait 1 with trait 2 was -0.29, and the correlation between phenotypes was -0.28.

¹⁶¹ Genomic Estimated Breeding Values

For the example, Equation 1 gives a system of order equal to 4 contemporary group effects and 7 marker covariates. Thus, let $\widehat{\mathbf{m}}$ consist of $\widehat{m}_{i,j}$, the solution for the i^{th} trait and j^{th} marker. Let $\widehat{\mathbf{g}}$ (from Table 2) consist of $\widehat{g}_{j,k}$, the predicted genotype for the j^{th} marker genotype of the k^{th} animal. Then a ¹⁶⁶ genomic EBV (GEBV) for the k^{th} animal and the i^{th} trait is calculated as

$$GEBV_{i,k} = \sum_{j=1}^{7} \widehat{m}_{i,j} \times \widehat{g}_{j,k}.$$

167 Results are in Table 4.

168 Table 4 goes here.

The GEBV should become more accurate as more animals are genotyped and phenotyped over time. The predictions of $\hat{\mathbf{g}}$ will also become better as more animals are genotyped.

The correlations of the GEBV for trait 1 with the phenotypes for trait 1 (for 20 animals with records) was 0.89, and for trait 2 was 0.70. The correlations are less than unity because of the removal of contemporary group effects from the phenotypes.

Of interest is the correlation between the GEBV and the EBV from an animal model. The regular animal model EBV are given in the last two columns of Table 4, from single trait analyses using heritabilities of 0.25 for trait 1 and 0.30 for trait 2. The correlation for trait 1 between GEBV and EBV was 0.80, and for trait 2 was 0.56. There was no bias in the regular EBV from the animal model because none was built into the example data.

Note also that the GEBV have a greater range of values than the EBV
 for each trait.

184 Discussion

The animal model is suffering from biases due to pre-selection of young bulls in dairy cattle. Attempts to adjust the animal model equations for preselection result in adhoc questionable methods. Since 2011, proposals have been made to abandon animal models and switch to a model that estimates SNP genotype effects, but few efforts have been made in that direction.

The SGEM is simple from a statistical point of view, and easier than an animal model from a computational point of view. While the SGEM given in this paper is an additive genetic model, the model can be easily transformed to include dominance effects at each marker. Instead of one value per SNP, there would be three, one for each possible genotype. The next step would be to include interactions among SNP markers for additive by additive effects. The SGEM may become as complex as researchers dare to venture. With theanimal model, one is limited to additive genetic effects.

One of the limitations of SGEM is the fact that SNP genotypes need to be predicted for every animal that have a record. However, this author contends that some years into the future, every dairy cattle animal that is born will be genotyped, and that the SNP genotypes will either be directly available or imputed.

The estimated SNP genotype effects should be fairly constant from one year to the next, as long as there are more animals with records than there are SNP markers to estimate. There is no need to have reference sets of animals and validation sets of animals with SGEM models.

If each country uses a SGEM and the same SNP markers, then $G \times E$ 207 interactions can be studied using the estimated SNP genotype effects directly. 208 Genetic correlations between countries could also be estimated using those 209 solutions. GEBV may be calculated for each animal, sires and cows, within 210 each country using the estimated SNP genotype effects from each country, 211 without the need for SNP MACE (multiple across country evaluation) or any 212 MACE. Interbull would coordinate estimated SNP genotype effects and make 213 comparisons between countries. 214

The actual SGEM may differ from country to country accounting for the little differences in data collection and factors within the country. For example, adjustments for age and month of calving, days pregnant, year-months of calving, and contemporary groups.

The SGEM allow the simple calculation of GEBV for all animals, and not from a biased animal model. Rankings of animals should be more accurate, and hence selection decisions would be better made.

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248 249	Table 1Example Data To Illustrate Methods.CG = Contemporary Groups												
250	CG Anim Sire Dam SNP Markers									Trait 1	Trait 2		
	0.04		0110	Dam	1	2	3	4	5	6	7	110110 1	11010 -
		1											
		2											
		3			1	0	-1	0	-1	0	1		
		4											
		5											
		6											
		7	1	5	0	0	1	-1	0	1	-1		
		8	2	6									
	1	9	1	8								14.8	11.0
	1	10	1	8	0	-1	0	0	0	0	1	7.3	7.2
	1	11	1	5	0	0	1	-1	1	1	0	6.1	18.4
	1	12	2	6	-1	0	0	1	-1	0	0	17.5	8.2
051	1	13	2	7								22.5	6.2
251	1	14	2	7								10.9	9.0
	2	15	2	9	-1	0	1	0	-1	0	1	4.2	6.7
	2	16	2	10	1	-1	-1	1	0	-1	0	17.4	8.5
	2	17	2	11	0	0	0	0	1	0	-1	15.3	15.3
	2	18	3	5								17.5	12.5
	2	19	3	6								9.0	17.9
	3	20	1	9								10.0	1.7
	3	21	2	10	0	-1	0	0	1	-1	0	10.1	9.1
	3	22	3	15	0	0	0	0	-1	1	1	11.8	6.6
	3	23	3	16	1	-1	-1	1	0	-1	-1	26.4	3.7
	3	24	4	12								13.1	9.4
	3	25	4	13	0	1	1	-1	0	0	-1	17.7	13.1
	4	26	2	11	0	0	0	0	1	0	0	6.7	13.3
	4	27	3	17	0	-1	-1	0	0	1	0	28.7	7.5
	4	28	4	9								7.4	8.7

252	Table 2							
253						ll Animal		
	Anim			edicted SI	VP Marke	er Genoty	pes	
		1	2	3	4	5	6	7
	1	-0.0313	-0.2856	0.6008	-0.4591	0.4359	0.5017	0.2647
	2	-0.1621	-0.2103	-0.3917	0.7955	0.3528	-0.9342	-0.3509
	3	1.0390	0.0842	-0.9693	0.3478	-0.5457	0.0304	0.9795
	4	-0.1798	0.3845	0.2185	-0.6223	-0.1306	-0.2626	-0.5750
	5	-0.2561	-0.0845	0.2867	-0.7825	0.3021	0.3039	-0.9091
	6	-0.4403	0.0810	0.2243	0.6900	-0.4450	0.3301	0.5602
	7	0.0161	0.0655	0.8963	-0.7345	0.3365	0.8471	-0.9323
	8	-0.3858	-0.3622	-0.1236	0.7074	-0.1762	-0.4001	0.4946
	9	-0.5628	-0.2604	0.5479	-0.0126	-0.2724	0.1276	0.6879
	10	0.1268	-0.8323	-0.0004	0.3407	0.4223	-0.0720	1.0013
	11	-0.2287	-0.1890	0.6089	-0.9585	1.0345	0.5933	-0.2903
	12	-1.2407	-0.2698	-0.4032	0.8843	-0.9448	-0.4575	-0.3087
	13	0.0808	0.3636	0.6053	-0.0369	0.5231	0.0689	-0.6853
254	14	-0.0431	-0.0425	0.2822	0.0604	0.3745	-0.0136	-0.6117
	15	-0.9380	0.0247	0.8297	0.2508	-0.6314	-0.1167	0.9181
	16	0.8640	-0.9840	-1.0675	1.1482	0.2812	-1.1517	-0.0940
	17	0.0764	0.0962	0.0101	0.3176	1.3577	0.0107	-0.8386
	18	0.2581	-0.1335	-0.4746	-0.3507	-0.2552	0.0338	-0.0982
	19	-0.1200	-0.3368	-0.7919	0.0995	-0.9148	-0.2391	0.3505
	20	-0.1364	-0.1124	0.7350	-0.0752	0.2423	0.4753	0.6369
	21	0.0113	-0.9033	-0.0963	0.2764	1.2299	-1.0678	0.0284
	22	0.0000	0.0405	-0.1024	0.2346	-0.6942	0.7695	0.9762
	23	0.9483	-0.9540	-1.1396	1.1393	0.2112	-1.1298	-0.9220
	24	-0.3432	0.4244	0.2747	0.4980	-0.1707	0.0069	-0.0749
	25	-0.2333	0.7546	0.6264	-0.9559	0.0617	-0.3634	-1.2092
	26	-0.3051	-0.2652	-0.3688	-0.0828	0.9575	-0.4287	-0.3305
	27	0.1800	-0.7313	-0.9147	0.3714	0.4389	0.9144	0.1217
	28	-0.2171	0.2162	0.5374	-0.1633	-0.0473	0.0867	0.2106

255		Table 3	5					
256	Solutions from SGEM for example data.							
	Item	Trait 1	Trait 2					
	CG 1	14.337	13.358					
	CG 2	13.070	12.776					
	CG 3	14.264	9.221					
	CG 4	13.395	8.226					
	snp 1	-2.469	-2.000					
257	$\operatorname{snp} 2$	-6.542	10.721					
	$\operatorname{snp} 3$	-7.353	-8.887					
	$\operatorname{snp} 4$	-5.843	-3.921					
	$\operatorname{snp}5$	-7.073	5.600					
	snp 6	2.049	-2.037					
	$\operatorname{snp}7$	-10.701	4.603					

Table 4

GEBV from SGEM and EBV from animal model for animals in Example
Data

Anim	Sire	Dam	am GEBV I		EI	BV
	0110	2 0.11	Trait 1	Trait 2	Trait 1	Trait 2
1	0	0	-2.7319	-4.1105	-1.9585	-0.6330
2	0	0	-0.3825	0.6667	0.6001	-1.5113
3	0	0	1.1782	6.8458	2.6518	-0.2479
4	0	0	-0.3985	2.8792	-0.6874	0.9594
5	0	0	2.4322	-1.9717	0.1473	1.2853
6	0	0	-0.0976	-4.3094	-0.7533	0.1475
7	1	5	9.0977	-8.8208	-0.4379	0.0985
8	2	6	-2.8221	-2.8908	-0.6517	-1.2368
9	1	8	-5.7706	-5.1327	-2.0477	-1.4907
10	1	8	-4.9474	-4.0074	-1.7126	-1.4890
11	1	5	-6.9651	0.7668	-1.7672	1.9735
12	2	6	2.2444	-5.0614	0.3538	-0.8983
13	2	7	4.1583	-2.6375	1.4513	-0.9989
14	2	7	4.3576	-4.0771	-0.3537	-0.8692
15	2	9	-9.0638	-5.4972	-1.9913	-2.3189
16	2	10	2.3673	-3.8338	0.8522	-2.2174
17	2	11	2.4020	2.6446	0.7022	0.4658
18	3	5	1.8052	2.4371	1.9409	0.3842
19	3	6	0.5403	1.2682	0.3406	0.8686
20	1	9	-4.2512	-4.6216	-2.4174	-2.0047
21	2	10	-3.6847	-1.0145	-1.1629	-1.0598
22	3	15	-2.8965	-0.7468	-0.1337	-1.3204
23	3	16	11.9437	-7.2520	3.0689	-1.7633
24	4	12	0.9230	-1.0911	-0.4006	0.2537
25	4	13	1.4814	3.0000	0.7269	0.8652
26	2	11	-7.8608	7.0972	-1.5942	0.8065
27	3	17	13.5606	-1.1473	3.4863	-0.3176
28	4	9	-3.0845	-1.1268	-2.1662	-0.4144