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Use of partial least-squares regression to predict single-nucleotide polymorphism marker genotypes when some animals are genotyped with a low density panel C. Dimauro<sup>a</sup>, R. Steri, M. A. Pintus, G. Gaspa and N. P.P. Macciotta Dipartimento di Scienze Zootecniche, Università di Sassari, via De Nicola 9, 07100 Sassari, Italy <sup>a</sup>Corresponding author: Corrado Dimauro, Dipartimento di Scienze Zootecniche, Università di Sassari, via De Nicola 9, 07100 Sassari, Italy. Tel. +39 079229298; fax +39 079 229302. E-mail: dimauro@uniss.it Running head: Single nucleotide polymorphism prediction 

23 Abstract

24

High density SNP platforms are currently used in Genomic Selection (GS) programs to 25 enhance the selection response. However, the genotyping of a large number of animals 26 with high throughput platforms is rather expensive and may represent a constraint for a 27 large-scale implementation of GS. The use of low density marker platforms could 28 overcome this problem, but different SNP chips may be required for each trait and/or 29 breed. In this paper a strategy of imputation independent from trait and breed, is proposed. 30 A simulated population of 5,865 individuals with a genome of 6,000 SNP equally 31 distributed on six chromosomes was considered. First, reference and prediction 32 populations were generated by mimicking high and low density SNP platforms, 33 respectively. Then, the partial least squares regression (PLSR) technique was applied to 34 reconstruct the missing SNP in the low density chip. The proportion of SNP correctly 35 reconstructed by the PLSR method ranged from 0.78 to 0.97 when 90% and 50% of 36 genotypes were predicted, respectively. Moreover, data sets consisting of a mixture of 37 actual and PLSR-predicted SNP or only actual SNP were used to predict genomic 38 breeding values (GEBV). Correlations between GEBV and true breeding values varied 39 from 0.74 to 0.76 respectively. Results of the study indicate that the PLSR technique can 40 be considered a reliable computational strategy for predicting SNP genotypes in a low 41 density marker platform with reasonable accuracies. 42

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45 **Keywords**: genomic selection; SNP prediction

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### 49 Implications

In genomic selection programs, animals are genotyped with high-density SNP marker platforms with around 50-60K markers. However, being the number of phenotypes available markedly lower than the number of markers, several statistical shortcomings arise when data are analyzed. In this paper we propose the use of both high and low-density SNP marker platforms in combination with partial least squares regression (PLSR) technique to reconstruct the missing SNP in the low density chips. Savings obtained by using low density platforms could be used to enlarge the number of animals involved in the selection program. 

#### 75 Introduction

76

Traditional genetic evaluations for livestock combine phenotypic data with pedigree 77 relationships to estimate the probability that genes are transferred to the next generations. 78 Genomic selection (GS), on the contrary, exploits dense marker information represented 79 by single nucleotide polymorphism (SNP) to evaluate genomic breeding values (GEBV) by 80 estimating the effect of chromosome segments on phenotypes (Hayes and Goddard, 81 2008). Advances in high throughput technologies have led to the construction of dense 82 SNP platforms that could trace the inheritance of individual genes. High density marker 83 84 (HDM) platforms with 50 – 60 K SNP are currently used in GS programmes. However, the number of genotyped animals is considerably smaller than the number of markers. In dairy 85 cattle, the ratio number of animals vs. number of markers is, on average, between 0.08-86 0.15, apart from USA and Canada where it is around 0.45 (VanRaden et al., 2009). Such a 87 data asymmetry results in several statistical shortcomings, as collinearity among predictors 88 and issues in multiple testing procedures. Furthermore, the well known curse of multi-89 dimensionality should become now more relevant, due to the recent commercial 90 availability of the 777 K SNP Illumina Bead-chip. 91

The use of low density marker platforms (LDM) may represent a interesting technical 92 option to reduce the genotyping costs and enlarge the number of animals involved in GS 93 programmes. However, the reduction of SNP density is expected to decrease GEBV 94 accuracy. Weigel et al. (2009) reported a loss of about one-third in the gain of reliability of 95 GEBV for lifetime profit in cattle when a low-density assays with 750-1,000 SNP was used. 96 In this study, SNP were chosen either on the basis of their chromosomal location (evenly 97 spaced) or for their relevance on the considered trait. Habier et al. (2007) combined the 98 use of evenly spaced SNP and co-segregation information from LDM to track HDM 99

inheritance within families. On simulated data, they found a reduction in GEBV accuracy
 ranging from 1 to about 25%, depending on the considered scenario.

The use of the above mentioned methodologies can be useful to reduce the number of 102 SNP but, separate chips for each trait and/or breed may be required. In this paper an 103 alternative strategy, independent from trait or breed, is proposed. The method starts by 104 creating a reference (REF) and a prediction (PRED) population of animals genotyped with 105 HDM (containing N SNP) and LDM (n SNP) platforms, respectively (N > n). Missing k-106 markers (k = N-n) in PRED population are reconstructed by using a suitable mathematical 107 tool and, as a final result, a PRED population with N SNP as in HDM is obtained. These 108 109 markers are a mixture of actual and predicted SNP.

The most straightforward computational method for predicting unknown SNP markers in 110 the LDM platform is the multivariate multiple regression. However, considering that 111 adjacent SNP are highly correlated, the predictive capability of the model could be 112 compromised by the multicollinearity among predictors (Draper and Smith, 1981). Partial 113 least squares regression (PLSR), originally developed in the computational chemistry 114 context (Hoeskuldsson, 1988), has become an established tool for modeling linear 115 relations between multivariate measurements. It is characterized by an higher prediction 116 117 efficiency compared to ordinary multivariate regression or principal component regression (Macciotta et al., 2006). PLSR has been already used in GS studies by Solberg et al. 118 (2009) for reducing the dimensionality of predictors in the calculation of GEBV. In the 119 present study, the PLSR technique is applied to predict missing SNP when animals are 120 genotyped with a LDM platform. Actually, this statistical technique is particularly useful 121 when a set of correlated dependent variables (Y) have to be predicted from a set of 122 correlated independent variables (X). PLSR maximizes the correlation structures between 123 **Y** and **X** and overcomes the multicollinearity problems by combining features of principal 124 components analysis and multiple regression (Abdi, 2003). 125

126 The aim of this work is to test the ability of PLSR for predicting missing SNP genotypes 127 when a PRED population is created by using a LDM platform of SNP markers.

128

#### 129 Materials and methods

- 130
- 131 The data

Data were extracted from an archive generated for the XII QTLs – MAS workshop, freely 132 available at: http://www.computationalgenetics.se/QTLMAS08/QTLMAS/DATA.html. The 133 base population consisted of 100 individuals (50 males and 50 females). A genome of six 134 chromosomes (total length 6 M) with 6,000 biallelic SNP, equally spaced in the genome at 135 136 a distance of 0.1 cM, was generated. A total of 48 biallelic QTLs were included, with positions sampled from the genetic map of the mouse genome and effects derived from a 137 gamma distribution (Hayes and Goddard, 2001). Initial allelic frequencies of both SNP and 138 QTL were set to 0.5. Then 50 generations of random mating followed. Generations from 139 51 to 57 were used to create the definitive archive of 5,865 individuals. For each 140 generation 15 males and 150 females were randomly selected to be parents of the next 141 generation. Each male had 100 sons and was mated to 10 females (10 sons for female). 142 143 Animals belonging to the generations from 51 to 54 had pedigree, phenotype, and marker information available. For the last 3 generations only pedigree and marker information 144 were available. These animals constituted the PRED population and were obtained by 145 randomly selecting 400 animals for each generation (a total of 1200 individuals). True 146 breeding values (TBV) were created as the sum of all QTL effects across the entire 147 genome. Phenotypes were generated by adding to the TBV an environmental noise drawn 148 from a normal distribution with mean zero and variance equal to the residual variance 149 defined to obtain a heritability of 0.30. For further details on the data generation see Lund 150 et al. (2009). 151

153 The PLSR technique

PLSR is a multivariate extension of the multiple regression analysis. It is particularly useful when (i) the number of predictor variables is similar to or higher than the number of observations and/or (ii) predictors are highly correlated (i.e. there is strong collinearity). The basic model is:

158 **Y=XB+E** 

159 where **Y** is a  $n \times m$  response matrix, **X** is a  $n \times p$  design matrix, **B** is a  $n \times m$  regression coefficient matrix, and **E** is a  $n \times m$  error term. In PLSR, matrices **X** and **Y** are 160 simultaneously decomposed into a set of new variables (called latent factors). Factors are 161 extracted in order to explain as much as possible of the covariance between X and Y and 162 to minimize the covariance between variables inside each matrix. Extracted latent factors 163 account for successively lower proportions of original variance and are defined as linear 164 165 combinations of predictor and response variables (Hubert and Branden, 2003). Key elements in the different calculation steps of the PLSR are: the scores, i.e. values of the 166 extracted latent factors both for the dependent (U) and independent variables (T), and 167 factor loadings (Q) expressing correlations between extracted factors and original 168 dependent variables. Considering a REF and a PRED population, latent factor scores (Tref) 169 extracted from X<sub>ref</sub>, are used to predict scores of latent factors extracted from Y<sub>ref</sub> (U<sub>ref</sub>) 170

Then, the estimated regression coefficients **B** are used to predict values of **Y**<sub>pred</sub> in the PRED population as:

174 
$$\mathbf{Y}_{\text{pred}} = \mathbf{BT}_{\text{pred}}\mathbf{Q}'_{\text{ref}}$$
 (2)

where  $\mathbf{Q}'_{ref}$  is the transposed matrix of factor loadings extracted from  $\mathbf{Y}_{ref}$ .

The standard algorithms for computing latent factors are nonlinear and iterative (NIPALS and SIMPLS algorithms, for example) and require the use of dedicated software (for more details see Wold *et al.*, 2001; de Jong, 1993). In this work, the PLS procedure of SAS-STAT software (SAS Institute INC, Cary, NC) was used.

180

### 181 The PLSR method for SNP genotypes prediction

182 To simulate a PRED population genotyped with a LDM platform, the first k-SNP were assumed to be not known. SNP from k+1 to 1,000 represented the predictors (i.e. Xref and 183 **X**<sub>pred</sub>) and were known both for REF and PRED population. SNP from 1 to k were known in 184 REF (Y<sub>ref</sub>) and were used to calculate the matrix of regression coefficients **B** (equation 1). 185 Then, using the equation (2), the  $\hat{\mathbf{Y}}_{\text{pred}}$  matrix was predicted. Being that the genotype at 186 each SNP is coded as the number of allele 1 copies, i.e. 0, 1 or 2, results (columns 187 in  $\hat{\mathbf{Y}}_{\text{pred}}$  each containing the predicted SNP genotype) were rounded to the nearest integer. 188 The goodness of SNP prediction was evaluated by calculating correlations between real 189 ( $\mathbf{Y}_{pred}$ ) and PLSR predicted ( $\hat{\mathbf{Y}}_{pred}$ ) SNP genotypes. Considering that for k predicted SNP 190 k correlations were calculated, the average value of these correlations, for each prediction 191 scenario, was considered. Moreover, percentage of correct predictions across SNP and 192 mean percentage of corrected SNP predictions for each animal were calculated. 193

A crucial point in PLSR modeling is how many latent factors should be retained to correctly define the complexity of one experiment. When several and correlated predictors are used, the risk of obtaining a model able to fit data well but with a very poor predictive power is rather high. This problem is known as model "over-fitting". It is usually handled by testing the predictive significance of the successive extracted factors. Cross-validation in
combination with PRESS statistics is commonly used to this purpose (Wold *et al.*, 2001).
However, in the present study several scenarios involving a great number of predictors are
compared and, therefore, the use of the above cited tests become problematic in terms of
computation time and resources. For these reasons, the best number of extracted latent
factors in each scenario was fixed empirically by comparing the obtained results with real
data (the procedure will be explained in the next section).

205

#### 206 Setup of the PLSR method

Location of missing SNP along the chromosome, number of latent factors to be extracted for each scenario, number of SNP to be predicted and the minimum number of genotyped animals to use as REF population are relevant aspects for the method be efficiently performed in practice. They were tested in successive steps during the development of the PLSR method. All the computations were done separately per chromosome .

Step 1: four scenarios of chromosome location of SNP to be predicted (k = 100) in PRED population were tested: at the beginning (SNP1 – SNP100), in the middle (SNP451-SNP550), at the end (SNP901 – SNP1,000), or evenly spaced in the chromosome.

Step 2: once the best SNP location was assessed, the optimum number of latent factors to be extracted was evaluated. In PLSR procedure, the number of factors can not exceed the number of the independent variables. Therefore, for each chromosome, several simulations were performed where 100 SNP were predicted with a number of factors ranging from 10 to 900.

220 Step 3: prediction accuracy for different number of SNP to be predicted was investigated 221 using the following proportions for missing SNP in PRED population: 10%, 25%, 50%, 75% and 90%. At the end of the PLSR procedure, a series of new data sets for PRED
population, each containing 10%, 25%, 50%, 75% and 90% of PLSR predicted SNP, were
produced.

Step 4: the effect of the SNP reduction in the estimation of genomic breeding values was 225 tested by evaluating GEBV's either in original and in five data sets, generated in step 3, 226 which contain the mixture of actual and PLSR predicted SNP. Effects of SNP markers on 227 phenotypes in the REF population were estimated with a mixed linear model that included 228 229 the fixed effects of mean, sex (1,2) and generation (1,2,3,4), and the random effects of SNP genotypes (Meuwissen et al. 2001). Overall mean and effects of SNP genotypes 230 were then used to predict GEBV in PRED population (Macciotta et al., 2010). Accuracies 231 were evaluated by calculating Pearson correlations between GEBV and true breeding 232 values. 233

Step 5: finally, considering a possible application of the method on real data, accuracy of the PLSR predictions were tested for different sizes of the REF population, from 5,000 to 600 individuals. In all the simulations, the size of PRED population was kept constant (600).

238

### 239 Results and discussion

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Step 1: the effects of SNP location on prediction accuracy can be observed in Table 1 where average correlations between actual and PLSR-predicted SNP genotypes for different scenarios are reported. Lowest correlations were obtained when markers to be predicted are located at the beginning or at the end of the chromosome. A slight increase of accuracy can be observed when SNP are located in the middle of the chromosome. The highest value was found for evenly spaced missing SNP. These results were expected, 247 considering the decaying pattern of correlation between loci for increasing distances, and 248 are in agreement with figures reported by Habier *et al.* (2009) who had already used 249 evenly spaced SNP to simulate low density marker panels. In any case, the value of the 250 mean correlation for the best scenario is notably high and may represent a useful 251 indication for constructing a LDM platform without trait or breed constraints.

Step 2 : Figure 1 displays pattern of mean correlations between 100 actual and PLSR predicted SNP for increasing number of extracted latent factors for the first chromosome. There is a rapid increase of prediction accuracy from 10 up to 100 factors (from 47% to 93%). A plateau of 98% is then reached when about 150 - 200 factors are extracted. These results indicate that the number of latent factors to be extracted should be higher or, at least, equal to the number of predicted SNP.

Step 3: the variation of prediction accuracy for different number of SNP to be predicted is 258 reported in Table 2. Moving from 10% to 75% missing SNP, there is small decrease (about 259 6%) in the average correlation between actual and predicted genotypes. In any case, 260 prediction accuracy is higher than 90% even when two-third of the SNP are predicted. It 261 slightly falls below 0.80 when 90% of SNP have to be predicted. However, even in this 262 case, the accuracy can be considered satisfactory. If confirmed on real data, results of the 263 264 present study may indicate that a chip with 5.4 K SNP evenly spaced across the genome could represent a suitable base for reconstructing, with a reasonable accuracy, the profile 265 of an high density platform of 54 K SNP (i.e. the one currently used for cattle). In a recent 266 study carried out with the bovine 54 K SNP, Weigel et al. (2010) using the algorithm 267 implemented in fastPHASE 1.2 software (University of Washington TechTransfer Digital 268 Ventures Program, Seattle, WA), reported a proportion of correctly reconstructed missing 269 SNP of about 0.88 when 90% SNP were predicted. Druet and Georges (2010) combined 270 fastPHASE and Beagle (Browning and Browning, 2007) algorithms to take into account 271 both population (linkage disequilibrium) and familial (Mendelian segregation and linkage) 272

information to predict missing genotypes. They found, with 50% missing genotypes, an imputation error of 3% and 1% for sparse and dense marker map, respectively. In the present work, the proportion of correctly reconstructed SNP for 90% and 50% missing genotypes was 0.86 and 0.98, respectively (Table 2).

The SNP genotype profile of each animal was also well reconstructed by the PLSR method. When 90% SNP were predicted, more than 84% of animals presented a percentage of corrected SNP reconstruction ranging from 80 to 100%. Moreover, when predicted SNP were lower then 75%, all animals had a proportion of corrected reconstructed SNP ranging from 95 to 100%.

Step 4: accuracies displayed in Table 3 indicate that the use of PLSR-predicted SNP does not affect the estimation of genomic breeding values. Correlations between true breeding values and GEBV remain basically the same moving from the scenario where all used SNP are actual to the one where 90% of marker genotypes are PLSR-predicted (Table 3). These results are similar to those obtained by Habier *et al.* (2009) who reported a reduction in GEBV accuracy of about 4% moving from a SNP panel density of 0.05 cM to 10cM.

Step 5: finally, Figure 2 displays accuracies of SNP prediction obtained with different sizes 289 of REF population. As the number of fully genotyped animals becomes smaller, 290 correlations between actual and predicted SNP slowly decrease reaching a value of 93% 291 when the number of REF animals is twice (2,000) the total number of SNP per 292 chromosome. Correlations dramatically drop (<70%) for a number of fully genotyped 293 animals equal to 600. Considering that on real data each bovine chromosome has on 294 average 1000-1200 SNP after data editing, a minimum number of 2,000-2,500 fully 295 genotyped animals could be enough to obtain reliable predictions from the PLSR method. 296

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298 Conclusions

300 The use of LDM platforms in combination with a suitable computational algorithm able to predict the missing genotypes with respect to HDM chips is an option for reducing 301 genotyping costs in GS programs. Savings could be used to enlarge the genotyped 302 population thus enhancing the efficiency of the breeding scheme. In this paper, the ability 303 of PLSR technique for predicting missing SNP genotypes in LDM platforms was tested. 304 The method correctly assigned from 86 to 98% of missing genotypes, when 90 and 50% 305 SNP were predicted, respectively. Moreover, only a slight difference (2%) in GEBV 306 accuracies was observed using actual SNP or a mixture of actual and predicted SNP. 307 Finally, a size of around 2,000-2,500 fully genotyped animals with a 54 K SNP chip was 308 found to be a reliable REF population to reconstruct the SNP profile of a PRED population 309 of animals genotyped with a LDM chip containing 5,4 K evenly spaced SNP. 310

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**Table 1** *Mean correlations (and related standard deviations) between 100 actual and predicted* 

367 SNP in each chromosome

Missing	Corre	elations
SNP position	Mean	St. Dev.
First 100	0.57	0.17
Middle 100	0.75	0.11
Last 100	0.68	0.14
One every 10	0.93	0.09

368

**Table 2** *Mean correlations (and related standard deviations) between actual and predicted SNP for* 

Percentage of	Corr	elations	Proportion of
predicted	Mean	St. Dev.	correct SNP
SNP			prediction
10%	0.98	0.07	0.99
25%	0.98	0.07	0.99
50%	0.97	0.08	0.98
75%	0.92	0.08	0.95
90%	0.78	0.13	0.86

371 increasing percentage of predicted SNP. Proportions of correct SNP prediction are also reported

372

**Table 3** *GEBV* accuracies for different ratio of available/predicted SNP.

	Real SNP	Predicted SNP	GEBV accuracy
	100%	0%	0.76
	75%	25%	0.76
	50%	50%	0.76
	25%	75%	0.75
	10%	90%	0.74
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381 Figure captions:

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Figure 1 Pattern of the mean correlations between actual and predicted SNP for increasing
 number of extracted factors during the PLSR procedure

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Figure 2 Mean correlations between actual and predicted SNP for different numbers of fullygenotyped animals

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