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Use of Principal Component approach to predict Direct Genomic Breeding Values for Beef Traits in Italian Simmental Cattle

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ABSTRACT

In the current study, principal component (PC) analysis was used to reduce the number of predictors in the estimation of direct genomic breeding values (DGV) for meat traits in a sample of 479 Italian Simmental bulls. SNP marker genotypes were determined with the 54K Illumina beadchip. After edits, 457 bulls and 40,179 SNPs were retained. PC extraction was carried out separately for each chromosome and 2,466 new variables able to explain 70% of total variance were obtained. Bulls were divided into reference and validation population. Three scenarios of the ratio reference:validation were tested: 70:30, 80:20, 90:10. Effect of PC scores on polygenic EBVs was estimated in the reference population using different models and methods. Traits analyzed were daily live weight gain, size score, muscularity score, feet and legs score, beef index (economic index), calving ease direct effect, and cow muscularity. Accuracy was calculated as correlation between DGV and polygenic EBV in the validation bulls. Muscularity, feet and legs, and the beef index showed the highest accuracies calving ease the lowest. In general, accuracies were slightly higher when reference animals were selected at random and the best scenario was 90:10 and no substantial differences in accuracy were found among different methods. Accuracies of direct genomic values were higher than those of traditional PA. Results of the present study suggest possible advantages of the use of genomic index in the pre-selection of performance test candidates for beef traits.

Key Words: cattle, genomic selection, beef traits, principal component analysis

INTRODUCTION

In the last years, the development of high density SNP platforms has had a relevant impact on genetics and breeding research programs for many livestock species. Genotypes of thousands of marker loci are currently used in dairy cattle to search for genomic regions associated with yield and functional traits (Raadsma, et al., 2009; Bolormaa et al., 2010a; Cole et al., 2009) and for predicting genomic enhanced breeding values (GEBV) in genomic selection (GS) schemes. For beef cattle, most of studies have dealt with genome-wide scans for associations between SNP and beef traits such as residual feed intake, average daily gain, hip height, and carcass traits (Bolormaa et al., 2011b, Bolormaa et al., 2011c) or to detect signature of selection able to discriminate between beef and dairy cattle (Hayes et al., 2009a). Until now, less pressure has been put on the implementation of GS programs, even though this technology may represent a valuable option also for beef cattle, allowing to increase breeding value accuracy and to enlarge breeding goals by including traits that are difficult or expensive to measure routinely.

Possible constraints to the application of GS in beef cattle are the limited number of genotyped animals (Garrick, 2011) due to the limited size of male population, and the genotyping costs. The latter issue can be partially addressed by developing a low density SNP chip specific for beef breeds (Rolf et al., 2010), and imputing the 54k chip (Weigel et al., 2010, Berry and Kearney, 2011, VanRaden, 2011). An approach to deal with the disproportion between the limited sample size and SNP number, relevant also for GS programmes in dairy cattle, may be represented by the use of strategies able to reduce predictor dimensionality. Principal component analysis (PCA) and partial least squares regression have been suggested for reducing the number of predictors in DGV calculations both for simulated and actual data (Long et al., 2011; Moser et al., 2009; Solberg et al., 2009). In particular, PCA allows for a considerable reduction (>90%) of the number of independent

variables in DGV estimation with accuracies similar to those obtained using directly all SNP genotypes available in simulated and real data (Macciotta et al., 2010a; Solberg et al., 2009; Long et al., 2011).

Aim of this work was to calculate DGV for beef traits in the dual purpose Italian Simmental cattle breed. A reduced set of predictors based on linear combinations of SNP genotyped on Illumina platform was obtained by PCA. Moreover, this method was compared with two other approaches commonly used to predict DGV in genomic selection programmes that use directly SNP genotypes as predictors.

MATERIALS AND METHODS

Data

A total of 465 Italian Simmental bulls were genotyped at 54,001 SNP loci using the Illumina Bovine SNP50TM bead-chip (Illumina, San Diego, CA). Animals with more than 1,000 missing genotypes and with inconsistencies in the mendelian inheritance were excluded from the analysis. SNP selection was more conservative and edits were based on the number of missing records (< 0.025), mendelian inheritance conflicts, absence of heterozygous individuals, minor allele frequency (> 0.05), deviance from Hardy-Weimberg equilibrium ($P < 0.01$) (Wiggans et al., 2009). After editing, 8 animals (2 for mendelian inheritance conflicts, 6 for missing genotypes) and 13,822 SNP (21 SNP for mendelian inheritance conflict, 999 SNP with missing exceeding the threshold, 12,215 SNP with MAF≤ 0.05 and 587 not in HW equilibrium) were discarded. Final number of bulls and SNP used were 457 and 40,179 respectively. Missing genotypes were replaced with the most frequent allele at that specific locus.

Phenotypes used were polygenic EBV provided by Italian Simmental association (evaluation of December 2009). Seven traits were considered: average daily weight gain (ADWG, kg/d), size score (SS), muscularity score (MS), feet and legs score (FLS), beef index (BI = 0.40*ADWG + 0.10*SS + 0.40*MS + 0.10*FLS), calving ease direct effect (CED), cow muscularity score(CWM). Table 1 reports EBV average value and reliability. EBV for CED and CWM were derived from progeny test whereas the other traits were measured on performance test. The scale of EBV analyzed were equivalent for different traits (standardized with mean 100 and genetic standard deviation 12).

Animals were sorted by year of birth (range 1972-2002) and the whole dataset was split into two subsets, reference (REF) and validation (VAL), containing the oldest and youngest animals, respectively. Different sizes of REF population were tested. Bulls born before 1999, 2000 or 2001 were included in the REF population (Figure 1), corresponding to the ratios REF/VAL of 70:30, 80:20 and 90:10 respectively.

Statistical model

PC-BLUP (BLUP on Principal Components). Data matrix $\mathbf{M}_{nxm}$ of marker genotypes was set up (n = total number of individuals, m = number of marker genotypes). Each element m_{ij} corresponded to the genotype at the j-th marker for the i-th individual. Genotypes were coded as -1, 0 or 1, where -1 and 1 are the two homozygotes and 0 the heterozygote, respectively (Solberg et al., 2009). PC extraction was carried out separately for each chromosome The number of PCs retained was based on the percentage of variance explained (Macciotta et al., 2010a). Scores of the selected PC were calculated for all individuals. The estimation of effects of the PC on the REF data set was carried out using a BLUP model.

$$\mathbf{y} = \mathbf{1}\mu + \mathbf{Zg} + \mathbf{e} \qquad [1]$$

where **y** is the vector of polygenic EBVs, **1** is a vector of ones, μ is the overall mean, **Z** is the matrix of PC scores, **g** is the vector of PC regression coefficients treated as random, and **e** is the vector of random residuals. Random PC effects (**g**) were assumed identically and normally distributed with $g_i \sim N(0, \mathbf{I}\sigma_{gi}^2)$ where $\sigma_{gi}^2=\sigma_a^2/k$ (σ_a^2 = additive genetic variance, k=number of PC retained). Random residuals were assumed normally distributed with $e_i \sim N(0, \mathbf{I}\sigma_e^2)$. Variance components were supplied by breed associations. BLUP mixed model equations were solved by using Gauss-Seidel iterative method.

PC-BLUP_EIGEN. It is the same method as above, but the (Co)variance matrices of random PC effects (G) and residuals (R) were modeled as diagonal $\mathbf{I}\sigma^2_{gi}\lambda_j$ and $\mathbf{I}\sigma_e^2$ respectively. In particular, the contribution of each j-th principal component to the genetic variance was assumed to be proportional to its corresponding eigenvalue (λ_i) $\sigma_{gi}^2 = (\sigma_a^2/k)*\lambda_j$ (Macciotta et al., 2010a).

To evaluate the effect of the reduction of predictor dimensionality on genomic predictions DGV were calculated also with other two approaches that directly uses all markers available (R-BLUP and BAYES A), but with different theoretical assumptions on the distribution of marker effects. Hereafter, these are named “full models”.

R-BLUP. In this model, marker effects were estimated using the same structure of model [1]. In this case, **Z** is the design matrix of SNP genotypes – coded as 0,1 and 2 according to the number of copies of the second allele. Marker effects were assumed to be sampled from the same normal distribution. (Co)variance matrix of SNP effects (**G**) was modelled as diagonal $\mathbf{I}\sigma_{gi}^2$, where $\sigma_{gi}^2 = \sigma_a^2/n$, with n equal to the number of SNP. Mixed model equations were solved using a Gauss-Seidel iterative algorithm until convergence.

BAYES A. A Bayes A model (BAYES A) that allows for variance to differ across chromosome segments (Meuwissen et al., 2001) was fitted:

$$\mathbf{y} = \mathbf{1}\mu + \mathbf{Zg} + \mathbf{Wu} + \mathbf{e} \qquad [2]$$

where **W** is the incidence matrix that allocate the animal with their phenotypic record and **u** is a vector of polygenic breeding values assumed to be normally distributed, with $u_i \sim N(0, \mathbf{A}\sigma_a^2)$, where **A** is the numerator relationship matrix and σ_a^2 is the additive genetic variance. The other symbols were the same as in model [1]. Prior structure and hyper-parameters were chosen according to Meuwissen et al., (2001). A scaled inverted chi-squared prior distribution was assumed for SNP specific variances, under the hypothesis that most of markers have nearly zero effects and only few have large effects. A total of 20,000 iterations were performed, discarding the first 10,000 as burn-in and considering no thinning interval. A residual updating algorithm was implemented to reduce computational time (Legarra and Misztal, 2008).

DGV estimation and accuracy assessment. The overall mean (μ) and the vector ($\hat{\mathbf{g}}$) of the PC scores (or marker effects in full models) estimated in the REF animals with the above described methods were used to calculate the DGV for VAL bulls as:

$$\hat{\mathbf{y}} = \mu + \mathbf{Z}\hat{\mathbf{g}}$$

where $\hat{\mathbf{y}}$ is the vector of DGV, **Z** is the matrix of PC scores (or marker genotypes in full models) for validation bulls.

The accuracy of the genomic prediction in the validation set was evaluated through analysis of Pearson correlation between EBV and DGV. To evalue the difference between DGV and traditional polygenic evaluations, DGV accuracies were compared with correlations between EBV and Parent Average (PA) calculated for beef traits included in the BI.

Bias was assessed by examining regression coefficient of EBV on predicted DGV, and 95% confidence interval for b estimates was calculated. Mean squared error of prediction (MSEP) and its partition in different sources of variation related to systematic and random errors (Tedeschi, 2006) were used to evaluate the goodness of prediction.

RESULTS

Accuracy of genomic prediction

The number of principal components to retain was assessed based on the pattern of DGV accuracies for increasing amounts of explained variance (Figure 2). A slight increase of DGV accuracy can be observed for larger proportions of explained variance, with a peak at 0.70 for some traits. This value, that corresponded to 2,466 extracted PC from the whole genome, was further used in the study. Actually it minimized the computational demand of DGV estimation without losing in accuracy. The distribution of extracted PC basically was proportional to the number of markers present in the chromosome (Figure 3).

Table 2 reports the Pearson correlation coefficients between DGV and polygenic EBV across four different estimation methods and for different REF:VAL ratios. Accuracies were moderate to high except for CED, which showed lowest values (on average 0.24) across all different validation sets and estimation methods. In particular, highest accuracies were obtained for traits related to muscularity: average $r_{EBV, DGV}$ across estimation methods were 0.82, 0.73, 0.76 and 0.66 and for CWM, MS, FLS BI, respectively. ADWG and SS showed moderate values (0.45 and 0.51, respectively). Values for ADWG are higher than those reported by Rolf et al. (2010) for Angus cattle. Accuracies found for SS were similar to those for stature reported by Olson et al. (2011) in Brown Swiss using BAYES B. Liu et al. (2011) reported a values of 0.71 in German

174 Holstein. Values for CED were close to those reported for Piedmontese (Ajmone-Marsan et al.,
175 2010) and Brown Swiss (Olson et al., 2011). Higher values were reported for Angus bulls (Garrick,
176 2011; Saatchi et al., 2011) but with population sizes greater than 2,000 bulls.

177 In general, DGV accuracy tended to increase for larger REF:VAL ratios in almost all traits.
178 Best values were obtained with a ratio 90:10 (Table 2). A slight effect of the estimation method
179 could be observed, even though without a clear pattern. R-BLUP performed best for ADWG
180 (accuracy of 0.49 averaged across REF:VAL ratios) compared to the other methods. A similar
181 pattern can be observed for BI, due to the relevance of ADWG in its composition. The two methods
182 that used all the markers available showed better average accuracies than the PC based approaches
183 for size score (average values of 0.54 vs 0.48 respectively). No substantial differences can be
184 observed for the other traits. The use of eigenvalues of SNP covariance matrix as prior variance did
185 not result in higher DGV accuracy, except for CED. For this trait, accuracy ranged from 4% to 10%
186 passing from REF:VAL 70:30 to 90:10. In general, for the other traits the PC-BLUP_EIGEN
187 performed the same or slightly worse than PC-BLUP (the maximum difference between the two
188 methods was 7%).

189 Accuracies obtained with methods that used simultaneously all markers as predictors were
190 substantially equivalent. Basically, slightly higher accuracies were found using BAYES A with a
191 maximum difference of 6%. DGV accuracies were substantially higher than $r_{PA,EBV}$ for all traits
192 (Table 2). On average the mean correlation across traits was 0.60 (PC-BLUP), 0.58 (PC-
193 BLUP_EIGEN), 0.60 (R-BLUP) and 0.61 (BAYES A), and these figures were higher than the
194 average accuracy of PA (0.49).

195

196 ***Bias and goodness of prediction assessment.***

Regression coefficients between EBV and DGV were quite variable across methods (Figure 4). In particular, PC-BLUP and PC-BLUP_EIGEN estimates showed the smallest regression coefficients, in most of cases lower than 1 (on average 0.82±0.27 and 0.89±0.28 respectively) (Figure 4). On the contrary, the methods that use SNP genotypes showed $b_{EBV,DGV}$ higher than 1 (on average 1.78±0.54 R-BLUP and 1.42±0.36 BAYES A) indicating that positive values of DGV underpredict EBV and vice versa for negative DGV values. The effect on prediction bias of CED was less defined compared to all other traits: regression slopes tended to be closer to one only for the full models, whereas they became worse for the PC based approaches. Furthermore, Figure 4 shows the lowest variability of the regression coefficients of PC based approaches across different traits in all REF:VAL ratios. Moreover, the PC-based estimates were less inflated than SNP based estimates, in particular PC-BLUP-EIGEN performed slightly better than PC-BLUP, especially when the reference population was larger (REF:VAL 90:10).

Table 3 reports the mean squared error of prediction of DGV and its decomposition for all traits and estimation methods. MSEP did not show large variation among traits excepted for MS (average of 60.8) that experienced the lower figure and BI with the highest MSEP (average of 32.7). Within traits, MSEP of DGV obtained using PC as predictors were on average higher than those calculated with SNP. Exceptions were observed for SS, FLS and CWM. PC-BLUP_EIGEN showed MSEP always lower than PC_BLUP except for CWM. In any case, MSEP differences among methods were rather small. On the other hand, larger differences in the MSEP decomposition can be highlighted. In general, mean bias was not very high (highest average value, 0.33, was found for ADWG) and for some traits it was close to zero. The systematic bias was very low for all traits being the maximum obtained for CWM (27% and 23% of the MSEP for BLUP and BAYES A respectively). A large incidence of random errors can be observed among traits with values ranging

from 60% (ADGW) to 98% (CED). Methods that use PC as predictors showed the lowest incidence of components related to prediction bias, as inequality of variance, and the highest for sources of random variation as incomplete co-variation.

DISCUSSION

In this paper, principal component analysis was used for reducing predictor dimensionality and computational demand in calculating DGV for beef traits. The number of PC retained was about 6% of the number of original variables. The magnitude of such a reduction was similar to the one reported for US Holsteins by Long et al. (2011). The dimension of about 2,500 predictor is quite recurrent in studies aimed at simplifying the predictor space in genomic selection application. For example, Rolf et al. (2010) indicated a minimum threshold of 2,500 SNP markers for estimating a reliable genomic relationship matrix in cattle population.

In general, DGV accuracies here obtained were moderate to high. Results on DGV accuracy in literature are scarce and mainly related to feed efficiency and body weight. However, the magnitude of correlations are in agreement with previous reports obtained on Angus (Garrick et al., 2010; Rolf et al., 2010; Saatchi et al., 2011). An exception is represented by direct calving ease which was much smaller in the present study if compared to aforementioned researches. It is rather hard to relate DGV accuracy to some genetic features of the traits, i.e. h^2. However, best values have been obtained for variables related to muscular development and to the robustness of legs. Intermediate are those related to the size and weight of the animals. In any case, DGV accuracies were higher than those of traditional parent averages, thus evidencing the superiority of the GS over traditional evaluations.

Other possible interpretation of the presented DGV accuracy may be the effects of the relatedness between reference and validation bulls which affects the accuracy as shown by Habier et al. (2010) that split the observed accuracy into two component, one related to LD and the other due to the relatedness of bulls in training and prediction population. Being 69 the number of sire-son pairs a possible effect of the relatedness might be envisaged. A high number of phenotypic records are needed to achieve reasonable accuracy as to overcome the curse of dimensionality and GS implementation.

Among the factors that affected DGV accuracies, size of REF population and heritability of the traits were the most important. The increase of the size of the reference population has been widely reported to improve the accuracy of genomic prediction (Meuwissen et al., 2001; Liu et al. 2011). Also in the present study, for larger sizes of REF population a moderate increase of $r_{EBV,DGV}$ was observed. In general, the lower the heritability the larger the references population needs to be (Hayes et al., 2009b). Simulation studies showed how the heritability of the trait affects positively the estimation accuracy (Calus and Veerkamp, 2007; Kolbehdari et al., 2007) as confirmed also by theoretical expectations (Daetwyler et al., 2008). The combination of low heritability and reduced population size may be able to explain the results presented here on CED accuracy.

In general, no large differences in DGV accuracies were found between estimation methods (on average 0.03, range 0.02-0.10). Methods used in this research basically differed in two aspects. The first is the kind of predictors, i.e. SNP or PC scores. Results here obtained confirm the substantial equivalence between the two approaches, already observed on simulated (Macciotta et al., 2010a; Solberg et al., 2009) and real data for milk traits (Long et al., 2011; Macciotta et al., 2010b). The second point deals with the distribution of predictor effects. Two methods, PC-BLUP and R-BLUP, assume an equal contribution of each predictor (SNP or PC score) on the variance of

265 the trait whereas the BAYES A and PC-BLUP_EIGEN relies on a heterogeneity of variance across
266 predictor effects. Early results on simulated data have highlighted the net superiority of the BAYES
267 method over the BLUP approach, confirming the suitability of the finite locus model. However,
268 also in the present work the two approaches yielded the same results, in agreement with reports on
269 real data for dairy cattle (VanRaden et al., 20009).

270 On the other hand, difference between the kind of predictors was evident in the evaluation of
271 prediction bias. PC based approaches were characterized by the lowest variability of $b_{EBV,DGV}$
272 within traits and by the predominance of the random components in the composition of the MSEP.
273 These results are probably due to the orthogonality of PC scores that prevent problems of
274 mullticollinearity between predictors. Apart from the relevant impact on calculation time (about 2
275 minute for PC-BLUP with 2.33 GHz Quad core processor and 4 Gb RAM; 3-8 hours for the R-
276 BLUP 4x4 with Quad core processors and 128 Gb RAM; 3 hours for BAYES A using 3.2 GHz
277 processor 8GB RAM), the PCA approach carried out by chromosome was effective also in reducing
278 the gap between predictors and observations, which is a cause of bias for the application of
279 multivariate techniques on non positive definite correlation matrices (Dimauro et al., 2011).
280 Furthermore, PC-BLUP approach is a trait independent methods as the reduced set of variable may
281 be used for different set of phenotypic measures.

282

283 **CONCLUSIONS**

284 Direct genomic values accuracies for some beef traits in the dual purpose Italian Simmental
285 cattle breed exhibited high to moderate values. DGV accuracies were higher than those of PA.
286 These figures may open interesting perspectives for the implementation of GS in this breed not only

for dairy but also for beef traits. The early availability of DGV with high or moderate accuracies may allow for a better selection of young bulls entering performance test.

The reduction of predictor dimensionality by using principal component had a relevant impact in reducing computational time without reduction in accuracies. Difference in assumptions of predictor effect distribution does not seem to affect DGV accuracies

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382 **Table 1.** Heritability of average daily weight gain (ADWG), feet and leg score (FLS), Calving Ease
383 direct (CED), Beef Index (BI), Muscularity Score (MS), Size Score (SS) and Cow Muscularity
384 (CWM). Mean and standard deviation of EBV used as phenotypes and their average reliability

Trait	h^2	Mean EBV[a] ± SD	Mean Reliability ± SD
ADWG[b]	0.35	104.08 ± 6.57	0.43 ± 0.12
SS[b]	0.32	103.07 ± 6.45	0.43 ± 0.12
MS[b]	0.61	106.45 ± 9.17	0.60 ± 0.16
FLS[b]	0.25	104.72 ± 7.31	0.42 ± 0.12
BI[c]	-	104.99 ± 6.29	0.43 ± 0.12
CED[d]	0.05	99.13 ± 6.98	0.59 ± 0.17
CWM[d]	0.36	100.76 ± 9.10	0.71 ± 0.21

385
386 a) all traits are reported as standardized breeding values with mean 100 and genetic standard deviation 12
387 b) EBV estimated in performance test
388 c) Aggregate index of ADWG, SS, MS and FLS
389 d) EBV estimated in progeny test
390

391 **Table 2.** Correlation coefficient between DGV on EBV of average daily weight gain (ADWG), feet
392 and leg score (FLS), Calving Ease direct (CED), Beef Index (BI), Muscularity Score (MS), Size
393 Score (SS) and Cow Muscularity (CWM) for three estimation methods tested and 3 composition
394 ratios of reference/validation set.

Trait[1]	PC-BLUP	PC-BLUP_EIGEN	R-BLUP	BAYES A	395 r_{PA-EBV}
			REF:VAL 70:30		
ADWG	0.39	0.39	0.43	0.41	0.24
SS	0.43	0.44	0.49	0.50	0.19
MS	0.73	0.67	0.73	0.73	0.72
FLS	0.72	0.73	0.70	0.72	0.61
BI	0.63	0.59	0.67	0.67	0.64
CED	0.23	0.27	0.18	0.23	-
CWM	0.80	0.73	0.80	0.81	-
			REF:VAL 80:20		
ADWG	0.36	0.35	0.45	0.39	0.23
SS	0.47	0.47	0.53	0.53	0.08
MS	0.67	0.64	0.70	0.72	0.71
FLS	0.74	0.70	0.74	0.76	0.63
BI	0.57	0.54	0.66	0.64	0.64
CED	0.23	0.27	0.20	0.20	-
CWM	0.85	0.84	0.83	0.85	-
			REF:VAL 90:10		
ADWG	0.53	0.51	0.58	0.54	0.24
SS	0.53	0.53	0.61	0.60	0.21
MS	0.81	0.79	0.78	0.81	0.71
FLS	0.85	0.84	0.79	0.83	0.60
BI	0.74	0.71	0.75	0.76	0.64
CED	0.24	0.34	0.22	0.27	-
CWM	0.83	0.81	0.81	0.83	-

396

397 **Table 3.** Mean squared error of prediction (MSEP) of DGV and its decomposition for beef traits in
398 the validation bulls using different estimation method.

	MSEP[1]	RMSEP	MB	UV	IC	SB	RE
Methods			**ADWG**				
PC-BLUP	44.68	6.68	0.33	0.05	0.63	0.08	0.60
PC-BLUP_EIGEN	41.04	6.41	0.30	0.08	0.63	0.06	0.65
BLUP	38.79	6.23	0.33	0.39	0.28	0.01	0.66
BAYES A	41.14	6.41	0.37	0.26	0.38	0.00	0.64
			SS				
PC-BLUP	43.71	6.61	0.09	0.21	0.71	0.02	0.90
PC-BLUP_EIGEN	42.42	6.51	0.08	0.27	0.66	0.01	0.92
BLUP	44.92	6.70	0.08	0.72	0.20	0.10	0.82
BAYES A	42.93	6.55	0.11	0.57	0.33	0.05	0.85
			MS				
PC-BLUP	63.15	7.95	0.23	0.17	0.61	0.00	0.77
PC-BLUP_EIGEN	61.84	7.86	0.10	0.28	0.63	0.01	0.90
BLUP	59.66	7.72	0.06	0.57	0.38	0.17	0.79
BAYES A	58.70	7.66	0.10	0.47	0.44	0.11	0.79
			FLS				
PC-BLUP	40.01	6.33	0.33	0.11	0.56	0.00	0.67
PC-BLUP_EIGEN	34.50	5.87	0.22	0.25	0.54	0.03	0.76
BLUP	39.73	6.30	0.18	0.46	0.37	0.11	0.72
BAYES A	40.75	6.38	0.27	0.35	0.39	0.07	0.67
			BI				
PC-BLUP	36.25	6.02	0.36	0.08	0.56	0.01	0.64
PC-BLUP_EIGEN	32.76	5.72	0.25	0.15	0.61	0.00	0.75
BLUP	29.93	5.47	0.23	0.42	0.35	0.08	0.70
BAYES A	31.86	5.64	0.31	0.28	0.41	0.03	0.66
			CED				
PC-BLUP	49.13	7.01	0.02	0.14	0.85	0.13	0.86
PC-BLUP_EIGEN	46.54	6.82	0.02	0.17	0.82	0.09	0.89
BLUP	44.79	6.69	0.04	0.69	0.28	0.00	0.97
BAYES A	43.44	6.59	0.03	0.55	0.43	0.00	0.98
			CWM				
PC-BLUP	42.02	6.48	0.01	0.23	0.77	0.02	0.98
PC-BLUP_EIGEN	55.16	7.43	0.02	0.33	0.66	0.04	0.96
BLUP	58.39	7.64	0.03	0.64	0.33	0.27	0.70
BAYES A	51.04	7.14	0.01	0.59	0.41	0.23	0.77

399 1) MB = Mean Bias; UV = Unequal variances; IC = Incomplete covariation; SB = Slope bias; RE = Random
400 errors. Note that MB + UV+ IC= MB + SB + RE = 1

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403 **Figure 1**

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405 **Figure 1**

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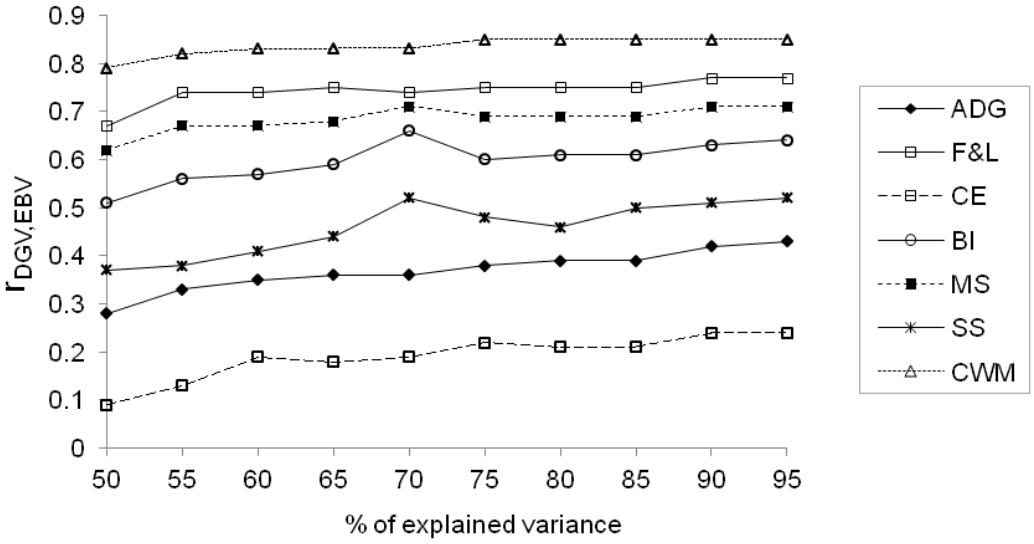
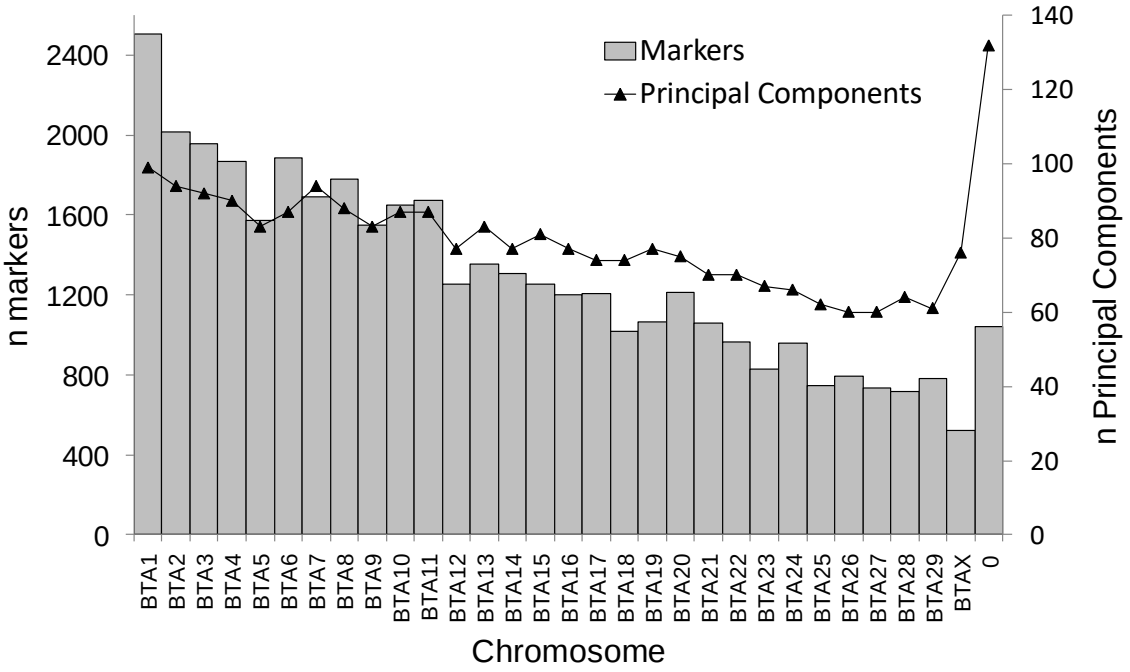


Figure 2.



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411 **Figure 3.**

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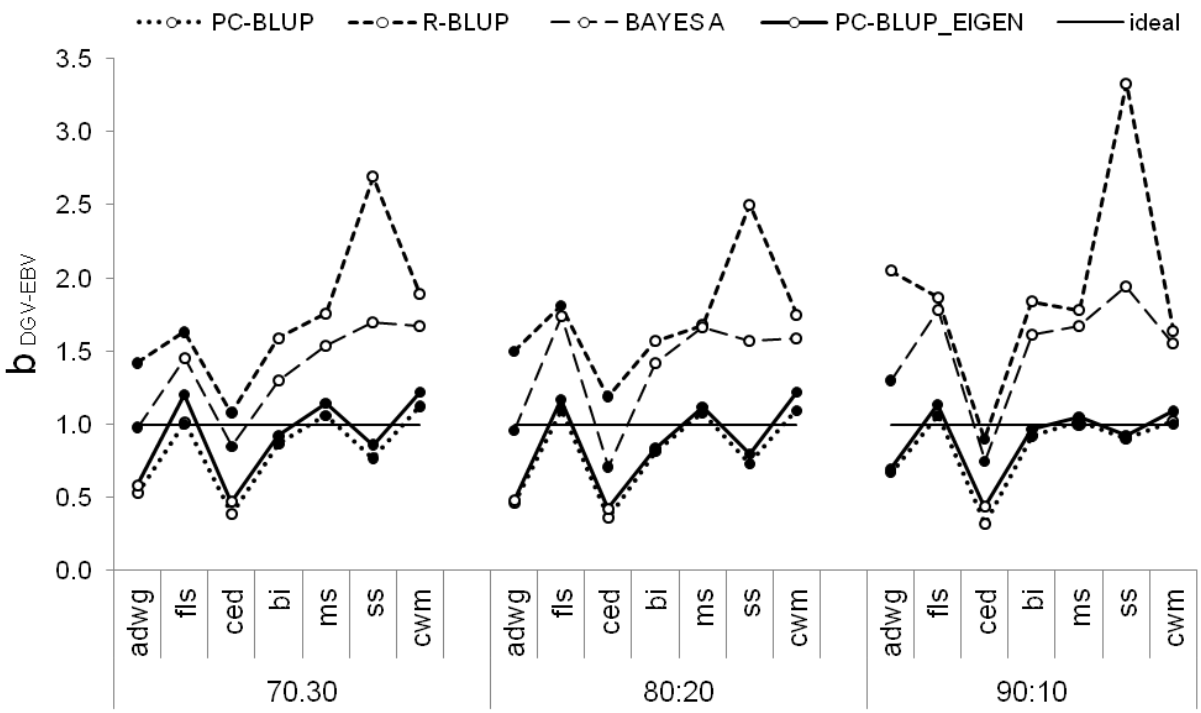

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416 Open circle = values of regression coefficient (b) out of the 95% CI including b=1 (p-value <0.001)

417 Solid circle = values of regression coefficient (b) inside the 95% CI including b=1 (p-value <0.001)

418 **Figure 4.**

Figure 1. Distribution of bulls by birth's year.

Figure 2. Number markers and number of PC components retained by chromosome.

Figura 3. Pattern of DGV correlation ($r_{DGV,EBV}$) function of % of variance explained by the PC of 7 meat traits (ADWG=average daily weight gain, FLS=Feet and leg score, CED=calving ease direct effect, MS=muscularity score, SS=Size Score, CWM=cow muscularity).

Figura 4. Pattern of regression coefficient of EBV vs DGV ($b_{EBV,DGV}$) of 7 meat traits (ADWG=average daily weight gain, FLS=Feet and leg score, CED=calving ease direct effect, MS=muscularity score, SS=Size Score, CWM=cow muscularity) both for estimation methods and different REF:VAL ratios.