Non Parametric vs. GBLUP Model for Genomic Evaluation with Large Reference Population in Holstein Cattle

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Abstract

In the last years, genomic selection has become an important component in dairy cattle breeding programs. Accordingly, different approaches are currently being developed, and used, to estimate genomic breeding values. The objective of this study was to compare the predictive ability of four methodologies to perform genomic evaluations in 25phenotypic traits (including productive, type and functional traits) using a large reference population of dairy cattle. The four evaluated approaches were Bayesian Reproducing Kernel Hilbert Spaces (RKHS), simple G-BLUP (GB), G-BLUP including a polygenic effect of 5% (GBP-5%) and G-BLUP including a polygenic effect of 10% (GBP-10%).The first two approaches use only genomic information, and the last two use both genomic and pedigree information. The data consisted on de-regressed proofs for 18,443genotyped bulls.A cross-validation was performed dividing the bulls into a training and a testingdata setborn before or after 2005, respectively. The results show that within the approaches using only genomic information, RKHS performs better than a simple GBLUP model. However, including polygenic effect improved GBLUP results. In general, RKHS performed slightly better, with larger predictive accuracy and lower mean square error, for the production traits, while GBP-5% performed better for type traits.Further research is needed to include pedigree information and to optimize the computational requirements of RKHS approach for routinely genomic evaluations.

Key words:model comparison, genomic evaluation, polygenic effect, predictive ability

1. Introduction

Selection based on dense SNP (Single Nucleotide Polymorphism) markers across the genome has become an important component in dairy cattle breedingprograms (Hayes *et al.*, 2009). In several genomic selection programs,thousands of progeny tested bulls have been genotyped and are being used as nationalreference populations. This has been extended through sharing data across countries for larger reference populations,such as the North American cooperation, Eurogenomics, or the joint Brown Swiss project (Gao *et al.*, 2012).

Different approaches are currently being used to estimatebreeding values based on genomic information. The first type of methodologies impliesprocedures that regress phenotypic records on SNP markers directly (Meuwissen *et al.*, 2001; Park and Casella, 2008). The second group of approaches encloses techniques that estimate genetic values using genomic relationship matrices, instead of marker estimation (de los Campos *et al.*, 2009; Misztal *et al.*, 2009). The last type of alternatives for dealing with large data sets and complex interactions between SNP are machine learning algorithms. Nonparametric or semi-parametric methods of this type can be implemented by regressions on markers (e. g., Boosting as in González-Recio *et al.*, 2010) or by building appropriate (co)variance structures (e. g. Reproducing Kernel Hilbert Spaces regression as in Gianola *et al.*, 2006). These nonparametric or semi-parametric approaches have been suggested as an alternative to predict genomic breeding values because these methods may require weaker assumptions when modeling complex quantitative traits.

Official genomic evaluation in Spain started in 2012 (Jiménez-Montero *et al.*, 2012a) by

implementation of a Random Boosting approach (González-Recio *et al.*, 2010). However, this procedure has shown a trend to yield predictions of genomic values that underestimate the true values. Alternative semi-parametric methods such as Bayesian Reproducing Kernel Hilbert Spaces (RKHS) and current popular parametric methods such as G-BLUP are being considered. Inclusion of genealogical information could also enhance accuracy of current genomic evaluations. When comparing the alternative approaches, it will be important to evaluate the accuracy of those methodologies to identify the approach having the highest predictive ability and feasible computational implementation for routinely genomic selection.

The aim of this study was to check the predictive ability of four different models for genomic evaluations in different economically important traits in a large reference population of dairy cattle. The accuracy of a RKHS regression method is compared with a simple G-BLUP. These two methodologies used only SNP information. In addition, the inclusion of genealogical information, together with genomic information, may improve genomic predictions because the SNP information may not account for all additive genetic variance. For this reason, also a G-BLUP model including a residual polygenic effect with two weights (5 and 10%) was also evaluated.

2. Materials and Methods

Genotypes

Genomic information from 22,300 Eurogenomics progeny-tested sires was used in this study. The Bovine 50K chip (Illumina inc., San Diego) was used to genotype 54,609 SNPs in each sire. SNPs with an incidence of missing genotypes across individuals greater than 5% or SNP with minor allele frequency less than 5% were discarded, leaving 36,971 SNP for the analyses. After editing, 0.01% of the SNP genotypes were missing. These genotypes were then imputed with Beagle 3.3.2 (see Jiménez-Montero *et al.*, 2013a for more details). Only sires with reliability higher than 75% in their progeny proofs were included. Genotypes of 18,443 bulls, and pedigree data of 63 721 animals were used.

2.2 Phenotypes

Sire deregressed proofs (DRP) for 25 phenotypic traits were used as phenotypes. The phenotypic traits included 5 productive traits: milk yield (MY), fat yield (FY), protein yield (PY), fat percentage (FP) and protein percentage (PP); 17 type traits: stature (STA), chest width (CW), body depth (BD), angularity (ANG), rump angle (RA), rump width (RW), rear legs, side view (RLSV), rear legs, rear view (RLRV), foot angle (FA), fore udder attachment (FUA), rear udder attachment (RUA), suspensory ligament (SL), udder depth (UD), fore teat placement (FTP), rear teat placement (RTP), teat length (TL) and feet and legs (FL); and 3 functional traits: somatic cell score (SCS), longevity (LONG) and days open (DO).

2.3 Training and testing data sets

The gain in predictive ability was assessed by a cross-validation.Sires were divided in two groups, a training and a testing data set, according to the year of birth. The January 2009 DRP were used as response variables in the training, whereas, December 2011 DRP were used as a prediction goal in the testing set. The testing data set included only sons of sires in the training set. This classification gave 14,487 training bulls born before 2005 and 3,956 testing bulls born after 2005. The minimum number of effective daughter contribution (EDC) allowed per sire was 15. The EDC wasalso used as weighting factor to account for differences in progeny group size when computing the correlation between direct genomic values and DRP (Jiménez-Montero *et al.*, 2012b). Design of the training and testing data sets followed the recommendations of Mäntysaari *et al.* (2010).

2.4 Statistical models for genomic evaluation

Bayesian Reproducing Kernel Hilbert Spaces (RKHS)

The model can be formulated as follows:

$$\mathbf{y} = \mathbf{X\beta} + \mathbf{K\alpha} + \mathbf{e}$$

where $\mathbf{y}$ is a vector of the mean adjusted records for progeny of sires in the training set. The first term ($\mathbf{X\beta}$) is a parametric term with $\boldsymbol{\beta}$ as a vector of systematic effects or nuisance parameters (only μ was fitted in this case, since the data were pre-corrected), and $\mathbf{X}$ is the incidence matrix. The nonparametric term is given by $\mathbf{K\alpha}$, where $\mathbf{K}$ is a positive definite matrix of kernels, and $\boldsymbol{\alpha}$ is a vector of nonparametric coefficients that are assumed to be distributed as $\boldsymbol{\alpha} \sim N(0, \mathbf{K}^{-1}\sigma_\alpha^2)$, with σ_α^2 representing the reciprocal of a smoothing parameter. The genome-enhanced breeding values can be calculated as $\mathbf{u} = \mathbf{K\alpha}$. The residuals $\mathbf{e}$ were assumed to be distributed as $N(0, \mathbf{R} = \mathbf{N}^{-1}\sigma_e^2)$, where $\mathbf{N} = \{n_i\}$ is a diagonal matrix with elements n_i representing the number of progeny of sire *i* and σ_e^2 is the residual variance.

In this study, the positive definite matrix of kernels was the genomic matrix (VanRaden, 2008; Yang *et al.*, 2010). This genomic relationship matrix can be calculated as

$$G_{ij} = \frac{1}{L}\sum_{k=1}^{L}\frac{(g_{ik} - \hat{p}_k)(g_{jk} - \hat{p}_k)}{\hat{p}_k(1-\hat{p}_k)}$$

where g_{ik} refers to the gene frequency value genotypes *AA*, *Aa* and *aa*, coded as 1, 0.5 and 0, respectively, of individual *i* at locus *k* where *i* = 1, *n* and *k* = 1, *L*. Gene frequency is half the number of copies of the reference allele *A*. The estimate of the allele frequency in the current population is designed as $\hat{p}_k$. This RKHS model was solved in a Bayesian context using Gibbs Sampling.

Simple G-BLUP (GB)

A basic G-BLUP model, using genomic matrix built following method 1 of VanRaden (2008),was used to predict direct genomic values:

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

where $\mathbf{g}$ a vector of random additive is genetic effects from genomic data and $\mathbf{e}$ is the random residual. The matrix $\mathbf{Z}$ is the incidence matrix linking breeding values $\mathbf{g}$ to the observations.

The random effects have the following assumptions: $\mathbf{g} \sim N(\mathbf{0}, \mathbf{G}\sigma_g^2)$ and $\mathbf{e} \sim N(\mathbf{0}, \mathbf{I}\sigma_e^2)$ where $\mathbf{G}$ is the genomic co-variance matrix.

G-BLUP with polygenic effect (GBP)

This model was the same as the above with a residual polygenic effect not captured by the SNPs as follows:

$$\mathbf{y} = \mathbf{1}\mu + \mathbf{Zg}_\omega + \mathbf{e},$$

where

$$\mathbf{g}_\omega = \mathbf{u} + \mathbf{g}$$

with $Var(\mathbf{g}_\omega) = \mathbf{A}\sigma_u^2 + \mathbf{G}\sigma_g^2$, where $\mathbf{A}$ is the pedigree-based relationship matrix.

Defining $\sigma_{g_\omega}^2 = \sigma_u^2 + \sigma_g^2$ and $\omega = \sigma_u^2 / \sigma_{g_\omega}^2$,then $\sigma_u^2 = \omega\sigma_{g_\omega}^2$ and $\sigma_g^2 = (1-\omega)\sigma_{g_\omega}^2$, and $Var(\mathbf{g}_\omega) = [\omega\mathbf{A} + (1-\omega)\mathbf{G}]\sigma_{g_\omega}^2$

The matrix $\mathbf{Z}$ is the incidence matrix as in GB, and $\mathbf{e}$ is the random residual following the distribution $\mathbf{e} \sim N(\mathbf{0}, \mathbf{I}\sigma_e^2)$ .The $\mathbf{G}$ matrix was adjusted to be on the same scale as $\mathbf{A}$ (Gao *et al.*, 2012).

The evaluated values for ω ranged between 0.05 and 0.30 for milk yield (h^2 = 0.28) and rear legs rear view (h^2 = 0.07), although only the results for 0.5 (GBP-5%) and 0.10 (GBP-10%) are shown below for all traits.

Both GB and GBP were implemented using Mix99 software (Lidauer and Strandén, 1999).

2.5 Criteria for model comparison

The reliability of the genomic predictions was computed usingthe predicted direct genomic values (DGV) of bulls in the testing set and their December 2011 DRP. Three parameters were evaluated. First, the correlation was computed as a weighted Pearson correlation taking into account the EDC (Mantysaari *et al.*, 2010) as follows:

$$r = \sqrt{r^2(1 + k / \overline{EDC})}$$

where r^2 is the square of Pearson's coefficient of correlation and $k = (4 - h^2)/h^2$. Secondly, the regression coefficientof the realized DRP on the estimated DGV was also evaluated. And finally, the mean square error (MSE) of predictions was also estimated.

Accuracy of comparisons

Means and confidence intervals were estimated using bootstrapped samples (Efron and Tibshirani, 1986) in each evaluated trait and methodology. Pairs for comparisons were the predicted DGV of bulls in the testing set and their December 2011 DRP.

One thousand samples were drawn with replacement from the whole testing set. For each bootstrapped sample the correlation, the regression coefficient and the MSE was computed.

Finally, the confidence intervalsfor the comparison criteria were computed as the narrowest interval containing 95% of the bootstrap replicates.

Selection effectiveness

This measure was evaluated as $\alpha_{top} / \alpha_{sel}$, where α_{sel} represents a given percentage of bulls ranked by their predicted DGV and α_{top} is the percentage of bulls selected by the model that were in the same percentile according to their realized DRP. This parameter can be interpreted as the fraction of young bulls as ranked by DGV that actually included at least 1 truly top bull, or similarly, as the fraction of truly top bulls that was included in a given set of top young bulls as predicted by DGV(see Jiménez-Montero *et al.*, 2013b for more details).

3. Results

The observed values for correlation, regression coefficient and MSE were very similar to those obtained from bootstrapped replicates (data not shown). Consequently, the mean and confidence interval from bootstrapped replicates are presented and discussed below.

3.1 Correlation

Table 1 shows the results for correlation obtained with the four methods considered.

From the methodologies only including genomic information, RKHS showed the best accuracy in fourteen out of 25 traits. However, GB only showed the best precision in 4 traits.

The methodologies including genomic and genealogical information showed larger correlation in 17 and 14 traits for GBP-5% and GBP-10%, respectively.

Regarding those traits with a larger weight on the Spanish selection index ICO, both RKHS and GBP-5% showed similar accuracy for PY and UD, whereas RKHS achieved better correlation for MY and GBP-5% for LONG. In general, RKHS showed better accuracy in production traits, while GBP-5% behaved better in Type Traits.
GBP-5% and GBP-10% showed similar accuracy in most traits.

3.2 Regression coefficient

The slopes obtained from the analysed approaches are shown in Table 2. A regression

coefficient of DRP on genomic predictions lower than one indicates overestimation of the genomic predictions, while a coefficient larger than one indicates underestimation.

It has been indicated that inflation of genomic predictions is critical in practice (Patry and Ducrocq, 2009) because it can give a biased advantage to juvenile over older progeny tested bulls (Aguilar *et al.*, 2010).

In this study, RKHS provided regression coefficients below 1 except for DO, while GB yielded regressions over 1 in all cases and GBP also provided values above 1 (except for FL) indicating underestimation of the genomic predictions.

Summarizing, the mean observed regression coefficient for GBP-5% and GBP-10% were 1.10 (0.84 – 1.27) and 1.12 (0.86 – 1.29), respectively. In addition, the averaged slope for GB was 1.31 (1.08 – 1.48). On the contrary, the regression coefficients obtained from RKHS were mostly below the unity (observed mean = 0.88, ranging between 0.63 – 1.03).

The only two traits where no relevant differences (overlapping bootstrap confidence intervals) were detected between RKHS and the other three evaluated methods were LONG and DO. The reason could be that LONG and DO have a higher uncertainty when compared with other traits.

Bayesian RKHS showed a higher endpoint of 95% confidence interval in practically all traits slightly lower than 1, whereas GBP-5% showed a lower endpoint of 95% confidence interval in practically all traits slightly greater than 1.

More fine-tuned for both models will be probably needed to achieve INTERBULL validation test criteria (Mäntysaari *et al.*, 2010) for combined proofs.

3.3 Mean square error

The mean square error for each trait and methodology is shown in Table 3. From the methodologies only including genomic information, RKHS showed smaller MSE in 15 out of 25 traits, and GB only in one trait.

In addition, from the methodologies including both pedigree and genomic information, GBP-5% showed a better performance in 13 traits and GBP-10% only in 8 traits out of 25. The confidence intervals indicated a large MSE for the GB approach in the majority of the evaluated traits.

For the traits with larger weight in the Spanish ICO, RKHS showed better MSE for MY and PY, whereas GBP-10% was better for LONG.

3.4 Selection effectiveness

Three approaches (RKHS, GBP-5% and GBP-10%) performed in a similar manner at selecting top-ranked bulls regarding their observed DRP (Figure 1). Most relevant differences were observed for GB methodology.

4. Discussion

Results of this study show that non-parametric model was more accurate than the simple G-BLUP. G-BLUP method needs the inclusion of a polygenic effect to obtain similar results to

those achieved with RKHS. More specifically, a weight of 5% of the polygenic effect showed a similar precision to RKHS approach. This is in agreement with Liu *et al.* (2010), which indicated a weight of 5% - 10% for the polygenic effect.

Respect the weighting of the residual polygenic effect, Gao *et al.* (2012) indicated that increasing the weighting factor reduces bias and gives highest reliability but the optimal weighting factors differed between traits. However, our results showed small differences between 5% and 10% weight results. Therefore, trait-specific weighting factors should be also investigated in models including a polygenic effect.

In addition, further research is also needed to optimize the computational requirements of RKHS approach for routinely genomic evaluations, because the elapsed CPU time and the random access memory used were higher than the GBLUP requirements.

Conclusions

The results of this study showed that within the methodologies evaluated, RKHS performs better than GB, and matches the performance of GBP approaches. More specifically, a weight of 5% of the polygenic effect on the GBP model showed a similar accuracy to RKHS approach. It might be expected that the inclusion of pedigree information and the optimization of the computational requirements in RKHS could further improve the performance of this semi-parametric method for routine genomic evaluations.

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Table 1. Correlation of predictions. Mean of the 1000 bootstrap replicates. Parenthesis indicate confidence interval containing 95% of replicates. In bold: best method within trait.

Trait	RKHS	GB	GBP-5%	GBP-10%
MY	**0.84** (0.82 - 0.86)	0.77 (0.75 - 0.79)	0.82 (0.81 - 0.84)	0.82 (0.80 - 0.84)
FY	**0.82** (0.80 - 0.84)	0.78 (0.76 - 0.80)	**0.82** (0.80 - 0.83)	0.81 (0.79 - 0.83)
PY	**0.81** (0.79 - 0.83)	0.78 (0.76 - 0.80)	**0.81** (0.79 - 0.83)	**0.81** (0.79 - 0.83)
FP	**0.92** (0.91 - 0.93)	0.84 (0.83 - 0.86)	0.90 (0.88 - 0.91)	0.89 (0.88 - 0.91)
PP	**0.92** (0.91 - 0.93)	0.86 (0.84 - 0.87)	0.90 (0.88 - 0.91)	0.90 (0.88 - 0.91)
STA	**0.84** (0.83 - 0.86)	0.79 (0.77 - 0.80)	0.83 (0.81 - 0.84)	0.83 (0.81 - 0.84)
CW	0.83 (0.80 - 0.85)	0.81 (0.79 - 0.84)	**0.84** (0.81 - 0.86)	**0.84** (0.82 - 0.86)
BD	0.84 (0.82 - 0.86)	0.84 (0.81 - 0.85)	**0.85** (0.83 - 0.87)	**0.85** (0.83 - 0.87)
ANG	0.90 (0.88 - 0.92)	0.91 (0.89 - 0.93)	**0.92** (0.90 - 0.94)	**0.92** (0.90 - 0.94)
RA	**0.79** (0.77 - 0.81)	0.75 (0.73 - 0.77)	**0.79** (0.77 - 0.81)	**0.79** (0.77 - 0.81)
RW	**0.80** (0.78 - 0.82)	0.76 (0.74 - 0.79)	**0.80** (0.78 - 0.81)	**0.80** (0.78 - 0.81)
RLSV	0.74 (0.72 - 0.77)	0.75 (0.72 - 0.77)	**0.77** (0.74 - 0.79)	**0.77** (0.74 - 0.79)
RLRV	0.63 (0.60 - 0.66)	**0.65** (0.62 - 0.68)	**0.65** (0.62 - 0.69)	**0.65** (0.62 - 0.68)
FA	0.69 (0.65 - 0.72)	0.72 (0.69 - 0.75)	**0.71** (0.68 - 0.74)	**0.71** (0.68 - 0.75)
FUA	0.83 (0.80 - 0.85)	0.83 (0.81 - 0.86)	**0.85** (0.82 - 0.87)	**0.85** (0.82 - 0.87)
RUA	0.83 (0.81 - 0.86)	0.83 (0.81 - 0.85)	**0.85** (0.84 - 0.88)	**0.85** (0.83 - 0.87)
SL	0.86 (0.84 - 0.89)	0.85 (0.82 - 0.87)	**0.87** (0.85 - 0.89)	**0.87** (0.85 - 0.89)
UD	**0.81** (0.79 - 0.83)	0.77 (0.75 - 0.78)	**0.81** (0.79 - 0.83)	0.80 (0.79 - 0.82)
FTP	**0.83** (0.81 - 0.85)	0.77 (0.75 - 0.79)	0.82 (0.80 - 0.84)	0.82 (0.80 - 0.84)
RTP	**0.78** (0.76 - 0.80)	0.72 (0.70 - 0.74)	0.77 (0.75 - 0.79)	0.77 (0.75 - 0.79)
TL	**0.79** (0.77 - 0.81)	0.76 (0.74 - 0.78)	**0.79** (0.77 - 0.81)	**0.79** (0.77 - 0.81)
FL	0.59 (0.55 - 0.63)	**0.63** (0.60 - 0.67)	0.62 (0.57 - 0.66)	0.62 (0.58 - 0.66)
SCS	**0.81** (0.79 - 0.83)	0.77 (0.75 - 0.79)	**0.81** (0.79 - 0.83)	0.80 (0.78 - 0.82)
LONG	0.71 (0.51 - 0.88)	**0.87** (0.70 - 1.00)	**0.87** (0.71 - 1.00)	**0.87** (0.72 - 1.00)
DO	**0.73** (0.68 - 0.76)	**0.73** (0.69 - 0.77)	0.71 (0.67 - 0.75)	0.71 (0.67 - 0.75)

MY: milk yield; **FY**: fat yield; **PY**: protein yield; **FP**: fat percentage; **PP**: protein percentage; **STA**: stature; **CW**: chest width; **BD**: body depth; **ANG**: angularity; **RA**: rump angle; **RW**: rump width; **RLSV**: rear legs, side view; **RLRV**: rear legs, rear view; **FA**: foot angle; **FUA**: fore udder attachment; **RUA**: rear udder attachment; **SL**: suspensory ligament; **UD**: udder depth; **FTP**: fore teat placement; **RTP**: rear teat placement; **TL**: teat length; **FL**: feet and legs; **SCS**: somatic cell score; **LONG**: longevity; **DO**: days open.

Table 2. Slope of predictions. Mean of the 1000 bootstrap replicates. Parenthesis indicate confidence interval containing 95% of replicates. In bold: best method within trait.

Trait	RKHS	GB	GBP-5%	GBP-10%
MY	**0.95** (0.92 - 0.97)	1.20 (1.16 - 1.23)	1.11 (1.07 - 1.14)	1.12 (1.09 - 1.15)
FY	**0.90** (0.87 - 0.93)	1.25 (1.21 - 1.30)	1.09 (1.06 - 1.13)	**1.10** (1.07 - 1.14)
PY	**0.91** (0.88 - 0.93)	1.21 (1.17 - 1.25)	**1.09** (1.06 - 1.12)	1.10 (1.07 - 1.14)
FP	**0.93** (0.91 - 0.95)	1.22 (1.18 - 1.25)	1.10 (1.07 - 1.12)	1.11 (1.08 - 1.14)
PP	**0.95** (0.92 - 0.97)	1.28 (1.25 - 1.32)	1.14 (1.10 - 1.16)	1.15 (1.12 - 1.18)
STA	0.81 (0.79 - 0.83)	1.13 (1.09 - 1.16)	**1.00** (0.97 - 1.02)	1.01 (0.98 - 1.04)
CW	**0.89** (0.86 - 0.92)	1.43 (1.38 - 1.48)	1.17 (1.12 - 1.21)	1.19 (1.14 - 1.23)
BD	**0.88** (0.85 - 0.91)	1.32 (1.28 - 1.37)	**1.12** (1.08 - 1.16)	1.14 (1.10 - 1.18)
ANG	**0.89** (0.86 - 0.93)	1.35 (1.30 - 1.39)	1.14 (1.10 - 1.18)	1.16 (1.12 - 1.20)
RA	**0.90** (0.88 - 0.93)	1.29 (1.25 - 1.34)	1.12 (1.08 - 1.15)	1.13 (1.10 - 1.17)
RW	**0.88** (0.85 - 0.91)	1.30 (1.26 - 1.35)	**1.12** (1.08 - 1.16)	1.13 (1.09 - 1.17)
RLSV	0.82 (0.79 - 0.86)	1.35 (1.29 - 1.40)	**1.10** (1.06 - 1.14)	1.12 (1.07 - 1.16)
RLRV	0.74 (0.69 - 0.78)	1.30 (1.23 - 1.37)	**1.02** (0.97 - 1.08)	1.05 (0.99 - 1.11)
FA	0.81 (0.77 - 0.86)	1.42 (1.34 - 1.50)	**1.10** (1.04 - 1.17)	1.13 (1.06 - 1.19)
FUA	0.84 (0.82 - 0.88)	1.35 (1.30 - 1.40)	**1.13** (1.08 - 1.17)	1.15 (1.11 - 1.19)
RUA	**0.91** (0.88 - 0.94)	1.35 (1.30 - 1.40)	1.19 (1.15 - 1.23)	1.20 (1.16 - 1.25)
SL	**0.99** (0.95 - 1.03)	1.47 (1.41 - 1.53)	1.26 (1.22 - 1.31)	1.28 (1.24 - 1.33)
UD	0.85 (0.82 - 0.88)	1.24 (1.20 - 1.28)	**1.08** (1.04 - 1.11)	1.09 (1.06 - 1.13)
FTP	**0.88** (0.86 - 0.91)	1.30 (1.25 - 1.34)	**1.12** (1.08 - 1.16)	1.13 (1.09 - 1.17)
RTP	0.86 (0.84 - 0.89)	1.28 (1.23 - 1.33)	**1.13** (1.09 - 1.17)	1.14 (1.10 - 1.18)
TL	**0.92** (0.89 - 0.95)	1.40 (1.36 - 1.45)	1.17 (1.14 - 1.21)	1.19 (1.15 - 1.23)
FL	0.63 (0.59 - 0.68)	**1.08** (1.00 - 1.15)	0.84 (0.78 - 0.90)	0.86 (0.80 - 0.92)
SCS	**0.94** (0.91 - 0.97)	1.35 (1.31 - 1.40)	1.15 (1.10 - 1.18)	1.16 (1.12 - 1.20)
LONG	0.87 (0.63 - 1.11)	1.36 (1.04 - 1.64)	**1.01** (0.82 - 1.19)	1.04 (0.81 - 1.23)
DO	**1.03** (0.98 - 1.10)	1.48 (1.40 - 1.57)	1.11 (1.04 - 1.18)	1.14 (1.06 - 1.21)

Abbreviations as in Table 1.

Table 3. Mean square error of predictions. Mean of the 1000 bootstrap replicates. Parenthesis indicate confidence interval containing 95% of replicates. In bold: best method within trait.

Trait	RKHS	GB	GBP-5%	GBP-10%
MY	**177438.45** (169456.35 - 185618.44)	237846.66 (227314.84 - 247675.13)	196069.36 (187370.43 - 204453.62)	198435.17 (190483.75 - 207213.51)
FY	**300.36** (287.43 - 315.38)	358.92 (343.71 - 374.58)	307.86 (295.32 - 322.29)	310.79 (297.58 - 325.50)
PY	**210.49** (200.32 - 219.33)	271.67 (260.71 - 283.52)	227.00 (217.10 - 237.71)	229.06 (217.27 - 239.22)
FP	**0.02** (0.02 - 0.02)	0.03 (0.03 - 0.03)	**0.02** (0.02 - 0.02)	**0.02** (0.02 - 0.03)
PP	**0.01** (0.01 - 0.01)	**0.01** (0.01 - 0.01)	**0.01** (0.01 - 0.01)	**0.01** (0.01 - 0.01)
STA	0.51 (0.49 - 0.54)	0.54 (0.52 - 0.56)	**0.47** (0.45 - 0.49)	**0.47** (0.45 - 0.49)
CW	1.39 (1.33 - 1.46)	1.50 (1.43 - 1.57)	**1.37** (1.31 - 1.44)	1.38 (1.32 - 1.44)
BD	1.03 (0.98 - 1.08)	1.08 (1.03 - 1.13)	**0.99** (0.95 - 1.04)	1.00 (0.95 - 1.04)
ANG	0.83 (0.78 - 0.87)	0.91 (0.86 - 0.96)	**0.82** (0.77 - 0.86)	**0.82** (0.77 - 0.87)
RA	0.82 (0.78 - 0.86)	0.91 (0.87 - 0.95)	**0.81** (0.77 - 0.85)	0.82 (0.78 - 0.86)
RW	**0.84** (0.80 - 0.88)	0.94 (0.89 - 0.98)	**0.84** (0.80 - 0.88)	**0.84** (0.81 - 0.89)
RLSV	1.31 (1.24 - 1.37)	1.32 (1.25 - 1.39)	**1.24** (1.18 - 1.30)	**1.24** (1.19 - 1.31)
RLRV	2.02 (1.93 - 2.12)	2.02 (1.92 - 2.11)	**1.93** (1.83 - 2.02)	1.94 (1.85 - 2.03)
FA	2.21 (2.11 - 2.32)	2.23 (2.12 - 2.34)	**2.15** (2.06 - 2.27)	**2.15** (2.05 - 2.25)
FUA	**1.25** (1.19 - 1.31)	1.44 (1.38 - 1.51)	1.27 (1.21 - 1.33)	1.28 (1.22 - 1.33)
RUA	**0.99** (0.94 - 1.04)	1.20 (1.14 - 1.25)	1.03 (0.98 - 1.08)	1.04 (0.99 - 1.09)
SL	**1.30** (1.24 - 1.37)	1.57 (1.50 - 1.65)	1.40 (1.33 - 1.47)	1.42 (1.35 - 1.49)
UD	**0.71** (0.68 - 0.74)	0.85 (0.81 - 0.89)	**0.71** (0.68 - 0.75)	0.72 (0.69 - 0.76)
FTP	**0.67** (0.64 - 0.71)	0.81 (0.77 - 0.85)	0.69 (0.66 - 0.72)	0.70 (0.67 - 0.73)
RTP	**0.60** (0.58 - 0.63)	0.70 (0.67 - 0.74)	0.61 (0.58 - 0.64)	0.62 (0.59 - 0.64)
TL	**0.79** (0.75 - 0.83)	0.90 (0.85 - 0.94)	0.80 (0.76 - 0.84)	0.81 (0.77 - 0.85)
FL	2.32 (2.22 - 2.44)	2.39 (2.27 - 2.52)	**2.29** (2.17 - 2.39)	2.30 (2.18 - 2.40)
SCS	**93.78** (89.75 - 98.55)	109.93 (104.78 - 114.54)	96.95 (92.72 - 101.12)	97.84 (93.66 - 102.54)
LONG	546.86 (448.09 - 649.12)	470.10 (383.25 - 553.54)	463.45 (376.62 - 548.32)	**461.52** (381.03 - 550.24)
DO	**409.63** (384.94 - 434.70)	413.87 (387.97 - 438.51)	410.64 (387.59 - 435.65)	412.10 (387.93 - 437.77)

MY: milk yield; **FY**: fat yield; **PY**: protein yield; **FP**: fat percentage; **PP**: protein percentage; **STA**: stature; **CW**: chest width; **BD**: body depth; **ANG**: angularity; **RA**: rump angle; **RW**: rump width; **RLSV**: rear legs, side view; **RLRV**: rear legs, rear view; **FA**: foot angle; **FUA**: fore udder attachment; **RUA**: rear udder attachment; **SL**: suspensory ligament; **UD**: udder depth; **FTP**: fore teat placement; **RTP**: rear teat placement; **TL**: teat length; **FL**: feet and legs; **SCS**: somatic cell score; **LONG**: longevity; **DO**: days open.

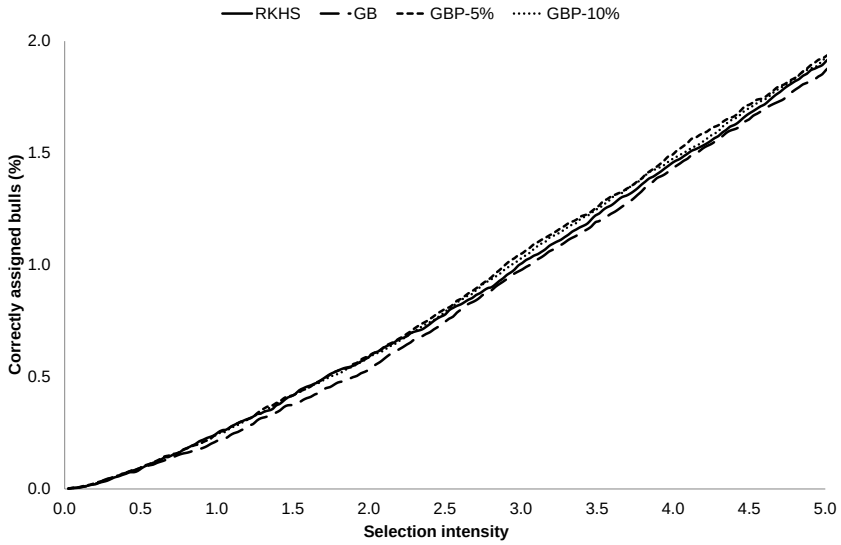

Figure 1. Percentage of correctly assigned bulls over the total population for a given selection intensity (averaged across traits, except LONG).