Comparison of selective genotyping strategies for prediction of breeding values in a population undergoing selection

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ABSTRACT: Genomewide marker information can improve the reliability of breeding value predictions for young selection candidates in genomic selection. However, the cost of genotyping limits its use to elite animals, and how such selective genotyping affects predictive ability of genomic selection models is an open question. We performed a simulation study to evaluate the quality of breeding value predictions for selection candidates based on different selective genotyping strategies in a population undergoing selection. The genome consisted of 10 chromosomes of 100 cM each. After 5,000 generations of random mating with a population size of 100 (50 males and 50 females), generation G0 (reference population) was produced via a full factorial mating between the 50 males and 50 females from generation 5,000. Different levels of selection intensities (animals with the largest yield deviation value) in G0 or random sampling (no selection) were used to produce offspring of G0 generation (G1). Five genotyping strategies were used to choose 500 animals in G0 to be genotyped: 1) Random: randomly selected animals, 2) Top: animals with largest yield deviation values, 3) Bottom: animals with lowest yield deviations values, 4) Extreme: animals with the 250 largest and the 250 lowest yield deviations values, and 5) Less Related: less genetically related animals. The number of individuals in G0 and G1 was fixed at 2,500 each, and different levels of heritability were considered (0.10, 0.25, and 0.50). Additionally, all 5 selective genotyping strategies (Random, Top, Bottom, Extreme, and Less Related) were applied to an indicator trait in generation G0, and the results were evaluated for the target trait in generation G1, with the genetic correlation between the 2 traits set to 0.50. The 5 genotyping strategies applied to individuals in G0 (reference population) were compared in terms of their ability to predict the genetic values of the animals in G1 (selection candidates). Lower correlations between genomic-based estimates of breeding values (GEBV) and true breeding values (TBV) were obtained when using the Bottom strategy. For Random, Extreme, and Less Related strategies, the correlation between GEBV and TBV became slightly larger as selection intensity decreased and was largest when no selection occurred. These 3 strategies were better than the Top approach. In addition, the Extreme, Random, and Less Related strategies had smaller predictive mean squared errors (PMSE) followed by the Top and Bottom methods. Overall, the Extreme genotyping strategy led to the best predictive ability of breeding values, indicating that animals with extreme yield deviations values in a reference population are the most informative when training genomic selection models.

Key words: Bayesian least absolute shrinkage and selection operator, genomic selection, molecular markers, predictive ability, selective genotyping

INTRODUCTION

Genomic selection is a modern selection method used just in animal breeding that makes use of genomewide marker information in prediction of breeding values (Meuwissen et al., 2001). Its implementation requires marker genotypes and phenotypes in a reference population, which are used to estimate effects of a large number of markers spread across the genome. These estimated effects are then used to predict breeding values of selection candidates based on their marker genotypes. Several studies using simulation and real data have shown the poten-
tial of genomic selection to improve response to selection by allowing estimation of breeding values of selection candidates without requiring individual phenotypic or progeny data (Meuwissen et al., 2001; Habier et al., 2007; Calus et al., 2008; Weigel et al., 2009; Kizilkaya et al., 2010; Toosi et al., 2010; Vazquez et al., 2010).

In practice, due to the cost of commercial genotyping, only subsets of selected animals in the reference population are genotyped. For instance, in dairy cattle only the superior animals typically are genotyped (e.g., AI sires and elite cows); in other situations, such as with beef cattle, phenotypic measurements for certain traits (e.g., carcass and meat quality traits) may be available only on animals that have been culled based on poor performance for correlated traits (e.g., growth traits). However, how such selective genotyping (or phenotyping) affects prediction ability in genomic selection is still unclear.

The objective of the present study was to evaluate the ability of predicting genetic values of candidates for selection resulting from different selective genotyping strategies in a population undergoing selection with different selection intensities.

MATERIAL AND METHODS

No live animals were used for this study, and therefore, institutional animal care and use committee approval was not required.

Simulation Settings

Fifty replicated data sets were simulated from a base population of 100 animals (50 males and 50 females). The genome was assumed to consist of 10 chromosomes of 100 cM each. A chromosome begins with 2 markers and then 1 putative QTL followed by 2 markers, a putative QTL, and so forth, giving a total of 302 loci (100 QTL and 202 markers) per chromosome (M₁-M₂-Q₁-M₃-M₄-...-M₁₉₉-M₂₀₀-Q₁₀₀-M₂₀₁-M₂₀₂). In the starting population, there were no polymorphisms in either markers or QTL. In each generation, mutations occurred randomly at the QTL loci, with a rate of $2.5 \times 10^{-3}$ per locus, and at the marker loci, with a rate of $2.5 \times 10^{-3}$ per locus. Both QTL and markers were assumed to be biallelic. For each new mutation at a QTL, an allelic effect was drawn from a normal distribution with mean of 0 and variance of 0.1. This generated an additive genetic variance of 1 at mutation-drift balance after the populations evolved for 5,000 generations (t = 5,000), with sires and dams mated randomly without selection. The number of offspring born at generation $t = 5,001$ was increased to 2,500 by mating each of the 50 sires to each of 50 dams from $t = 5,000$, with 1 offspring per mating pair. This generation was referred to as $G₀$ (reference population).

Offspring of $G₀$ generation ($G₁$) was obtained by directional (i.e., animals with largest yield deviation values) or random selection in $G₀$. These selection intensities were considered: Top2% (top 25 males × top 25 females), Top6% (top 75 males × top 75 females), Top10% (top 125 males × top 125 females), Top14% (top 175 males × top 175 females), Top20% (top 250 males × top 250 females), Top26% (top 325 males × top 325 females), and Top34% (top 425 males × top 425 females). After animals were selected, they were randomly mated to produce $G₁$, with population size kept at 2,500 animals.

Motivation for Genotyping Strategies

Genomewide marker information can improve the reliability of breeding value prediction in a sample of selection candidates using genomic selection (VanRaden et al., 2009; Weigel et al., 2009). However, genotyping entire commercial populations are not feasible due to the cost of genotyping or other practical reasons. Hence, only a fraction of the available animals are typically genotyped, and these may be chosen at random or based on some criterion (e.g., yield deviation values) within a selective genotyping strategy. Information on phenotypes and genotypes of selected animals is then used for training genomic selection models or for development of smaller and cheaper genotyping arrays to be used in commercial herds (Weigel et al., 2009). For example, in dairy cattle only superior animals are typically genotyped (e.g., AI sires and elite cows) whereas in beef cattle and pigs phenotypic measurements for certain traits (e.g., carcass traits) may be available only on animals that have been culled based on poor performance for correlated traits (e.g., growth traits). In any case, little is known regarding how such selective genotyping or phenotyping strategies affect the predictive ability of genomic selection models, especially for young selection candidates. Therefore, in a genomic selection program using a partially genotyped reference population it is important to decide which animals should be genotyped as well as to assess the effects of this genotyping strategy on the resulting ability of predicting genetic values.

In this simulation study, 5 genotyping strategies were applied to choose 500 individuals in $G₀$, which were genotyped and used as a training set. The selective genotyping strategies were 1) Random: randomly selected animals, 2) Top: animals with largest yield deviation values, 3) Bottom: animals with lowest yield deviations values, 4) Extreme: animals with the 250 largest and the 250 lowest yield deviations values, and 5) Less Related: less genetically related animals. The animals in $G₁$ (selection candidates) did not have yield deviations records but had marker genotype information.

The 5 selective genotyping strategies were evaluated at different levels of heritability in the narrow sense. Yield de-
viations records in G₀ were obtained by adding a normally distributed residual term to the genetic value (sum of genetic values at all QTL loci) of each individual. The variance of the residual term (which represents environmental effects) was set to 9.3, or 1 times the genetic variance, such that heritability values were 0.10, 0.25, and 0.50, respectively. Furthermore, an additional scenario with 2 correlated traits was considered, in which different selection intensities and selective genotyping strategies were based on 1 of the traits (indicator trait), but the selection objective refers to the other trait (target trait). An example of a real situation would be selection for meat quality (e.g., tenderness) in beef cattle. Culling decisions may be performed on an indicator trait related to growth, and yield deviations for the target trait can be evaluated only in slaughtered animals. In this specific case, selective genotyping (and selective phenotyping as well) is focused on the bottom of the distribution of the indicator trait. However, for completeness of the simulation, we considered all 5 selective genotyping strategies described previously (Random, Top, Bottom, Extreme, and Less Related) applied to the indicator trait in generation G₀. Results were evaluated for the target trait in generation G₁. Heritability of both the indicator and target traits was set to 0.50, and the genetic correlation between these traits was 0.50. The 5 genotyping strategies applied to individuals in G₀ were compared in terms of their ability to predict the true (target trait) genetic values of the animals in G₁.

Analysis

The genomic-based estimates of breeding values (GEBV) were obtained using the Bayesian least absolute shrinkage and selection operator (LASSO) model proposed by Park and Casella (2008). Specifically, this general model was considered:

\[ y = 1_n \mu + X\beta + e, \]

in which y is the number of response vector lines (n) × 1 response vector (yield deviations), \( \mu \) is an effect common to all yield deviations, \( X \) is an incidence matrix of order \( n \times p \), \( \beta = (\beta_1, \ldots, \beta_p)' \) is a vector of unknown regression coefficients vector lines (p) × 1 vector of unknown regression coefficients, and e is a residual vector that follows the distribution \( N(\mathbf{0}, \sigma^2_e) \), in which \( \sigma^2_e \) is the residual variance. The incidence matrix \( X \) refers to genetic marker genotypes, in which each column represents a specific SNP (i.e., genotypes for a specific locus across all animals) and each row represents a specific animal (i.e., the genotypes of an individual across SNP loci); SNP genotypes were coded as 0, 1, and 2 for homozygous for a specific allele, heterozygous, and homozygous for the alternative allele, respectively. The elements of vector \( \beta \) refer to the additive allelic substitution effect of each of p SNP.

Given \( \mu, \beta, \) and \( \sigma^2_e \), y has a multivariate normal distribution given by

\[ y \mid \mu, \beta, \sigma^2_e \sim N_n(1_n \mu + X\beta, \sigma^2_e I_n). \]

The priors assigned to the unknowns in the Bayesian LASSO model followed the parameterization of Park and Casella (2008), given by

\[ p(\mu) \sim \text{constant} \]

\[ p(\beta \mid \sigma^2_e, \tau_1^2, \tau_2^2, \ldots, \tau_p^2) \sim N(\mathbf{0}, \sigma^2_e \text{diag}(\tau_1^2, \tau_2^2, \ldots, \tau_p^2)), \]

\[ p(\tau_j^2) \sim \text{Exp}(\lambda) \propto \lambda \exp(-\lambda \tau_j^2), \text{for } j = 1, 2, \ldots, p, \]

\[ p(\lambda \mid a, b) \sim \text{Gamma}(a, b) \propto \lambda^{a-1} \exp(-b\lambda) \]

\[ p(\sigma^2_e \mid \nu_e, S^2_e) \sim \nu_e S^2_e \chi^2_{\nu_e} \sim \infty \]

\[ (\sigma^2_e)^{-1/2} \left[ \frac{1}{\nu_e/2} + 1 \right] \exp \left[ -\left( \frac{S^2_e}{2\sigma^2_e} \right) \right]. \]

A Gibbs sampling algorithm was implemented to obtain samples from the joint posterior distribution of the model unknowns (i.e., \( \mu, \beta, \tau^2, \lambda^2, \) and \( \sigma^2_e \)), in which \( \tau^2 = (\tau_1^2, \ldots, \tau_p^2) \) is the vector of variances of the prior Normal distributions of marker effects. Hyperparameters were chosen as follows: \( a = 1, b = 0.0001, \nu_e = 1, \) and \( S^2_e = 0.1. \) Full conditional posteriors of model parameters are in Appendix I. Inferences for each analysis were based on 40,000 samples, after a burn-in period of 30,000 iterations, and with a thinning rate of 10. Convergence of each chain was checked by visual inspection of the trace plots.

In the simulation, the predictive abilities for different selection intensities and genotyping strategies in G₀ were measured by the correlation between the true breeding value (TBV) of G₁ animals and their predicted values (GEBV) and by the predictive mean squared error (PMSE). For each combination of selection intensity and genotyping strategy in G₀, the simulation and analyses were repeated 50 times.

RESULTS AND DISCUSSION

The linkage disequilibrium (LD) levels in G₀ according to genetic distance between markers are presented in Figure 1. The estimated LD was similar to its expected value with a population in recombination drift balance and allows for mutations (Tenesa et al., 2007). The LD increased with decreasing the genetic distance between markers, as expected.

Figure 2 shows correlations between GEBV and TBV of the animals in G₁ for different levels of heritability. Such correlations varied between 0.14 and 0.46 (heritability = 0.10), 0.15 and 0.57 (heritability = 0.25),
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0.17 and 0.66 (heritability = 0.50), and 0.12 and 0.45 (2 correlated traits) across the 5 genotyping scenarios.

For all simulated traits, the lowest correlations between GEBV and TBV were obtained with the Bottom strategy, irrespective of selection intensity (except for the no selection case, in which Bottom had the same correlation as Top). One possible reason is that different levels of selection intensities (2, 6, 10, 14, 20, 26, and 34% of animals with greatest yield deviation performance) were used to produce generation G1. On the other hand, in the no selection case, the animals in G0 were chosen randomly for use as parents of the next generation (G1), which explains the similar correlations when Top or Bottom genotyping strategies are applied.

For all genotyping strategies in G0, except for Bottom, the correlation between GEBV and TBV became slightly greater as selection intensity decreased and reached the largest value when no selection (random sampling) occurred, especially at greater heritability. Among the genotyping strategies considered, genotyping individuals with extreme yield deviations values produced the greatest correlation and smallest PMSE. This can be explained by the fact that animals with extreme yield deviations values are the most informative about the regression line.

Results for the Random and the Less Related strategies were similar. A likely explanation is that the population simulated in the present study was fairly small, with a relatively high (and constant) level of genetic relationships among all animals and high inbreeding coefficient. In larger populations comprising clusters of animals (e.g., families) with greater genetic relationships among individuals within clusters than between clusters, the Less Related strategy might yield better results.

The effects of selection intensity on the correlation between GEBV and TBV were also analyzed in the situation where only the Top or Bottom animals were genotyped (Figure 2). In the first case, there was no clear change in the correlation when moving from the most intense selection (Top2%) to no selection. On the other hand, when only the worst animals were genotyped, the correlation increased (or stayed the same) as selection intensity decreased. As expected, greater correlations between GEBV and TBV were obtained with genomic information on the animals with best yield deviations values, as opposed to the worst, except for the hypothetical situation of no selection, in which results were the same.

For all selection intensities and levels of heritability, the Random, Extreme, and Less Related genotyping strategies yielded better results than the Top strategy. However, the difference was smaller with selection than without selection. Currently, in dairy cattle it is common to genotype only the most widely used animals (the Top strategy) compared with rarely used animals (the Bottom strategy), Extreme, Less Related, or Random animals. In general, the results of this simulation study indicate that genomic information of animals with extreme yield deviations tends to be more useful for breeding value prediction as compared with that of animals chosen at random or with the best yield deviations values, irrespective of the level of heritability.

A simulation study by Ehsani et al. (2010) showed that selective genotyping of the best animals provides

Figure 1. Means of linkage disequilibrium (r^2) in the reference population (G0) according to genetic distance between markers.

Figure 2. Correlations between true and predicted breeding values of offspring (G1) based on different selection intensities and genotyping strategies applied to the reference population (G0). Different heritability levels (0.10, 0.25, and 0.50) were considered (panels a, b, and c) in addition to a situation in which selection was applied to an indicator trait and results were evaluated for the target trait, with a genetic correlation between traits of 0.50 (panel d). Each point represented the mean of 50 replicates. Top2% = top 25 males × top 25 females; Top6% = top 75 males × top 75 females; Top10% = top 125 males × top 125 females; Top14% = top 175 males × top 175 females; Top20% = top 250 males × top 250 females; Top26% = top 325 males × top 325 females; Top34% = top 425 males × top 425 females; Random = randomly selected animals; Top = animals with largest yield deviation values; Bottom = animals with lowest yield deviations values; Extreme = animals with the 250 largest and the 250 lowest yield deviations values; Less Related = less genetically related animals.
poorer predictions of breeding values for animals in the next generation compared with random sampling of animals. In addition, these authors did not find important differences between genotyping individuals with high phenotypic values and individuals with low phenotypic values in the reference population. Using simulated data, Jiménez-Montero et al. (2012) concluded that the magnitude of predictive accuracy of GEBV depends on the number of animals genotyped and the selective genotyping strategy used. According to these authors, divergent genotyping strategies in females could be worth to increase the genomic program efficiency, together with the current male genotyping strategies.

Across all different selection intensities applied in G₀, the Extreme genotyping strategy in the reference population yielded the greatest correlations between GEBV and TBV in offspring for all simulated traits, with values ranging from 0.38 to 0.66. Habier et al. (2007) showed similar correlations when 1,000 markers and phenotypes with a heritability of 0.50 were simulated in the reference population and used to predict GEBV in their progeny. Similarly, Solberg et al. (2008) reported a correlation of 0.79 when GEBV were predicted for the offspring of individuals in the training data. However, in these 2 studies all animals in the reference population were genotyped and included in the analysis, unlike the present study, in which different selection strategies were considered and only a fraction of the animals in the reference population were genotyped.

The efficacy of 5 different genotyping strategies was evaluated considering information on one trait (with low, medium, and high heritability). However, it was unclear how effective these strategies would be in situations involving correlated traits. Therefore, we also examined the effects of selective genotyping applied to an indicator trait and evaluated results for the target trait (with a genetic correlation of 0.50 between traits). The results showed that genotyping only the animals with Extreme yield deviations values for 1 trait (indicator trait) is also the best strategy to obtain the greatest correlation between GEBV and TBV for a correlated trait (target trait) in the next generation (Figure 2) among the scenarios considered. In general, for all selection intensities and genotyping strategies, low to medium correlations were obtained using information on correlated traits.

Overall, for Extreme, Related and Random genotyping strategies, lower values of correlations between GEBV and TBV were obtained when different selection intensities were applied in G₀ in comparison with no selection. It is important to note that the present study considered only one generation of selection (breeding animals in G₀ selected based on their yield deviations values) whereas in commercial herds the animals are selected for 1 or more traits for many generations. In this context, using a simulated population that resembled a commercial dairy cattle population over 25 years, Ansari-Mahyari et al. (2008) showed that it is possible to use selective genotyping in practical dairy cattle breeding programs and decrease genotyping costs with a minimal loss of response as compared with complete genotyping of the reference population. In dairy cattle, considering that the number of genotyped animals is less than the number of non-genotyped animals with phenotypes, Patry and Ducrocq (2011) showed that the inclusion of genomic pseudoperformance based on GEBV for all the selection candidates strongly reduced or removed biases, regardless of their magnitude. These authors proposed an alternative method for combining genomic, phenotypic, and pedigree data in a multiple-step procedure that is easy to implement, to remove bias due to genomic preselection of young sires.

The percentage of co-selected animals selected using the GEBV and TBV for different selection intensities and selective genotyping strategies for a trait with heritability of 0.25 are presented in Table 1. The greatest and lowest percentages of co-selected animals were obtained using the Extreme and the Bottom strategies, respectively. As expected, the Random and the Less Related genotyping strategies showed similar proportions of co-selected animals. When selecting the top 10, 25, and 50% of the animals based on TBV, 33 to 38%, 49 to 51%, and 67 to 70% of the same animals, respectively, would have been selected if GEBV were obtained genotyping individuals with extreme yield deviations values. In general, the same trends were observed for low and high heritability traits and correlated traits (results not shown).

The predictive ability from different genotyping strategies applied in G₀ was also assessed by PMSE (Figure 3). When the animals were genotyped randomly, lower PMSE were obtained. Differences were minimal with respect to selection intensity with values ranging from 0.65 to 3.32 for different levels of heritability and correlated traits. Similar results were obtained with the Less Related strategy (PMSE ranging from 0.67 to 3.95). Genotyping only those animals with extreme yield deviation values yielded GEBV with slightly greater PMSE than when using the Random or Less Related strategies in each of the 8 selection intensities. In contrast, when selection intensity was high in the reference population (Top2%), the difference in PMSE between Random or Less Related and the Extreme genotyping strategies were slightly larger, especially for traits with low heritability.

For the Top genotyping strategy, PMSE values remained constant or increased with a reduction in selection intensity, reaching a maximum when no selection was applied. Although similar trends were observed for different levels of heritability, greater values of PMSE were obtained for less heritable traits and correlated traits, regardless of the intensity of selection applied.
Comparing the Top strategy with Random or Extreme, for traits with heritability of 0.25 or greater, similar PMSE is expected. However, genotyping only the animal with best yield deviation appears to be a poor choice for low heritability traits, especially when selection intensity is low in the reference population.

The Bottom genotyping strategy resulted in greatest values of PMSE, with a tendency toward decreasing PMSE with weakening of selection intensity. For all levels of heritability and of selection intensity (except for the no selection case), lower correlations and larger PMSE were obtained using the Bottom genotyping strategy than with other selection strategies. On the other hand, the Bottom and the Top strategies gave roughly the same correlations and PMSE in the absence of selection.

The PMSE results discussed above were based on different genotyping strategies and selection intensities applied to a single trait. A similar trend in PMSE was observed when the animals in reference population were selected for one trait and the genotyping information was used to predict GEBV for a correlated trait measured in the progeny (Figure 3).

The results in terms of correlations between GEBV and TBV and PMSE disagreed with each other when comparing the Random and Extreme strategies. For all selection intensities, the Random approach was poorer in terms of correlation but better or equal in terms of PMSE. For these 2 strategies, greater differences were obtained for correlations than for PMSE. Among the 5 genotyping strategies considered, the Extreme genotyping approach yielded the greatest correlation (Figure 2) and lowest PMSE (Figure 3) for GEBV prediction.

The efficiency of genomic selection for different genotyping strategies was evaluated for a simulated trait with heritability of 0.10, 0.25, or 0.50 and using 2 correlated traits. These results can be extended to strategies in which several quantitative traits are of interest, with different levels of genetic correlation between them. It is known that the correlation between GEBV and TBV is influenced by heritability, with an expected reduction in the correlation for traits with low heritability, as shown in this study. Nonetheless, as indicated by Solberg et al. (2008), a decrease in the correlation between GEBV and TBV for traits with low heritability can be compensated by using a larger number of observations to estimate the marker effects.

The results obtained in this simulated study can be applied in many practical situations. For example, in beef cattle it is practically impossible to achieve reasonable reliabilities for young animals for carcass traits because such traits are generally expressed late in life, require the slaughter of animals, and incur a high cost of measurement. In such cases, it is possible to use marker information from a set of animals in previous generations to predict performance in the next generation. The results of this study show that the predictive ability of...
breeding values will depend, among other factors, on which animals are genotyped in the reference population. Considering predictive ability, the best strategy appears to be genotyping extreme animals in terms of yield deviations values in the reference population.

The results reported in this simulation study can be extended to different scenarios, such that they can be useful for researchers and breeders working with different species, population structures, and number of molecular markers. The specific values of accuracy or mean square errors reported will change with different levels of LD, heritability of the trait, genetic correlation with indicator trait, population size, selection intensity, number of genotyped animals or selection applied to multiple generations, among other factors. However, the ranking of performance of the selective genotyping strategies considered should be maintained across a wide range of combinations of such factors. For example, performing simulations with multiple generations of selection would certainly increase the levels of LD and consequently increase the prediction accuracy values, but this would not change remarkably the relative efficiency of the methods compared.

LITERATURE CITED


APPENDIX I

Here, \( a, b, \nu_e, \) and \( S_e^2 \) are hyperparameters, and \( \tau_j^2 \) is a variance associated with regressor \( \beta_j \). After integrating out \( \tau_j^2, \tau_j^2, \ldots, \tau_p^2 \) in Eq. [1] using Eq. [2], one obtains a double exponential distribution on \( \beta_j \):

\[
p(\beta_j | \lambda) = \prod_{j=1}^{p} \left[ \frac{(2\lambda)^{1/2}}{2} \right] \exp[-(2\lambda)^{1/2} |\beta_j|].
\]

The fully conditional distributions for a Gibbs sampler are

\[
p(\mu | \text{else}) \sim \mathcal{N}[1/n(1'_n y - 1'_n X\beta), \sigma_e^2/n]
\]

\[
p(\beta_j | \text{else}) \sim \mathcal{N}\left\{\frac{X'_j x_j + (\sigma_e^2 / \tau_j^2)^{-1} X'_j (y - 1'_n y - X\beta) \beta_j - 1}{\tau_j^2 \sigma_e^2 / \tau_j^2}\right\},
\]

for \( j = 1, 2, \ldots, p \), in which \( x_j \) is the \( j \)th column of \( X \), \( X_{-j} \) is \( X \) without its \( j \)th column and \( \beta_{-j} \) is \( \beta \) without its \( j \)th element. Furthermore,

\[
p(\tau_j^2 | \text{else}) \sim \text{Inverse Gaussian}\left[(2\lambda)^{1/2} \beta_j \right]^{-1}, \quad \text{for} \quad j = 1, 2, \ldots, p
\]

\[
p(\lambda | \text{else}) \sim \text{Gamma}(a + p, b + \sum_{j=1}^{p} \tau_j^2)
\]

and

\[
p(\sigma_e^2 | \text{else}) \sim [\nu_e S_e^2]^{-1} \chi^2_{\nu_e + p},
\]