Walloon Single-Step Genomic Evaluation System Integrating Local and MACE EBV

F.G. Colinet[1], J. Vandenplas[1,2], P. Faux[1], S. Vanderick[1], R. Renaville[1], C. Bertozzi[4], X Hubin[3], and N. Gengler[1]

[1] University of Liege, Gembloux Agro-Bio Tech, 5030 Gembloux, Belgium
[2] National Fund for Scientific Research, 1000 Brussels, Belgium
[3] Walloon Breeding Association, 5590 Ciney, Belgium

Abstract

Walloon dairy cattle could be considered as a small scale population where the majority of AI bulls are imported from several foreign countries. Single-step Genomic Best Linear Unbiased Prediction (ssGBLUP) methods allow the simultaneous use of genomic, pedigree and phenotypic information and should reduce potential biases in the estimation of Genomically Enhanced Breeding Values (GEBV). Therefore, in the context of developing a Walloon genomic evaluation system, it was considered as the best option. However, in opposition to multi-step genomic predictions, ssGBLUP only uses local phenotypic information and is unable to use directly important other sources of information coming from abroad, *e.g.* Multiple Across Country Evaluation (MACE) results provided by Interbull. Therefore, single-step Genomic Bayesian Prediction (ssGBayes) was used as an alternative method for the Walloon genomic evaluation system. The ssGBayes approach allows combining simultaneously all available genotype, pedigree, local and foreign information in a local evaluation by considering a correct propagation of external information avoiding double counting of contributions due to relationships and due to records. In the Walloon genomic evaluation system, local information refers to Walloon EBV and associated reliabilities (REL) and foreign information refers to MACE EBV and associated REL. Furthermore, the Bayesian approach has the advantage to directly combine EBV and REL without any deregression step. The ssGBayes method computed more accurate predictions for all types of animals. For example, for genotyped animals with low Walloon REL (< 0.25) without MACE results and sired by genotyped bulls with MACE results, the average increase of REL for the studied traits was 0.39 points of which 0.14 points could be traced to the inclusion of MACE information. For other categories of genotyped animals, the contribution by MACE information was high too. The new Walloon genomic evaluation system passed the Interbull GEBV tests for several traits in July 2013. This approach has the potential to improve current genomic prediction strategies as it can be used in other settings where the combination of different sources of information is required.

Key words: Bayesian integration, MACE, genomic prediction

Introduction

Simultaneous use of all data by Best Linear Unbiased Prediction is a condition to predict unbiased estimated breeding values (EBV; Henderson, 1984). However, this condition is not always fully met. For example, small scale local populations lead to evaluations based only on local data while foreign bulls are used (*e.g.*, 87 % of cows in 1st to 3rd parity in 2012 were sired by AI bulls born outside of Walloon Region of Belgium). Although these bulls were strongly preselected, foreign raw data used to select them is unavailable leading to potential biases in local evaluations. Local EBV will be also less accurate because only incomplete data (*i.e.*, foreign raw data not included) is available. Genomic selection could increase these problems for local genomic evaluations.

Most current genomic evaluation systems are multi-step, relying heavily on the use of Multiple Across Country Evaluation (MACE) results as the primary source of foreign phenotypic information. However, these implementations of genomic prediction using MACE results mitigated these issues only for sires with high REL which are introduced during the SNP prediction equation estimation step.

Single-step genomic evaluations (ssGBLUP) should reduce potential biases in the estimation of genomically enhanced breeding values (GEBV) by the simultaneous combination of genomic, pedigree and all local phenotypic information (VanRaden, 2012), also because fewer approximations are made than in multi-step methods. Therefore, in the context of developing a Walloon genomic evaluation system, ssGBLUP was considered as the best option. However, in opposition to multi-step genomic prediction, ssGBLUP uses only local phenotypic information and is unable to use directly important others source of information coming, *e.g.* Multiple Across Country Evaluation (MACE) results. Nevertheless, the recovery of such important sources of information in the Walloon genomic evaluation system was required, *i.e.* due to the widespread use of imported AI bulls.

Therefore, in the context of the Walloon genomic evaluation system, the aim of this research was to assess the potential of a Bayesian approach, based on ssGBLUP, to simultaneously combine all available genotype, pedigree, local and foreign information in a local genomic evaluation. This approach also avoids deregression steps, allows a correct propagation of external information and avoids multiple considerations of contributions due to relationships and due to records.

Materials and Methods

In this study, local information will refer to local EBV and associated reliabilities (REL) estimated from all available local data and foreign information will refer to MACE EBV and associated REL.

Currently, in the Walloon Region of Belgium, genomic evaluations for the Holstein breed are performed for all traits submitted to MACE. In this study, results are reported showing the strategy and the results obtained in the July 2013 run for milk, fat and protein yields, somatic cell score, longevity and two conformational traits (stature and udder support).

The genomic evaluation system implemented in the Walloon region of Belgium consisted in several steps. First, a group of genotyped animals was defined as those animals born after the year 1998. Ancestors for these animals were extracted from the database used for the official Walloon genetic evaluation and covered up to 6 known ancestral generations. After extraction, the pedigree file contained 16 234 animals of which 1 909 animals (1 378 bulls and 525 cows) were genotyped. The genotyped cows were in a large majority not from selective genotyping but representing local variability of Holstein animals. A total of 38 604 SNP markers were selected after editing.

Local information included EBV and associated REL for cows and bulls estimated from data provided by the Walloon Breeding Association (subscript W; EBV_W, REL_W) for the official Walloon evaluation of April 2013 (Auvray and Gengler, 2002; Croquet *et al.*, 2006). Table 1 shows the number of animals associated to Walloon information for which EBV_W were available for each studied trait.

Foreign information included EBV and REL for sires provided by the April 2013 MACE evaluation performed by Interbull (subscript M; EBV_M, REL_M; Table 1).

Table 1. Used genetic parameters, local and foreign information available for the genomic evaluation for the seven reported traits.

Trait	Heritability	Genetic variance	No. of animals			No. of genotyped animals		
			EBV_W	EBV_M	EBV_{WC}	EBV_W	EBV_M	EBV_{WC}
Milk yield	0.38	280 425	12 046	1 981	601	1 762	1 205	278
Fat yield	0.43	523	12 046	1 981	601	1 762	1 205	278
Protein yield	0.41	262	12 046	1 981	601	1 762	1 205	278
SCS	0.13	0.2060	12 047	1 941	575	1 762	1 167	261
Longevity	0.11	0.0797	11 641	1 914	520	1 758	1 155	238
Stature	0.52	1.1984	12 671	1 922	595	1 706	1 158	277
Udder support	0.19	0.3212	12 226	1 911	573	1 699	1 158	277

For every trait, contributions of Walloon information into MACE were determined based on the domestic effective daughter equivalents (EDC) associated to EBV_M and REL_M as reported by Interbull. MACE information free of Walloon information had therefore a reported domestic EDC equal to 0. For all animals and traits with a domestic EDC different from 0, Walloon EBV and associated REL contributing to the April 2013 MACE routine-run (subscript Wc; EBV_{Wc}, REL_{Wc}) were considered to avoid double counting of contributions due to records (Table 1). Information was harmonized between the local and MACE traits by adjusting scale and mean difference towards the original expression of the trait in the Walloon genetic evaluation computations. As shown in Table 1, numbers of available local and foreign records were slightly different among the traits.

The Bayesian procedures to integrate external information into genetic evaluations were outlined by Vandenplas and Gengler (2012a) and were adapted to blend Walloon and MACE information into a modified ssGBLUP (Vandenplas and Gengler, 2012b; Vandenplas *et al.*, 2012) for each trait separately. This method, called here single-step Genomic Bayesian Prediction (ssGBayes), was used as an alternative method for the Walloon genomic evaluation system. As in our implementation Walloon and MACE information were added and Walloon information contributing to MACE subtracted, the used Genomic evaluation will be called $ssGBayes_{W+M-Wc}$ and can be described by the following system of equations:

$$\left(\mathbf{G}^{*-1} + \mathbf{\Lambda_W} + \mathbf{\Lambda_M} - \mathbf{\Lambda_{Wc}}\right) \hat{\mathbf{a}}_{\mathbf{W+M-Wc}} = \mathbf{D_W^{-1}}\hat{\mathbf{u}}_{\mathbf{W}} + \mathbf{D_M^{-1}}\hat{\mathbf{u}}_{\mathbf{M}} - \mathbf{D_{Wc}^{-1}}\,\hat{\mathbf{u}}_{\mathbf{Wc}} \quad (1)$$

where $\mathbf{G}^* = \mathbf{H}\,\sigma^2_a$ is the combined genomic-pedigree based (co)variances matrix, **H** is the combined genomic-pedigree based relationship matrix (*e.g.*, Aguilar *et al.*, 2010), σ^2_a is the genetic additive variance, $\hat{\mathbf{a}}_{W+M-Wc}$ is the vector of Walloon GEBV based on Walloon and MACE information, $\hat{\mathbf{u}}_W$ is the vector of EBV_W, $\hat{\mathbf{u}}_M$ is the vector of EBV_M, $\hat{\mathbf{u}}_{Wc}$ is the vector of EBV_{Wc}, $\mathbf{\Lambda}_i$ (i=W, M and Wc) is a matrix miming least square part of hypothetical BLUP, and $\mathbf{D}_i^{-1}$ is the inverse of the prediction error (co)variances matrix of $\hat{\mathbf{u}}_i$. For the 3 sources of information (*i.e.*, W, M and Wc), animals having known EBV were called external animals. This was an extension from the theory outlined by Vandenplas and Gengler (2012a) as so-called local contributions to the formation of the left-hand side and right-hand side were replaced by information summarized by EBV_W, REL_W translated into $\mathbf{\Lambda}_W$ and $\mathbf{D}_W^{-1}\hat{\mathbf{u}}_W$.

The inverse of the combined genomic-pedigree based relationship matrix **H** was computed using the inverse of the additive pedigree relationship matrix and a modified genomic relationships matrix using a weight of 95 % for raw genomic relationships and of 5 % for pedigree relationships. For matrix compatibility, both diagonal and off-diagonal values were respectively centered on the average of diagonal and off-diagonal elements of the subpart of the additive relationship matrix among genotyped animals.

For each information source, animals not associated to available EBV were called internal animals and their EBV were predicted following the multivariate normal (MVN) prior distribution:

$$p\left(\hat{\mathbf{u}}_{\mathbf{i(I)}} \middle| \hat{\mathbf{u}}_{\mathbf{i(E)}}\right) = MVN\left(\mathbf{G}_{\mathbf{i(IE)}}\,\mathbf{G}^{-1}_{\mathbf{i(EE)}}\,\hat{\mathbf{u}}_{\mathbf{i(E)}}, \left(\mathbf{G}_{\mathbf{i}}^{(\mathrm{II})}\right)^{-1}\right)$$

where the subscript I refers to internal animals not associated to the i^{th} source of information and E refers to external animals associated to the i^{th} source of information.

For the 3 sources of information (*i.e.* W, M and Wc), the matrix $\mathbf{D}_i^{-1}$ was approximated by $\mathbf{D}_i^{-1} = \mathbf{G}^{-1} + \mathbf{\Lambda}_i$ where $\mathbf{G}^{-1}$ is the pedigree-based additive (co)variances matrix and $\mathbf{\Lambda}_i$ is a diagonal variance matrix with one element per animal (Quaas and Zhang, 2006). Each diagonal element of Λ_i is equal to RE_{ij}/σ^2_e for j=1, 2, …, J animals. The element σ^2_e is the residual variance and the element RE_{ij} is the effective number of records, so-called record equivalents, for the j^{th} animal. Record equivalents expressed the amount of contributions for an animal (Misztal and Wiggans, 1988).

As both Walloon and MACE information were associated to related animals, double counting of contributions due to relationships among related animals could exist. Therefore, the combination of Walloon and MACE information was performed by taking into account contributions due to relationships among related animals. These contributions were estimated by a two-step algorithm (TSA; Vandenplas and Gengler, 2012a). It takes into account all relationships between animals associated to information and their ancestors. Therefore, for the internal animals, RE_{ij} is equal to 0. All contributions for these animals were only due to their relationships with external animals. For the external animals, RE_{ij} was estimated through TSA and only express the amount of contributions due to records.

Because a major feature of the Walloon genomic evaluation system is its ability to use MACE information, the influence of the use of this information was tested. To test this influence, ssGBayes was run considering only Walloon information ($ssGBayes_W$) using the following system of equations:

$$\left(\mathbf{G}^{*-1} + \mathbf{\Lambda}_{\mathbf{W}}\right)\hat{\mathbf{a}}_{\mathbf{W}} = \mathbf{D}_{\mathbf{W}}^{-1}\hat{\mathbf{u}}_{\mathbf{W}} \quad (2)$$

where $\hat{\mathbf{a}}_W$ is the vector of Walloon GEBV only based on Walloon information.

Approximation of genomic REL (GREL) for GEBV in Genomic evaluation systems is not always straight forward (Misztal *et al.*, 2013). Because systems of equations (1) and (2) associated to model $ssGBayes_{W+M-Wc}$ respectively $ssGBayes_W$ represented hypothetical mixed model equations, the computation of REL was tested using the standard formula:

$$GREL = 1 - PEV/\sigma_g^2 \quad (3)$$

where σ^2_g is the genetic variance for the corresponding trait based on the diagonal element of the $\mathbf{G}^*$ matrix and PEV is the prediction error variance obtained from the diagonal element of the inverted left-hand-side of the equations (1) and (2), respectively. By using elements of $\mathbf{G}^*$ to get the genetic variance, the method corrected for inbreeding estimated using combined pedigree and genomic information.

The two ssGBayes were performed using BLUPF90 (Misztal, 2013) modified to implement equations (1) and (2).

Results & Discussion

For all traits, among the approximately 12 000 animals associated to available Walloon information around 1 950 bulls were also evaluated by Interbull. Walloon information for around one third of these bulls contributed to the April 2013 MACE routine-run. Table 1 also indicates that more than 80 % of the 1 378 genotyped bulls and around 10 % of the 16 234 animals in the considered pedigree file had foreign information. This large amount of additional information was incorporated in the genomic evaluation system and would allow increasing the overall accuracy of the produced GEBV.

Table 2 gives details on the improvement of REL when estimating (G)EBV from different sources. First, the improvement due to including only genomic information was considered. For the genotyped bulls with low reliable official Walloon EBV (REL_W < 0.50), the genomic information allowed an substantial increase of between 0.13 and 0.19 points for average REL of these bulls according to the studied traits.

The genomic information also increased average REL of the two other categories of bulls with more accurate Walloon EBV. Indeed, the average REL was increased with 0.05-0.06 points for the bulls with REL_W between 0.50 and 0.75. Even for locally well proven bulls (*i.e.*, $REL_W \geq 0.75$), the genomic information added 0.01 to the average REL.

Table 2. Average REL (SD) associated to EBV_W, $GEBV_W$ and $GEBV_{W+M-Wc}$ for genotyped bulls for the seven studied traits

Trait	REL_W											
	]0.00 - 0.50[				[0.50 – 0.75[				[0.75 – 0.99]			
	N	EBV^1_W	$GEBV^2_W$	$GEBV^3_{W+M-Wc}$	N	EBV^1_W	$GEBV^2_W$	$GEBV^3_{W+M-Wc}$	N	EBV^1_W	$GEBV^2_W$	$GEBV^3_{W+M-Wc}$
Milk yield	647	0.25 (0.12)	0.44 (0.09)	0.80 (0.09)	173	0.63 (0.07)	0.69 (0.06)	0.87 (0.05)	390	0.90 (0.07)	0.91 (0.06)	0.94 (0.04)
Fat yield	642	0.26 (0.12)	0.45 (0.09)	0.80 (0.09)	158	0.63 (0.07)	0.69 (0.05)	0.87 (0.04)	412	0.90 (0.07)	0.91 (0.06)	0.94 (0.04)
Protein yield	644	0.26 (0.12)	0.44 (0.09)	0.80 (0.09)	162	0.63 (0.07)	0.69 (0.06)	0.87 (0.04)	404	0.90 (0.07)	0.91 (0.06)	0.94 (0.04)
SCS	682	0.25 (0.12)	0.43 (0.09)	0.84 (0.12)	186	0.63 (0.07)	0.68 (0.06)	0.90 (0.08)	337	0.90 (0.07)	0.91 (0.06)	0.96 (0.04)
Longevity	889	0.23 (0.12)	0.36 (0.09)	0.51 (0.09)	146	0.61 (0.08)	0.66 (0.07)	0.75 (0.07)	149	0.86 (0.06)	0.87 (0.06)	0.89 (0.04)
Stature	632	0.28 (0.10)	0.46 (0.08)	0.82 (0.13)	141	0.63 (0.07)	0.69 (0.05)	0.91 (0.06)	408	0.91 (0.07)	0.92 (0.06)	0.96 (0.04)
Udder support	699	0.28 (0.10)	0.43 (0.08)	0.71 (0.14)	189	0.63 (0.07)	0.68 (0.06)	0.84 (0.08)	286	0.91 (0.08)	0.92 (0.07)	0.95 (0.04)

[1] REL obtained from Walloon polygenic evaluation
[2] REL obtained from Walloon genomic evaluation using only EBV_W (eq. 1 and 3)
[3] REL obtained from Walloon genomic evaluation using EBV_W, EBV_M and EBV_{Wc} (eq. 2 and 3)

Considering the simultaneous combination of genomic and foreign information ($ssGBayes_{W+M-Wc}$), the increases of the averaged REL for each of the three mentioned categories of genotyped bulls (Table 2) were higher than those associated to $ssGBayes_W$. As expected, the highest increase of REL was observed for the bulls with the lowest REL_W. When comparing different traits, the use of $ssGBayes_{W+M-Wc}$ led to an increase of average REL between 0.20 points for longevity and 0.41 points for milk yield compared to $ssGBayes_W$. The increase was lower for genotyped bulls with REL_W included in the range [0.50-0.75[with 0.09 to 0.22 additional REL. Even for the already locally well proven bulls (*i.e.*, $REL_W \geq 0.75$), $ssGBayes_{W+M-Wc}$ still provided more reliable GEBV than $ssGBayes_W$. Additional points of REL ranged from 0.02 for longevity to 0.05 for fat yield (Table 2).

Table 3 shows the improvements for only genotyped animals with available EBV_W, without foreign information, and sired by genotyped bulls with MACE results. These

genotyped animals were typically Walloon cows and bulls and foreign or Walloon bulls to be tested. Again, similarly to Table 2, even if $ssGBayes_W$ allowed an increase of average REL with 0.16-0.28 additional points of REL, $ssGBayes_{W+M-Wc}$ led to higher REL. For most traits, the system combining all available information ($ssGBayes_{W+M-Wc}$) provided an average REL higher than 0.50 for these genotyped animals with a REL_W included in the range]0.00-0.25[.

Table 3. Average REL (SD) associated to EBV_W, $GEBV_W$ and $GEBV_{W+M}$ for genotyped animals without MACE results and sired by genotyped bulls with MACE result for the studied traits.

Trait	REL_W											
	]0.00 – 0.25[				[0.25 – 0.50[				[0.50 – 0.75[			
	N	EBV^1_W	$GEBV^2_W$	$GEBV^3_{W+M-Wc}$	N	EBV^1_W	$GEBV^2_W$	$GEBV^3_{W+M-Wc}$	N	EBV^1_W	$GEBV^2_W$	$GEBV^3_{W+M-Wc}$
Milk yield	43	0.11 (0.10)	0.38 (0.08)	0.52 (0.04)	123	0.43 (0.07)	0.54 (0.05)	0.60 (0.03)	101	0.52 (0.02)	0.61 (0.02)	0.64 (0.02)
Fat yield	43	0.11 (0.10)	0.39 (0.08)	0.53 (0.04)	77	0.41 (0.08)	0.54 (0.05)	0.60 (0.04)	147	0.54 (0.03)	0.62 (0.02)	0.65 (0.02)
Protein yield	43	0.11 (0.10)	0.39 (0.08)	0.53 (0.04)	91	0.42 (0.08)	0.54 (0.05)	0.60 (0.03)	133	0.53 (0.02)	0.61 (0.02)	0.65 (0.02)
SCS	52	0.11 (0.10)	0.36 (0.08)	0.54 (0.04)	194	0.43 (0.06)	0.53 (0.04)	0.61 (0.03)	30	0.53 (0.07)	0.61 (0.06)	0.66 (0.05)
Longevity	117	0.14 (0.08)	0.30 (0.06)	0.38 (0.04)	165	0.31 (0.04)	0.40 (0.04)	0.44 (0.03)	0	--- (---)	--- (---)	--- (---)
Stature	46	0.08 (0.09)	0.36 (0.10)	0.53 (0.05)	114	0.36 (0.06)	0.51 (0.05)	0.59 (0.03)	120	0.70 (0.04)	0.74 (0.03)	0.76 (0.03)
Udder support	65	0.11 (0.09)	0.34 (0.09)	0.48 (0.06)	158	0.38 (0.07)	0.50 (0.05)	0.56 (0.04)	73	0.53 (0.03)	0.60 (0.03)	0.64 (0.03)

[1] REL obtained from Walloon polygenic evaluation
[2] REL obtained from Walloon genomic evaluation using only EBV_W (eq. 1 and 3)
[3] REL obtained from Walloon genomic evaluation using EBV_W, EBV_M and EBV_{Wc} (eq. 2 and 3)

The Genomic evaluation addressed another category of genotyped animals including the newborn Walloon bulls (candidate for AI bulls) and recently imported AI bulls (or with a forecasted importation), both types of animals not being yet included in the routine genetic evaluations. Therefore, these bulls had no available external information due to their absence in the pedigree file at the last official Walloon genetic evaluation. These animals were incorporated in the genomic evaluation system by only using their available information (*i.e.*, pedigree and genotypes) and information available for their relatives.

If their sires had available MACE EBV, the accuracy of their GEBV was sufficiently increased for their GEBV to become publishable (Table 4). For each of the seven studied traits, the genomic evaluation system ($ssGBayes_{W+M-Wc}$) provided a publishable GEBV for more than two thirds of these bulls. Currently, the system is not yet optimized by genotyping additional related animals with information (*e.g.*, maternal grand-sires, brothers, half-brothers) in order to increase the links between these candidate animals and the genotyped animals with information. An appropriate strategy will be implemented to detect the most important animals to be also genotyped which should increase the proportion of publishable GEBV even further.

The Walloon genomic evaluation system was used and results tested inside the GEBV tests of Interbull. Results passed the tests for

several traits in April and July 2013. Currently, research is undertaken to optimize the formation of the modified genomic relationships matrix. Indeed, several tests showed that the weighting used has a large influence and that the optimal proportion between raw genomic and pedigree relationships directly reflects the critical partitioning of total genetic variance in variances explained by SNP effects or polynomial residuals.

Table 4. Average REL (SD) associated to $GEBV_{W+M-Wc}$ for genotyped bulls without external phenotype information (neither local EBV neither MACE EBV), sired by genotyped bulls with MACE results for the studied trait.

Trait	Publication rules: REL ≥	No. of bulls	Averaged REL_{W+M-Wc} (SD)	No. of publishable $GEBV_{W+M-Wc}$
Milk yield	0.50	17	0.53 (0.05)	13
Fat yield	0.50	17	0.53 (0.06)	13
Protein yield	0.50	17	0.53 (0.05)	13
SCS	0.45	20	0.54 (0.05)	19
Longevity	0.35	23	0.38 (0.05)	18
Stature	0.50	21	0.54 (0.06)	15
Udder support	0.50	21	0.47 (0.07)	15

REL_{W+M-Wc} and $GEBV_{W+M-Wc}$ from Walloon genomic evaluation using EBV_W, EBV_M and EBV_{Wc}

Conclusions

The ssGBayes method, through its Bayesian approach, integrated well MACE results into ssGBLUP and allowed recovering indirectly a large amount of phenotypic information. All available external sources of information were correctly propagated avoiding double counting of contributions due to relationships and due to own records. Therefore, the ssGBayes method proved to be a good choice for the Walloon genomic evaluation system integrating Walloon and MACE EBV. Additional optimizations are currently under development by genotyping important sires and by adapting the correct partitioning of additive total variance for a given trait in order to increase the number of traits that pass the Interbull GEBV test. The ssGBayes method used in the Walloon genomic evaluation system can also be adapted to a multi-trait setting allowing the genomic evaluation of only locally available traits (*e.g.*, fine milk composition, methane emissions) using external information from correlated traits (*e.g.*, traits evaluated by Interbull).

Finally, the ssGBayes approach has the potential to improve current genomic prediction strategies as it can be used in other settings (*e.g.*, beef cattle and pigs) where the combination of different sources of information is required.

Acknowledgements

The authors acknowledge the Ministry of Agriculture of Walloon Region of Belgium (Service Public de Wallonie, DGO3) for financial support through several grants, *i.e.* research projects D31-1233 and D31-1274. Jérémie Vandenplas, as a research fellow, and Nicolas Gengler, as an honorary senior research associate, acknowledge the former and ongoing support of the National Fund for Scientific Research (F.R.S.-FNRS, Brussels, Belgium) for their positions and through several grants. Pierre Faux acknowledges the financial support of National Research Fund, Luxembourg through project NextGenGES-PHD-09-118, as part of a private public partnership between CONVIS (Ettelbruck,

Luxembourg) and Gembloux Agro-Bio Tech of the University of Liège. Jérémie Vandenplas acknowledges I. Misztal for hosting him at Animal and Dairy Sciences Department of University of Georgia (Athens, USA), G. Gorjanc for hosting him at Animal Science Department of University of Ljubljana. The help of S. Tsuruta (University of Georgia, Athens, USA) and I. Aguilar (Instituto Nacional de Investigación Agropecuaria, Las Brujas, Urugay) concerning the BLUPF90 family of programs, on which the developed computing programs are based, is acknowledged. Computational resources have been provided by the Consortium des Équipements de Calcul Intensif (CÉCI) funded by the National Fund for Scientific Research (F.R.S.-FNRS, Brussels, Belgium) under Grant No. 2.5020.11.

References

Aiguilar, I., Misztal, I., Johnson, D.L., Legarra, A., Tsuruta, S. & Lawlor, T.J. 2010. Hot topic: A unified approach to utilize phenotypic, full pedigree, and genomic information for genetic evaluation of Holstein final score. *J. Dairy Sci. 93*, 743-752.

Auvray, B. & Gengler, N. 2002. Feasibility of a Walloon test-day model and study of its potential as tool for selection and management. *Interbull Bulletin 29*, 123-127.

Croquet, C., Mayeres, P., Gillon, A., Vanderick, S. & Gengler, N. 2006. Inbreeding depression for global and partial economic indexes, production, type, and functional traits. *J. Dairy Sci. 89*, 2257-2267.

Henderson, C.R. 1984. *Applications of linear models in animal breeding*. 2nd ed. University of Guelph, Guelph, ON, Canada.

Misztal, I. 2013. *BLUPF90 family of programs.* University of Georgia, Athens. Accessed Jan. 15, 2013. http://nce.ads.uga.edu/wiki/doku.php

Misztal, I. & Wiggans, G.R. 1988. Approximation of prediction error variance in large-scale animal models. *J. Dairy Sci. 71 (Suppl. 2)*, 27-32.

Misztal, I., Tsuruta, S., Aguilar, I., Legarra, A., VanRaden, P.M. & Lawlor, T.J. 2013. Methods to approximate reliabilities in single-step genomic evaluation. *J. Dairy Sci. 96*, 647-654.

Quaas, R.L. & Zhang, Z. 2006. Multiple-breed genetic evaluation in the US beef cattle context: methodology. CD-ROM Commun. 24-12 in *Proc. 8th World Congr. Appli. Livest. Prod.*, Belo Horizonte, Brazil.

Vandenplas, J. & Gengler, N. 2012a. Comparison and improvements of different Bayesian procedures to integrate external information into genetic evaluations. *J. Dairy Sci. 95*, 1513-1526.

Vandenplas, J. & Gengler, N. 2012b. Extension of Bayesian procedures to integrate and to blend multiple external information into genetic evaluations. *J. Dairy Sci. 95 (Suppl. 2)*, 449-450.

Vandenplas, J., Misztal, I., Faux, P. & Gengler, N. 2012. Bayesian integration of external information into the single step approach for genomically enhanced prediction of breeding values. *J. Dairy Sci. 95 (Suppl. 2)*, 682.

VanRaden, P.M. 2012. Avoiding bias from genomic pre-selection in converting daughter information across countries. *Interbull Bulletin 45*, 29-33.