

## Toward genomic breeding programs in French dairy sheep and goats

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### ▶ To cite this version:

Helene H. Larroque, Francis F. Barillet, Guillaume G. Baloche, Jean-Michel Astruc, Diane Buisson, et al.. Toward genomic breeding programs in French dairy sheep and goats. 10. World Congress on Genetics Applied to Livestock Production (WCGALP), Aug 2014, Vancouver, Canada. hal-02742056

### HAL Id: hal-02742056 https://hal.inrae.fr/hal-02742056

Submitted on 3 Jun2020

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**ABSTRACT:** Genomic selection opens new perspectives for breeding programs of dairy ruminants. In France, several projects have enabled the creation of reference populations in dairy sheep and goats. Early studies have shown that the reliability of genomic evaluations using a GBLUP method in these species is lower than in Holstein dairy cattle breed. The single-step approach gives best predictions for candidates at birth (genomic evaluation accuracy obtained by cross validation for milk yield of 0.47 in Lacaune dairy sheep and 0.43 in goats' breeds). The multi-breed approach is effective in goats by blending Alpine and Saanen breeds, but not in sheep. Finally, switching to genomic selection is planned in Lacaune dairy sheep and is under consideration for other sheep breeds. In goats, inclusion of major genes in genomic evaluations should be explored before switching to genomic breeding programs.

Keywords: Dairy goats Dairy sheep Genomic selection Genetics

#### Introduction

Genomic selection (GS) based on phenotypic, genotypic and pedigree data, opens new perspectives for breeding programs. This is especially true for dairy species where the selection of sires on dairy traits is conditioned by a progeny testing period. For dairy cattle, GS accelerates genetic progress through more accurate genetic breeding values of males at birth, an increase of selection intensity and a reduction of the generation intervals on the male pathway with a much earlier selection in life. Moreover, the cost of genotyping is relatively low compared to the economic value of animals and cost of progeny test. All these reasons make genomics schemes immediately profitable in many dairy cattle breeds. In small dairy ruminants the situation seems at first sight less favorable. Indeed, the relative higher cost of genotyping is still a strong economic barrier, but above all the potential to accelerate genetic progress is less obvious. Among the factors influencing the genetic progress, the proportion of candidates retained after genotyping (intensity of genomic selection) will play a key role and will be determined by the economic balance between the cost of genotyping and the reduction of artificial insemination (AI) livestock. However, the use of fresh semen for AI in dairy sheep and

the need to cope with the demand of insemination highly concentrated in time will limit the possibilities of reducing the number of males after first selection. The generation interval, already short in small ruminants (about four or five years compared to eight years in dairy cattle), will hardly decrease significantly. The last factor influencing genetic progress is the accuracy of genomic estimated breeding values (GEBV). GS should allow an increase in the genetic merit accuracy of candidates at birth by the knowledge of genomic information compared to the estimated breeding values (EBV) based only on pedigree. The quality of genomic predictions depends on the methods and evaluation models implemented but also on the characteristics of the reference population, i.e. genotyped progeny tested sires. These characteristics (size, accuracy of progeny test, kinship relationship within reference population, and with the population of candidates) result from the current breeding programs and from their effectiveness.

In France, several projects have allowed to establish reference populations for the main breeds of small dairy ruminants (4 in dairy sheep and 2 in dairy goats). We present in a first part the peculiarities of breeding programs of these breeds and the genetic characteristics of their reference populations that may impact on accuracy of genomic predictions. Then we discuss our recent studies to improve genomic evaluations in a single or multi-breed context. Finally, we give the fields yet to be explored to improve genomic evaluations, and describe changes under consideration in breeding programs of French small ruminants.

#### **Populations**

**Breeding programs.** In France, the majority of goat's and sheep's milk is processed into cheese of high quality under Protected Designation of Origin (PDO). The selection of dairy sheep has been implemented on the basis of local breeds. The largest is the Lacaune breed for the production of Roquefort cheese. The second population is located in the Western Pyrenees mountains and consists in 3 breeds: Blond-Faced Manech (Manech Tête Rousse: MTR) and Black-Faced Manech (Manech Tête Noire: MTN) and Basco-Béarnaise (BB). The Corsica breed, with the smallest breeding program, is not currently concerned by studies of genomic selection. In goats, breeding programs concern mainly two breeds, Alpine and Saanen, with a national geographical distribution. Purebred breeding programs of small dairy ruminants in France are based on a

pyramidal structure of populations with, at the bottom the production herds/flocks, and at the top the open nucleus herds/flocks. This part of the populations is the basis of genetic evaluations with official milk and pedigree recording. AI is mainly used in the nucleus, with fresh semen for sheep and frozen semen for goats. Breeders associations manage artificial insemination centers to raise young males, born from assortative matings in the nucleus, from weaning to the age at reproduction, and to organize their progeny test. The gene flow from the nucleus to the commercial herds/flocks is based partly on AI males and partly on natural mating males by sons of AI sires.

Breeding programs, set up in the sixties and seventies, are now fully efficient and are based on herds with official milk recording accounting for around 20% of the entire population for dairy sheep and 30% for goats (Table 1). For goats, sizes of breeding programs are similar in the two breeds, the number of herds and the AI rate (20% for population in official milk recording and 40% in nucleus herds) allow testing 40 bucks a year (Larroque et al., 2011). The dairy sheep breeding programs MTN and BB are similar to those of goats with respectively 30 and 50 rams progeny tested per year. Lacaune and MTR programs are of bigger scale with respectively 440 and 150 young rams progeny-tested each year, what amounts to size of French dairy cattle programs before beginning GS (Astruc et al., 2012). The use of fresh semen and seasonal reproduction force the sheep programs to use many rams, compared to the size of their females' population, which limits their dissemination as well as the accuracy of their progeny test based on only 30 to 40 daughters vs 80 in goats. The generation interval is around 6 years on the father-son pathway in goats and in MTN sheep vs only 4 years in Lacaune, MTR and BB dairy sheep.

Table 1 shows also results of a genetic diversity analysis based on pedigree of females born between 2006 and 2009 (Danchin at al., 2011). The pedigree depth is well known, from an equivalent generation number (EqG) of 5.52 in MTN to 9.9 in Lacaune. The Alpine, Lacaune and MTR breeds have the largest effective number of founders ( $f_e$ , from 162 to 191), showing a fairly high diversity of gene origin, while MTN and BB breeds have the lowest and the Saanen breed is in an intermediate situation. This ranking of genetic diversity remains the same for the realized effective population size (Ne) except for the Alpine breed with a Ne close to the Saanen one. The inbreeding coefficient for females born in 2009 in these populations is highest in the MTN breed (around 2.8%). With a similar number of equivalent generations of 7.86, the Holstein dairy cattle breed in France has an effective number of founders of 20.7, an effective population size of 62 and an inbreeding coefficient for females born in 2007 close to 4.3% (Danchin et al., 2009).

**Structure of the reference populations**. The availability, in 2009 for sheep and in 2011 for goats, of a SNP50 Bead-Chip (Illumina Inc., San Diego, CA) allowed the start of GS studies by constituting reference populations. Table 2 describes the populations of genotyped males. The effort focused on genotyping the latest progenytested cohorts with for example 77% of rams born between

2003 and 2009 in Lacaune breed and 94% of bucks born between 2001 and 2009 in Alpine breed. In addition, in goats, 1175 Alpine females and 810 Saanen females born in 2008 and 2009 were also genotyped as part of a program to detect quantitative trait loci (QTL).

Based on these genotypes, linkage disequilibrium (LD) was estimated because of its influence on the expected accuracy of genomic predictions (Baloche et al., 2013, Carillier at al., 2013). Due to accumulation of chromosomal recombination in time, LD at small distances depends on the effective population size several generations ago while the LD at long distances reflects the recent history of the population (Hayes et al. 2003). For our populations, the LD was estimated using the square of the correlation coefficient ( $r^2$ ) of Hill and Robertson (1968), by calculating the correlation between all pairs of SNPs on 10Mbp within each chromosome. These  $r^2$  were then averaged by intervals of 0.02Mbp between markers.

Figure 1 shows the LD calculated up to a distance of 2 Mbp between markers, for the Lacaune sheep breed and the Alpine and Saanen goat breeds (separately or together), and for a fictitious population with an effective population size of 1,000. The LD decreases with increasing the distance between markers and becomes constant beyond 1.2 Mbp. For goats, LD estimated for the two separate breeds is close, while it is lower for the blended population. At 0.05 Mbp (i.e. the average distance between two SNPs) the estimated LD in our different populations is equivalent: 0.12, 0.13 and 0.15 respectively in Lacaune, MTR and BB or MTN breeds; 0.17 in Alpine or Saanen breed and 0.14 in the blended goat population. But it remains lower than the one estimated in Holstein dairy cattle populations (0.26 at 0.07 Mbp in France, Hozé et al., 2013).

In comparison with the decay of LD for a population of Ne=1,000, the r<sup>2</sup> calculated in our populations is lower for small intervals between SNPs and larger for large intervals, indicating that these breeds showed high genetic diversity many generations ago and that selection has led to increase the LD recently. In Lacaune, this selection began with the definition of a standard Lacaune after pooling several small local breeds. In goats, the difference in LD extent between the multi-breed and single breed populations increases with the distance between markers. For small distances, this level of r<sup>2</sup> is due to the common origin of the two breeds, introduced in France in the 1910s and then extensively crossbred, while r<sup>2</sup> at large distances reflects separated selection schemes for each breed over the last 40 years.

In order to estimate the possibility of blending breeds with small sizes of the reference population, the persistence of LD phases across breeds was also examined by correlation of signed values of r between breeds. Between Alpine and Saanen breeds, this correlation ranges from 0.88 to 0.56 for distances 0-0.05 Mbp. It is close to the one between breeds relatively near genetically (0.68 between MTR and MTN breeds from 0.01 to 0.05Mbp). At larger distance, it decreases rapidly to reach a level of 0.08 (at 0.6 Mbp) close to the one between Lacaune and MTN breeds (0.09) genetically distant. This illustrates the proximity of the two goat breeds many generations ago and their most recent management into separate breeds. In goats, it was considered that this moderate correlation at 0.05 Mbp did not rule out the potential of genomic prediction across breeds given the small size of the reference populations. For MTR and MTN breeds Legarra et al. (2014) shows that these two breeds are closer to Spanish sheep populations Latxa Cara Rubia (LCR, for MTR) and Latxa Cara Negra Navarra (LCNNAF, for MTN) due to their geographical proximity and frequent exchanges.

Overall, extent of LD in our populations does not seem very favorable to genomic selection as well as the persistence of LD phases between breeds. Based on the characteristics of populations two types of situations seem to be emerging. First of all, breeding programs with relatively large size of reference population (close to those of some French medium-sized dairy cattle breeds) but with lower inbreeding coefficient and extent of LD, and a more limited accuracy of males' EBV after progeny test. This is the case of MTR and Lacaune breeds for which the relevance of a genomic selection program must be evaluated directly in a single-breed approach. The other breeding programs have a much smaller size of reference population, but also somewhat higher rates of inbreeding and small effective population sizes. We can also emphasize goats' breeding programs with a very accurate progeny test of bucks, and the BB's breeding program with a shorter generation interval and a higher rate of AI compared to MTN breed. For some of these smaller breeding programs a multi-breed approach seems relevant to assess when breeds are genetically close.

#### Improvement of genomic predictions quality

The results of French GS studies presented here concern four milk production traits calculated on a total lactation basis (provided by a part-lactation sampling design in sheep): milk yield (MY, h<sup>2</sup>=0.3 in both species), fat content (FC, h<sup>2</sup>=0.35 in sheep and 0.50 in goats), protein content (PC, h<sup>2</sup>=0.45 in sheep and 0.50 in goats) and somatic cell scores (SCS, h<sup>2</sup>=0.13 in Lacaune breed and 0.20 in goat breeds), and also two type traits common of both species: teat angle (TA, h<sup>2</sup>=0.33 in Lacaune breed and 0.31 in goats) and udder depth (UD, h<sup>2</sup>=0.19 in Lacaune and 0.29 in goats). The quality of predictions is assessed using a validation by splitting the population of genotyped and progeny-tested males in two sets: the training set with the oldest males and the validation set with youngest males (Table 2). A classical genetic evaluation and a genomic evaluation are performed on a subset of performances recorded before the birth of progeny-test daughters of validation's males. The quality of predictions is assessed on the validation population's males by comparing their GEBV estimated before recording performances of daughters, with their "pseudo-performances", i.e. daughter yield deviations (DYD, equal to the average performance of their daughters previously adjusted for the environmental effects and the genetic level of the dams). Two parameters are particularly considered: coefficients of Pearson correlation for reliability, and regression coefficients (slopes) of DYDs on sires' GEBVs for bias estimation.

**Single breed context.** The first studies were carried out in the breeds with the largest reference population (Lacaune and MTR) in a single-breed context with a genomic BLUP (GBLUP) using a two-step approach (Astruc et al., 2012 and Barillet et al., 2012). In the first step, DYDs of males of the reference population were computed and in the second step a genomic evaluation was performed on these DYDs.

Correlations between EBVs (or GEBVs) and DYDs for validation rams are presented in Table 3 for MY, FC, PC and SCS. They are always higher with GEBV ranging from 0.37 for FC in MTR breed to 0.57 for PC in Lacaune breed. These correlations show that GEBVs are better predictors of DYD than the EBVs based on phenotypes and pedigree data only. Correlations with GEBVs are higher in Lacaune breed for the three common traits but the gain in accuracy is higher for the MTR breed for milk yield. Regression coefficients for milk yield and SCS in Lacaune breed are quite different from 1 indicating an overdispersion of young rams GEBVs' (not shown). In comparison with the French dairy cattle breeds (Fritz et al., 2010), the level of correlation is low regarding the Holstein's results (0.60 for MY) but of the same order than Normande and Montbeliard breeds' results (0.36 and 0.47 for MY respectively). Nevertheless, the gain of reliability provided by molecular information is low in sheep breeds (0.07 and 0.11 for MY in Lacaune and MTR breeds respectively), compared with the gains in dairy cattle (0.27,0.17 and 0.15 for Hosltein, Montbéliarde and Normande breeds respectively). These small gains in reliability led us to explore other approaches for estimating GEBV.

Duchemin et al. (2012) compared the reliability of DYDs' predictions in Lacaune breed obtained according to three models (markers only, infinitesimal only and joint estimation of markers and infinitesimal effects) and four methods (BLUP, Bayes  $C_{\pi}$ , partial least squares (PLS), and sparse PLS (SPLS)). Based on correlations between GEBV and DYDs for validation rams, all methods showed a higher quality of prediction than BLUP method. No difference was found between the GBLUP, the PLS and the SPLS methods. The method Bayes  $C_{\pi}$  gave slightly better predictions than the others (0.44 vs 0.42 for MY in Bayes  $C_{\pi}$  and GBLUP, PLS or SPLS respectively). With this method the model including infinitesimal effects with estimated  $\pi$  gave slightly more accurate predictions for SCS. The inclusion of infinitesimal effects yields regression coefficients closer to 1. The method Bayes  $C_{\pi}$  thus provides best prediction accuracies, but is very time consuming compared with other methods, including GBLUP, for a relatively small gain.

Recently Baloche et al. (2013), still in Lacaune breed, have compared three BLUP-like models: 1) a pseudo-BLUP where phenotypes are DYDs of rams and the pedigree-based relationship matrix included all rams genotyped and non-genotyped; 2) a pseudo-ssGBLUP (pseudo single-step GBLUP) model same as above, but introducing a combined pedigree and genomic relationship matrix across rams (therefore all rams were included, regardless of whether they are genotyped or not); 3) a single-step GBLUP (ssGBLUP) model where phenotypes were directly the observed performances of sheep, and which includes fixed environmental effects as well as a random permanent environmental effect. For the two genomic models, correlations between GEBVs and DYDs are higher than in the two-step approach, around 0.6-0.7 except for MY (0.45) (Table 4). Compared to the pseudo-ssGBLUP, correlations with ssGBLUP GEBVs are slightly better. Moreover, except for SCS, ssGBLUP improves slopes (results not shown). The ssGBLUP takes into account information from dams of candidates, which is not the case with pseudo-ssGBLUP approach, and can increase quality of prediction. However, the slopes still not equal to 1.

Legarra et al. (2014) have also recently shown that pseudo-ssGBLUP approach is appropriate in the case of very small reference populations as the BB breed. Indeed, a two-step approach with only 194 males genotyped (for 656 non-genotyped) would not be better than a prediction based on pedigree. This study shows for this breed an improvement of reliability for MY from 0.41 on the basis of pedigree to 0.46 with genomic data. This result is probably due to a progeny testing well organized and a closed population, so that the candidates for selection have information from almost all parents.

Multi-breed context. In goats, given the small size of the reference population in each breed, studies began with a multi-breed genomic evaluation using a two-step approach applied to a GBLUP model (Carillier et al., 2013). Correlations between GEBVs and DYDs estimated in the validation population ranged from 0.32 for SCS to 0.53 for FC (Table 3). These levels of correlations, lower than in French Holstein dairy cattle breed, are similar to those of the MTR sheep breed and Normande dairy cattle breed, with equivalent reference population sizes. However, the results for SCS and type traits (compared to the Normande breed) are lower. Relative gains in reliability using genomic information are lower for milk production traits (from 3% for PC to 8% for FC) than for type traits, and are much lower than those of other species. This can be explained by a higher accuracy based on ascendance with a large number of daughters by sire (388 on average). The regression coefficients range from 0.73 to 0.96 and are higher than 0.90 for PC, FC and type traits indicating that bias is low for these traits (not shown). In this study, model accuracy of young bucks' candidates range from 52% to 56%, by also including genotypes of 1985 females. These accuracies are smaller than the ones derived from ascendance (0.62 for MY in average). This study also showed that inclusion of females' genotypes increases the accuracy of young candidates, especially in the goats' context with lack of preferential treatment. However, being daughters of only 20 sires, the genetic diversity between these females is not representative of the whole population and cannot be sufficient to greatly improve the accuracy of young candidates.

Low accuracies of GEBVs observed for young candidates and questions about adequacy of genomic multibreed evaluation for these breeds led us to explore other evaluation models. Thus, a one-step approach was tested by comparing three models (Carillier et al., 2014a and 2014b): a multi-breed model blending the two breeds together, a per-breed model, and a multi-trait model considering each trait in a breed correlated to a similar one in the other breed. correlation being estimated or set to 0 or 0.9. The coefficients of Pearson correlations between GEBVs and DYDs (Table 4) for validation males range from 0.43 (for MY) to 0.70 (for PC). Whatever the evaluation model, correlations are very close, those of per-breed model being slightly higher in some cases. In the multi-trait model the different correlations used have no impact on the accuracy correlations coefficients. The use of a single-step approach instead of a two-step one increases the correlations regardless of the traits. The best regression coefficients are obtained with the per-breed model. In the multi-trait model using a correlation of 0.99 improves the bias except for PC (and rear udder attachment). However, in all cases regression coefficients are not as good as in the two-step approach. Model accuracies for young bucks candidates are in all cases, and especially with the multi-breed model, higher than those derived from ascendance (from +28% for type traits and SCS to 37% for MY) and then higher than those obtained in the two-step approach.

Legarra et al. (2014) have extended the pseudossGBLUP approach to a multi-trait model blending MTR and LCR dairy sheep breeds on one hand, and MTN and LCNNAF breeds on the other hand with a genetic correlation of 0.95 (sameness) or estimated. The genetic correlation for MY was estimated at 0.5 between MTR and LCR, and at 0.3 between MTN and LCNNAF. The level of correlation in the multi-trait model does not change the results of predictions. For MTR and LCR breeds, predictions are not modified compared with a single-breed model. But, predictions are slightly improved for MTN and LCNNAF breeds, what was not expected in view of their connections.

#### **Discussion - Conclusion**

The results of the first studies in small dairy ruminants in France show that the reliability of genomic evaluations is not as high as for large breeds of dairy cattle. This can be linked with a smaller size of reference population and a lower level of LD with similar SNPs chip density, and for sheep a lower accuracy of progeny testing which leads to a less precise reference population. However, these results are similar to those obtained in dairy cattle breeds with smaller reference populations like the Montbéliarde or Normande breeds. They also show that the small size of the reference population may be balanced by a greater accuracy of progeny testing in the case of goats, or a larger inbreeding and a smaller effective population size in the case of BB sheep breed but also in Saanen's goats breed.

Clearly the single-step GBLUP approach seems more efficient to obtain highest correlations between DYDs and GEBVs because it takes into account information from dams of candidates, which is an asset for populations using partially AI. This approach also has the advantage of taking into account the selection and therefore to provide unbiased GEBVs. However, in this approach the regression coefficients of DYDs on GEBVs are often lower than 1 which leads to an overdispersion of young candidates compared to the oldest. Studies are ongoing to improve these coefficients. This approach should also be improved by taking into account the heterogeneity of variance primarily related to herd's effects and which are integrated into the current genetic evaluation model, but not in ssGBLUP. Finally, approaches combining knowledge of major genes and polygenic effects are to be developed in the future for goats, for whom genes with major effects for milk production traits (DGAT1 / caseins) were highlighted (Carillier et al., 2014a).

The multi-breed approach does not seem to give good results in sheep. Pooling MTR and LCR breeds in a multiple trait model does not improve reliability of their genomic evaluations. Indeed, the MTR breed already has a relatively large size of reference population. For the LCR breed, with a small reference population (148 genotyped rams), this can indicate that a lack of intensive crossbreeding and/or of common major genes can be a brake in the interest of the multi-breed approach (Legarra et al., 2014). In goats, multi-breed and per-breed models give equivalent reliability results in each of the two breeds except for FC (highest with a per-breed model in both breeds). Whatever the model, reliability of predictions are higher in Saanen breed than in Alpine breed, with slopes closer to 1, which can be explained by a higher inbreeding and a smaller effective population size. On the other hand in the multi-breed approach, GEBVs' accuracies of young candidates are higher than in a per-breed one, what is an advantage for this model besides easy to implement and less costly in computing time than the multiple trait model.

The current MTR and Alpine breeding programs were modeled, optimized and compared with alternative genomic breeding programs by Shumbusho et al. (2013). The comparisons were based on the annual genetic gain (AGG) for a dairy trait with heritability of 0.30 and after 10 generations of selection. In dairy breeds, genomic breeding programs outperformed conventional breeding programs when size of reference population exceeded 1,000 individuals with their own phenotypes. It was especially true when progeny testing was eliminated, the benefits of short generation interval being greater than the losses in accuracy. A reference population size of 2,000 individuals gave the best genomic scenario with an increase of AGG by 51.7% in MTR breed and 26.2% in Alpine breed compared to the current optimized breeding programs. In Lacaune breed, first results of a GS experiment (Baloche et al., 2014) have confirmed the superiority of genomic rams compared to conventional ones (0.52 total merit index standard deviation) after a genomic preselection of around one third. This could induce a culling pressure of 24% compared to the 48% for conventional rams, at the arrival of performances of their first daughters. In addition and in agreement, with a genomic selection pressure of 0.3 of young rams at 3 month old (completed by a selection rate of 0.8 after progeny-test results), Buisson et al. (2014) showed that a Lacaune genomic breeding program was economically balanced with an annual genetic gain increased by 15%.

In view of these early works, several situations seem to be emerging for the future in genomic selection of French small dairy ruminants. For the Lacaune breed a GS in purebred is envisaged with a switch programmed by breeders' organizations in 2015 held up by a reference population of 4,841 rams in 2013. For Pyrenean sheep breeds, switching to GS purebred in the near future is also considered. This seems coherent in MTR breed with a reliability of predictions of the same order than in Lacaune breed (and a reference population reaching 1,424 rams in 2013). The effectiveness of GS is more questionable for BB and MTN breeds. However, the BB breed with a very efficient breeding program has carried on its efforts with additional genotyping rams, bringing to 509 the reference population. In addition for these breeds, because of the use of fresh semen and the high costs of performances recording and AI, breeding programs require a lot of organization. Genomic selection is then a possibility to reduce the complexity of these breeding programs and the number of rams in selection centers through the elimination of progeny testing and a faster turnover of rams. In goats, clearly the single-step GBLUP method combined with a multi-breed approach provides opportunities for GS. However, the presence of major genes in this species also suggests that other genomic models should be explored.

#### Acknowledgements

Authors thanks the French Genovicap and Phenofinlait programs (ANR, Apis-Gène, CASDAR, FranceAgriMer, France Génétique Élevage and French ministry of agriculture), the European 3SR project, the French sheep programs SheepSNPQTL (ANR and Apis-Gène), Roquefort'In (Agrimip innovation/FUI, FEDER, CR Midi-Pyrénées region, CG Aveyron and Tarn, Communauté d'Agglomération du grand Rodez), GENOMIA (POCTEFA/FEDER, CG 64, CR Aquitaine), DEGERAM (FNAD, FEDER, CR Midi-Pyrénées, Auvergne et Limousin) that have founded the cited studies.

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# Table 1. Characteristics of French dairy small ruminants' breeding programs

Breeds <sup>*</sup>	ALP	SAA	LAC	MTR	MTN	BB
No <sup>a</sup> females	159,000	108,000	170,000	76,000	13,000	24,000
%No <sup>b</sup> females	30	30	19	29	16	32
%AI <sup>c</sup>	20	20	85	50	45	50
No <sup>d</sup> males PT	40	35	440	150	30	50
No <sup>e</sup> daughters PT	80	80	40	40	40	40
Generation interval	5.59	5.61	4.09	4.48	5.62	4.3
$EqG^{ m f}$	7.81	6.34	9.90	7.61	5.52	6.13
$fe^{g}$	191	124	190	162	73	102
Ne <sup>h</sup>	143	120	227	174	89	112

\*ALP=Alpine; SAA=Saanen; LAC=Lacaune; MTR: Manech Tête Rousse ; MTN=Manech Tête Noire ; BB=Basco-Béarnaise.

<sup>a</sup>: females in official milk recording; <sup>b</sup>: percentage of females in official milk recording compared to the entire population; <sup>c</sup>: rate of artificial insemination; <sup>d</sup>: males progeny tested each year; <sup>e</sup>: females of the progeny test by male; <sup>f</sup>: equivalent generation number; <sup>g</sup>: effective number of founders; <sup>h</sup>: effective population size.

#### **Table 2. Reference populations**

	No genotyped	Training	set	Validation set	
		Birth year	No	Birth year	No
ALP	470	1993-2005	236	2006-2009	148
SAA	355	1993-2005	194	2006-2009	99
LAC	2,887	1999-2005	1593	2008-2009	592 <sup>*</sup>
		1999-2005	1593	2007-2008	681**
MTR	1,295	1990-2006	1002	2007-2008	293
MTN	362	1990-2006	306	2007-2008	56
BB	281	1990-2005	194	2006-2007	87

\* : Baloche et al. (2013); \*\*: Astruc et al. (2012)

Table 3. Pearson correlations between DYD and EBV orGEBV (two-step approach of GBLUP).

LAC E	DYD*EBV DYD*GEBV	0.35 0.42	0.44	0.52		TA	UD
E	DYD*GEBV	0.42					
			0.50	0.57	~		
G	Gain			0.57	0.45		
		0.07	0.06	0.05	0.06		
MTR D	DYD*EBV	0.27	0.32	0.43			
Ľ	DYD*GEBV	0.38	0.37	0.48			
G	Gain	0.11	0.05	0.05			
ALP+SAA D	DYD*EBV	0.37	0.50	0.50	0.31	0.32	0.30
Ľ	DYD*GEBV	0.39	0.53	0.52	0.32	0.35	0.37
G	Gain	0.02	0.03	0.02	0.01	0.03	0.07

\*: MY= milk yield; FC=Fat content; PC=protein content; SCS= somatic cell score; TA=teat angle; UD=udder depth; ALP=Alpine; SAA=Saanen; LAC=Lacaune; MTR: Manech Tête Rousse.

Table 4. Genomic accuracies obtained with pseudo single step GBLUP (pss-GBLUP) or single-step GBLUP (ssGBLUP) approaches.

Breeds <sup>*</sup>	Traits <sup>**</sup>	MY	FC	PC	SCS	TA	UD
LAC <sup>1</sup>	pss-BLUP	0.32	0.58	0.54	0.49	0.47	0.47
	pss-GBLUP	0.43	0.65	0.62	0.59	0.58	0.57
	ss-GBLUP	0.47	0.71	0.70	0.59	0.66	0.61
	BLUP <sup>3</sup>	0.37	0.50	0.50	0.31	0.32	0.30
ALP+SAA <sup>2</sup>	ss-GBLUP	0.43	0.61	0.70	0.47	0.61	0.59
		0.43	0.63	0.69	0.47	0.59	0.59
	per breed						
<sup>1</sup> : standardized accuracies (Baloche et al. 2013): <sup>2</sup> : Pearson correlations							lations

<sup>1</sup>: standardized accuracies (Baloche et al., 2013); <sup>2</sup>: Pearson correlations between DYD and EBV or GEBV (Carillier at al., 2014a and 2014b); <sup>3</sup>: BLUP with the two-step approach.

\*: ALP=Alpine; SAA=Saanen; LAC=Lacaune.

\*\*: MY= milk yield; FC=Fat content; PC=protein content; SCS= somatic cell score; TA=teat angle; UD=udder depth.



