SMARTER

SMAll RuminanTs breeding for Efficiency and Resilience

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About the SMARTER research project

SMARTER will develop and deploy innovative strategies to improve Resilience and Efficiency (R&E) related traits in sheep and goats. SMARTER will find these strategies by: i) generating and validating novel R&E related traits at a phenotypic and genetic level ii) improving and developing new genome-based solutions and tools relevant for the data structure and size of small ruminant populations, iii) establishing new breeding and selection strategies for various breeds and environments that consider R&E traits.

SMARTER with help from stakeholders chose several key R&E traits including feed efficiency, health (resistance to disease, survival) and welfare. Experimental populations will be used to identify and dissect new predictors of these R&E traits and the trade-off between animal ability to overcome external challenges. SMARTER will estimate the underlying genetic and genomic variability governing these R&E related traits. This variability will be related to performance in different environments including genotype-by-environment interactions (conventional, agro-ecological and organic systems) in commercial populations. The outcome will be accurate genomic predictions for R&E traits in different environments across different breeds and populations. SMARTER will also create a new cooperative European and international initiative that will use genomic selection across countries. This initiative will make selection for R&E traits faster and more efficient. SMARTER will also characterize the phenotype and genome of traditional and underutilized breeds. Finally, SMARTER will propose new breeding strategies that utilise R&E traits and trade-offs and balance economic, social and environmental challenges.

The overall impact of the multi-actor SMARTER project will be ready-to-use effective and efficient tools to make small ruminant production resilient through improved profitability and efficiency.

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1 Summary

One of the major ambitions of WP6 was to perform the first across-country genomic evaluations in small ruminants, through 3 case-studies covering dairy sheep, meat sheep and dairy goats. For that we estimated the (co)variance components and calculated genetic correlations across countries where possible. In addition, we characterized the populations (dairy sheep and goats) using genotypes.

In meat sheep, we combined pedigree and phenotypes (live-weight, fat depth and muscle depth) of Texel, Suffolk and Charollais breeds from Ireland and the UK. In dairy sheep, we combined pedigree, phenotypes (milk yield) and genotypes of Latxa (blond – LCR - and black – LCN - strains) and Manech (blond – MTR - and black – MTN - strains) breeds from Spain and France, respectively. Finally in dairy goats, we pooled pedigree, phenotypes (milk yield, fat and protein yield and content, udder traits) and genotypes of Alpine and Saanen breeds from Canada, France, Italy and Switzerland.

Different methods for assessing the proximity of the populations were used. In dairy sheep, a PCA revealed a clear overlap of MTR and LCR with a smaller overlap between MTN and LCN. In goats, the overlap is important between France and Italy (whatever the breed), but to a lesser extent between French, Italian and Swiss Alpine; the Canadian populations are clearly separate from the European ones.

Animal models were run where each country represented a different trait, and the model used was that used in the routine genetic evaluation. Most of the genetic correlations were estimable and were stronger than 0.7 with some exceptions. However, covariance could not be properly estimated between some populations and were not consistent across analyses for milk yield in goats. In dairy sheep, the estimated genetic correlations were approximately 0.7, both in blond strains (MTN x LCR) and in black strains (MTN x LCN). This is sufficiently strong to justify an across country evaluation In meat sheep, the correlations, estimated in the Texel breeds, were stronger than 0.8 for Irish pre-weaning weight and British early-life weight (0.82), scan weight (0.88), muscle depth (0.85) and fat depth (0.85). The weak correlation between Irish weaning weight and British early-life weight (0.38) indicates that both traits are different. In goats, the genetic correlations were strong for the udder traits. For example, they were above 0.75 for rear udder attachment (in Saanen: 0.95 between Canada and France; 0.90 between Italy and Canada; 0.84 between France and Italy). Including genomic information had minimal effect on the estimated genetic correlations between populations.

Even if these results are encouraging for running routinely international evaluations, several limitations were identified: first, the question of the harmonization of the phenotypes is important. This is especially true for milk yield in goats with different ways of calculating the lactation yield. Second, exchanges (at least in dairy sheep) in germplasm was sometimes just unidirectional, and exchanges in both ways might strengthen the connection across countries. Third, in some cases, the size of the populations were very unbalanced.

However, strong genetic correlations estimated between two countries in most cases warrants possible benefits from a joint genetic evaluation. This also indicates that limited re-ranking of sires would be expected between countries.

2 Introduction

Selection in small ruminants is generally based on smaller breeding programs than that for cattle. The selection tools are not used as intensely as in cattle because of their cost (performance recording, especially milk recording in dairy small ruminants) compared to the gross margin per animal and because of physiological limits. Moreover, the usage of AI is less in small ruminants with fresh semen being preferred over frozen; this all limits the international exchange of germplasm to create genetic linkages. Genomics coupled with trait harmonisation and international cooperation may be one strategy to accelerate genetic progress in small ruminant populations. Even if some of the sheep and goat breeds are more or less exclusively local breeds, some of them are bred in several countries, including international breeds, such as the Alpine and Saanen goat breed, the Lacaune or Assaf dairy sheep breed as well as some terminal sire breeds in meat sheep (eg., Texel, Suffolk). Consequently it was important to study the feasibility of an international evaluation in sheep and goats as a means of increasing both the accuracy of selection but also possibly the selection intensity (as well as available genetic variability). This should translate to accelerated genetic gain.

Such across-country genetic evaluations were implemented in SMARTER on existing traits as a proof of concept for future efficiency and resilience traits. The purpose was to build the pipelines and estimate the parameters needed for such evaluation and to assess if the level of connectedness of the populations (genealogical connection across countries and characterization of the populations with SNP information) was sufficient to run the evaluation and to estimate the genetic correlations across-country. The different across country genetic evaluations implemented in SMARTER are presented in the MS26:

-in meat sheep, an international evaluation of early life weight, scan weight, muscle depth, fat depth (efficiency-related trait) involving Texel, Suffolk and Charollais from the UK and Ireland;

-in dairy sheep, an international evaluation of milk yield involving Red-Faced and Black-Faced Manech from France and Blond-Faced and Black-Faced Latxa from Spain (Manech and Latxa being two different names representing similar strains across the border.

-in goats, an international evaluation of milk yield (efficiency-related trait) and udder traits (efficiency-related trait) involving Alpine and Saanen from Canada, Italy, France and Switzerland.

The work presented in this deliverable is related to the estimation of the variance/covariance components of the three above case-studies.

4 articles are attached in the appendices:

-paper submitted in the Journal of Dairy Science Communications (dairy sheep). See Appendix section 7.1 : “High genetic correlation for milk yield across Manech and Latxa dairy sheep from France and Spain” by Garcia-Baccino et al.

-paper accepted in the Journal of Animal Breeding and Genetics (meat sheep). See Appendix section 7.2 : “Across-country genetic evaluation of meat sheep from Ireland and the UK” by Fitzmaurice et al.,

-paper submitted in Frontiers (goats). See Appendix section 7.3 : “Genetic Characterization and Population Connectedness of North American and European Dairy Goats” by Teissier et al.

-paper to be submitted very soon in the Journal of Dairy Science Communications (goats). See Appendix section 7.4 : “Genetic parameters across four countries in Alpine and Saanen goat breeds for milk production and type traits” by Teissier et al.

3 Conclusion

Thanks to the preliminary work achieved since the start of SMARTER (Task 6.1 and part of the task 6.2), it has been possible to pool data from different countries, using common file format and based on signed agreement, and to track the same animals presents in pedigree files form different countries.

For each putative same trait (e.g. “milk yield”, “fat depth”, “rear udder attachment”), the genetic covariance and the genetic correlation were estimated using two-trait models (each country was considered a different a trait).

In dairy sheep, the genetic correlations for milk yield were estimated at 0.7 both in the Red-Faced Manech x Blond-Faced Latxa and in the Black-Faced Manech x Black-Faced Latxa analyses.

In meat sheep, the genetic correlations between the UK and Ireland were estimated at 0.82 for pre-weaning weight (Ireland) and early-life weight (UK), 0.88 for scan weight, 0.85 for muscle depth and 0.85 for fat depth. But the genetic correlation was only 0.38 for weaning weight (Ireland) and early-life weight (UK) showing that both traits are not the same, probably because they correspond to different ages.

In goats, the genetic correlations are comprised between 0.76 and 0.95 for udder traits (example of rear udder attachment) depending of the countries. However, the covariance components could not be estimated with a sufficient level of accuracy for milk yield. Moreover the different estimations were not consistent according to the model and method.

When estimable, the genetic correlations appear sufficient for running an international evaluation, but not as high as found in cattle. For example, the genetic correlations for milk yield in cattle ranged (run of December 2021 in Interbull) from 0.67 for New Zealand to 0.84 for Canada (average of genetic correlations with other countries) with a general average of 0.79 (https://interbull.org/ib/maceev_archive).

As a result, across-country evaluation is feasible in most cases. When the genetic correlations are either too weak or not estimable, work of the harmonisation of the trait is required. In the goat case, improved connectedness should improve the correlation for milk yield. This is an incentive for harmonisation of the traits. This highlight the interest for harmonising novel resilience and efficiency traits through the recommendations that are due within the task 6.1.

4 Deviations or delays

The deliverable should initially be submitted on 31 October 2021. As the case-studies on across country evaluation were undertaken mostly in 2021, the publications on variance components were not submitted for the deadline. This explains the two months delay.

5 Acknowledgements

All the people working on the case studies have participated in this collaborative work. However, we may express a special thanks to those who were the linchpin for this work, and most of all to Carolina Garcia-Baccino, Marc Teissier and Shauna Fitzmaurice who estimated the variance components.

6 References

Not applicable

7 Appendix

7.1 Paper “High genetic correlation for milk yield across Manech and Latxa dairy sheep from France and Spain” submitted to Journal of Dairy Science Communications the 1st of December 2021

Temporary manuscript number: JDSC.2021-0195

Title: High genetic correlation for milk yield across Manech and Latxa dairy sheep from France and Spain.

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Submitted article inserted below

HIGH GENETIC CORRELATION FOR MILK YIELD ACROSS MANECH AND LATXA DAIRY SHEEP FROM FRANCE AND SPAIN

Short running title: genetic correlation across dairy sheep breeds

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ABSTRACT

Spanish Latxa and French Manech are dairy sheep breeds which split into Blond (Latxa Cara Rubia -LCR, Manech Tête Rousse -MTR) and Black (Latxa Cara Negra of Navarre –LCN, Manech Tête Noire – MTN) strains. Exchange of genetic material (AI doses) is more and more frequent across breeds, within color, in order to boost genomic precision from a larger reference population and genetic progress from a larger selection base. However, additional gains can only be achieved if the selected traits are genetically similar across countries. In this work we pool across-country, within-color records, pedigree and markers to estimate the genetic correlation across breeds for milk yield. The number of animals with records oscillates from 65,000 (LCN) to 544,000 (MTR), whereas the number of connecting AI rams (with more than 10 daughters in the other country) is 381 MTR rams in LCR and 58 MTN rams in LCN. Blond strains had a stronger and more extended in time connection. The number of genotyped rams goes from 328 (LCN) to 4,901 (MTR). Description of the relatedness of populations was done by Principal Component Analysis (PCA) and Fst coefficients. The genetic correlation was estimated using two (one per color) two-trait models (each country a trait) by profile likelihood, using a grid search while fixing other variance components to within-population estimates.

Results showed a closer relationship of MTR and LCR, both by PCA and Fst (0.01 for Blond strains *vs.* 0.05 for Black strains). Genetic correlation estimates were of 0.70 in both cases. We expected a lower correlation for Black strains due to dominance and epistasis. Thus, we attribute the correlation not being 1 mostly to genotype by environment interaction, including on-farm management and trait modelling. We conclude that the correlation of 0.7 across populations is encouraging for future joint work of Latxa and Manech breeders.

MAIN BODY

Across population (or countries) genetic and genomic evaluations and later selection can lead to several benefits. These include a greater genetic progress across the two populations (Smith and Banos, 1991), a possible increase in reliability in particular for genomic predictions (Brøndum et al., 2011; Lund et al., 2011), and fairer choice of animals for breeders (Goddard, 1985).

The dairy sheep breeds Manech (in France) and Latxa (in Spain) have a common origin in the Western Pyrenees mountains and they are structured in different populations (strains or ecotypes), each with its own selection scheme (Legarra et al., 2014). Previous studies showed that pooling the data did not boost genomic accuracies, and also that “Blond” (Manech Tête Rousse - MTR, and Latxa Cara Rubia - LCR) strains were genetically very similar, with “Black” strains (Manech Tête Noire – MTN, and Latxa Cara Negra of Navarre - LCN) being less similar (Legarra et al., 2014). There is nevertheless a common interest in sharing data and of modifying the selection schemes towards selection across and within country. In fact, there had been recent exchanges of semen to explore the feasibility of joint evaluation and selection (Pineda-Quiroga et al., 2020). These changes are within “color”.

A key parameter for an across-population genetic evaluation is the correlation across breeding objectives (Smith and Banos, 1991), where a high correlation indicates that an extra genetic gain can be achieved in both populations. Of interest is also the correlation across countries of the individual traits *per se* (Karoui et al., 2012; Wientjes et al., 2017), because the traits, even named identically, may differ across countries, due to genotype-genotype, genotype-environment, and statistical and trait-definition considerations (Nilforooshan and Jorjani, 2021). A soft threshold for the joint evaluation to be of interest is an across-population genetic correlation of

0.7 (Mulder et al., 2006), although this is highly dependent on the structure of the breeding scheme.

This work presents estimates of the genetic correlation across countries for milk yield (MY), the most important trait in the breeding objective, separately for the “Blond” and “Black” strains of Latxa and Manech.

Essentially, we combined all data available for all four populations evaluation into two international evaluations: a “Blond” one (MTR and LCR) and a “Black” one (MTN and LCN). An extraction of all records available in the databases resulted in the data shown in Table 1. Most rams are AI rams, although there is some natural mating; the average number of daughters among rams with >10 daughters is roughly 50. Concerning volume of data, it can readily be seen that the “Blond” strains are more numerous than the “Black” ones and that Manech has more data than Latxa. However, the volume of data within breed is not relevant for the accuracy of across-countries correlation estimation.

Pedigree was quite complete, with 15% to 30% missing sires. To consider missing sires, metafounders were defined every 3 years, separately for Manech and Latxa, resulting in 10 for each within color. Pedigrees were joined within “color”. It was possible to do so as official identifications of Manech rams were kept when using them in Latxa.

The genealogical connection across countries is essential for accurate estimation of the correlation. Thanks to the recent exchanges, there are 381 MTR AI rams with more than 10 daughters in LCR (15 % of total AI males used in LCR), and 58 MTN rams with more than 10 daughters in LCN (7% of total AI males used in LCN). Most of these rams are genotyped.

These AI exchanges occurred in the vast majority after 2000 (for MTR and LCR) and after 2010 (for MTN and LCN). They only occurred in one direction: from France (Manech) to Spain (Latxa). In our files, there is no trace of a trade of live animals, which if occurs is very rare.

Finally, we also used genotypes. Manech animals were genotyped with the 50 k Illumina chip OvineSNP50, whereas Latxa animals had been genotyped with two chips: 50 k Illumina chip OvineSNP50 and Affymetrix Axiom Ovine Genotyping Array, in proportions roughly half and half. Editing and quality control of the genotypes is done nationally. After combining the two genotype files for a set of common markers across all four populations, this resulted in 22,827 SNP loci being used for the across-country estimation. The genotyped animals in Table 1 are all progeny-tested AI males. The genotyped young animals without offspring were simply discarded because they contribute no information.

Using genotypes, we empirically assessed the proximity of the different populations, visually using PCA and also using Fst differentiation coefficients. We ran animal models using all available data, where each country represents a different trait, and each country uses the model for its routine genetic evaluation. The models consider contemporary group, lambing season, age and litter size at each lactation. We ran regular REML (with pedigrees) and Single-Step GREML (with pedigrees + markers) but results were essentially the same and only Single-Step GREML results are shown.

The across-country correlations were estimated as follows. First, we estimated the within-population variance components. These are estimated with high precision as there is a large volume of data. Then, we fixed the within-population variance components to these estimates, and we ran a grid search for genetic correlations from 0 to 0.9, with a step of 0.1. For each of these correlations, the likelihood was computed using airemlf90 (Misztal et al., 2002) using a single iterate (OPTION maxrounds 0). In this manner we obtain a profile likelihood as a function of the genetic correlation. The estimate of the genetic correlation is the peak of this likelihood, and approximate standard errors were obtained from its curvature. Note that there is no residual or permanent environment correlation, because no female with record ever belongs to the two populations. Also, we obtained an *a priori* (in absence of data and only due to structure) estimate of the genetic correlation, using eq. (8) in (Legarra et al., 2021): $r \approx \frac{\sqrt{h^2}}{\sqrt{h^2+\frac{8F_{st}}{1-F_{st}}c^2}}$. We used estimates of $h^2 = 0.28$ and guesses of variance due to epistasis of c^2 =0.10.

Fst coefficients across MTN and LCN were 0.053, and across MTR and LCR were 0.014. This is as expected as the MTR originated from LCR in the past century, which is not the case for MTN and LCN which evolved in parallel (at least for the 20th century)and also because of the larger and older use of MTR in LCR than of MTN in LCN. The other Fst coefficients were 0.052 (LCN – LCR), 0.061 (LCN – MTR), 0.065 (MTN-LCR) and 0.072 (MTN – MTR). The PCA in Figure 1 shows a clear overlap of MTR and LCR, as expected; indeed, due to introductions, there are LCR AI rams that are offspring of MTR AI rams. The overlap between MTN and LCN was smaller, as these breeds had less exchange and, in particular, almost no AI rams of LCN are offspring of MTN rams, although many females are.

Within-breed estimated heritabilities were 0.28 (MTN and LCN) and 0.27 (MTR and LCR). Interestingly, repeatabilities differ, with ≈0.60 for both Manech and ≈0.40 for both Latxa. This is probably due to different treatment of first and later lactations, first for filtering in computation of MY, and later in the respective linear models.

Figure 2 shows the profile likelihoods of genetic correlations for both LCN-MTN and LCR-MTR. In both cases the estimated genetic correlation is 0.7. Respective asymptotic standard errors were 0.05 for “Black” and 0.03 for “Blond”. Milk Yield is computed in different ways, from lambing to 120 days in

Latxa, whereas in Manech it is computed from weaning until the end of lactation, and then scaled to a constant lactation length. However, we verified that applying both definitions of MY to the same test-day data set lead to a correlation of the two measures of MY of 0.95, so this does not explain the value of 0.7.

In addition, in presence of non-additive genetic correlation, we expected a higher value of genetic correlation for “Blond” than for “Black”, because “Blond” populations are closer genetically as shown by the PCA in Figure 1 and by the Fst coefficient. The *a priori* estimates using Fst coefficients yield estimates for the correlation of 0.98 (for blond strains) and 0.93 (for black strains). Again, these values do not fully explain the estimate of 0.7.

Thus, we speculate that most of the genetic correlation is due to genotype-environment interaction, including models used. Differences in models among countries reside in the manner of combining the elementary effects flock, age, and period in the model, and also in the effect number of lambs born, which is considered as an effect in Latxa but not in Manech. On top of this there could be some differences in farm management and climate.

All in all, the correlation of 0.7 across populations is encouraging for future joint work of Latxa and Manech breeders. New studies need to address the individual accuracy of across-population prediction, in particular for candidates to selection, and practicalities such as the optimal time frame for joint predictions (Weigel and Banos, 1997).

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NOTES

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	Records (milk yield)	Pedigree (N animals)	Rams with more than 10 daughters	Of which, genotyped rams	Animals with records for MY
MTR	1,973,609	573,501	6,432	4,901	543,929
LCR	431,692	153,765	996	716	144,993
MTN	518,226	158,055	1,233	846	146,132
LCN	197,081	68,830	459	328	65,060

Table 1: Descriptive of used for analyses. MTR: Manech Tête Rousse; LCR: Latxa Cara Rubia; MTN: Manech Tête Noire; LCN: Latxa Cara Negra.

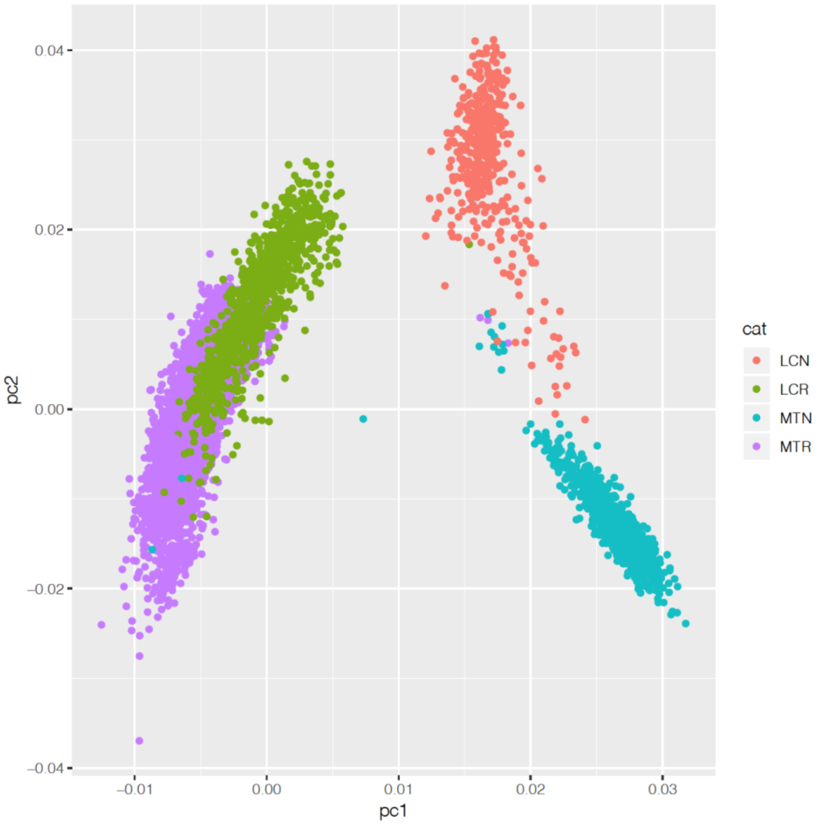

Figure 1: Principal components analysis showing Manech Tête Noire (MTN), Manech Tête Rousse (MTR), Latxa Cara Rubia (LCR) and Latxa Cara Negra (LCN).

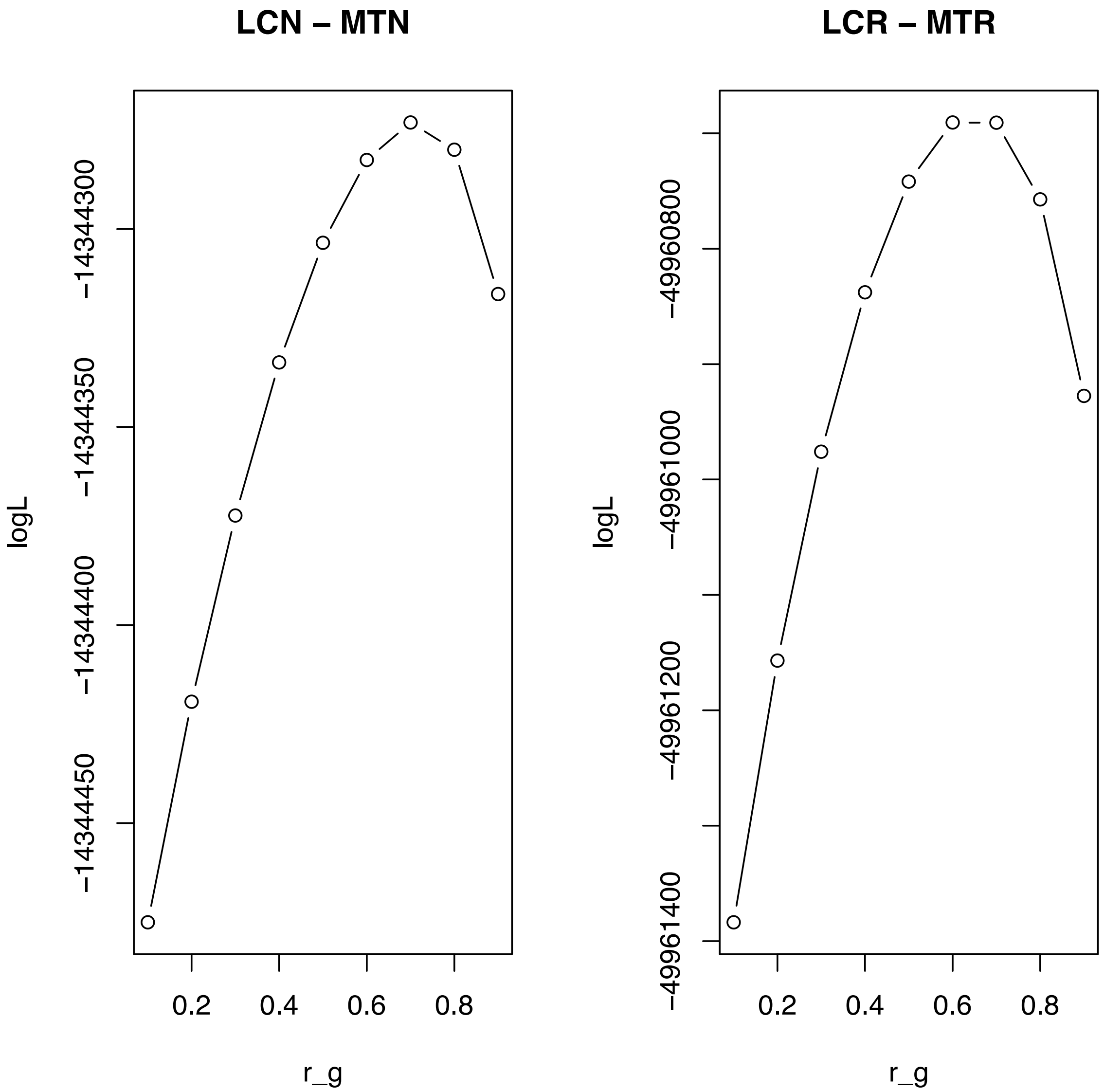

Figure 2: Profile log-likelihood of the genetic correlation (r_g) for Latxa Cara Negra -Manech Tête Noire (LCN-MTN) and Latxa Cara Rubia – Manech Tête Rousse (LCR-MTR)

7.2 Paper “Across-country genetic evaluation of meat sheep from Ireland and the UK” accepted in the Journal of Animal Breeding and Genetics

Title: Across-country genetic evaluation of meat sheep from Ireland and the UK

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Submitted article inserted below

Running head: Across-country sheep genetic evaluations

Across-country genetic evaluation of meat sheep from Ireland and the UK

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Abstract

Genetic evaluations in sheep have proven to be an effective way of increasing farm profitability. Much research has previously been conducted on producing within-country genetic evaluations, however, to date no across-country sheep genetic evaluations have been produced. The objective of the present study was to examine the feasibility of an across-country genetic evaluation of live body weight and carcass composition traits for Texel sheep raised in Ireland and the UK. The benefit of genetic selection based on across-country genetic evaluations, in comparison to within-country genetic evaluations, was also quantified. Animal traits included early-life and post-weaning live body weights, and muscle and fat depth ultra-sound measurements. Irish and UK data were combined, common animals were identified and a series of bivariate analyses were performed separately for each trait to produce across-country genetic evaluations. Fixed effects included contemporary group, age at first lambing of the dam, parity of the dam (Ireland), dam age at lamb's birth (UK), a gender by age of the lamb interaction, a birth type by rearing type of the lamb interaction and country of birth of the lamb. Random effects included the animal additive genetic, dam maternal, litter common environment and residual effect. The model for post-weaning weight, muscle depth and fat depth included only the animal additive genetic and litter common environmental random effects. Genetic correlations between the two countries ranged from 0.82 to 0.88 for the various traits. Across-country genetic evaluations were estimated for all animals and response to selection was predicted using the top 10 and top 20 sires in both within- and across-country analysis for the two countries. Overall, results showed that rates of genetic gain could potentially increase from between 2.59 and 19.63% from selection based on across-country genetic evaluations compared to within-country evaluations alone. Across-country evaluations are feasible and would be of significant benefit to both the Irish and UK sheep industries.

Key words: Across-country genetic evaluations, carcass composition, lamb growth, sheep

Introduction

Pedigree sheep breeding is an international activity with high levels of trade of breeding stock occurring between countries. Growth and carcass composition traits are of high economic importance worldwide (Cocks et al., 2002; Byrne et al., 2010) and genetic selection of these traits has led to substantial economic gains in the global sheep industry (Jones et al., 2004; Conington et al., 2004; Amer et al., 2007). International genetic evaluations will allow for across-country genetic selection of breeding stock. This will increase the rate of genetic gain achieved in comparison to within-country selection alone due to a higher selection intensity attained from the increased number of selection candidates (Banos and Smith, 1991; Smith and Banos, 1991; Lohuis and Dekkers, 1998). To date, no across-country genetic evaluations have been produced for sheep. On the contrary, across-country genetic evaluations have successfully been established for both beef and dairy cattle through the development of Interbeef (Interbeef, 2020) and Interbull (Interbull, 2020), respectively. Outcomes from these initiatives already inform selective breeding programmes in multiple countries worldwide.

In sheep, large amounts of performance recording have been undertaken particularly in pedigree flocks across Ireland (Sheep Ireland) and the UK (Agriculture and Horticulture Development Board - AHDB) resulting in a high volume of data being available particularly for live body weight and carcass composition traits measured on certain common breeds. Therefore, it could be of significant advantage to pool these data together into an across-country evaluation system to allow breeders to more accurately compare and select animals across-country.

The objective of the present study was to assess the feasibility of combining lamb live body weight and carcass phenotypic records and pedigree data from Ireland and the UK in order to develop an across-country genetic evaluation system for pedigree Texel sheep. An additional objective was to quantify the potential benefit of selection based on across-country genetic evaluations in comparison to within-country genetic evaluations.

Materials and Methods

Data

All data used in the present study were obtained from Sheep Ireland, the Irish national database (http://www.sheep.ie) and AHDB, the UK national Sheepbreeder database (https://ahdb.org.uk/beef-lamb). The study focused on purebred Texel lambs. Three live body weight traits, namely pre-weaning weight (20-65 days of age, 12-32 kg), weaning-weight (66-120 days, 20-55 kg) and post-weaning weight (121-180 days, 25-75 kg) and two carcass composition traits, namely muscle depth (121-180 days, 10-44 mm) and fat depth (121-180 days, 1-23 mm) from Ireland were examined. Similar traits were examined in the UK data including early-life body weight (40-85 days, 12-45 kg), post-weaning weight (121-180 days, 25-75 kg), muscle depth (121-180 days, 10-44 mm) and fat depth (121-180 days, 0.5-8 mm). In both cases, muscle and fat depth were assessed with ultrasound measurements.

Live body weight and carcass trait data records were available on 177,307 Irish and 521,244 UK lambs born between 2010 and 2017. A number of edits were applied to the two datasets. Average daily gain was calculated from live body weight records and only lambs with a daily live weight gain of between 100 and 650 g/day were retained for analysis. Live body weight and carcass composition trait records were discarded if sire, dam, maternal grandsire or flock of birth was unknown. For live body weight and carcass composition traits in the UK both the sire of the lamb and maternal grandsire of the lamb were required to have at least 5 progeny each. This was only applied to the UK data due to the high volume of data available and it allowed a more informative dataset to be created. Within the UK data, lamb records were discarded if dam age was unknown or aged >9 years. Similarly, within the Irish data dams with no known parity number or a parity number >10 were discarded. Both dam age (UK) and dam parity (Ireland) were subsequently categorised as 1,2,3,4, or ≥5. Age at first lambing was defined as the age of the ewe at her first lambing. In Ireland this was whether the dam first lambed down as a ewe lamb (8 to 18 months of age) or a hogget (18 to 28 months of age) whereas in the UK data this ranged from 1 to 3 years. Birth type was defined as the number of lambs born per lambing event; only lambs born with a birth type between 1 and 4 were retained for analysis. Rearing type was defined as the number of lambs reared per litter; only lambs with a rearing type of between 1 and 3 were retained for further analysis. Records from lambs that were artificially reared, reared by a non-genetic dam or born as a result of embryo transfer were discarded. For all traits, lambs were allocated to a contemporary group of flock-by-week of weighing. Contemporary groups were only retained for further analysis if they contained 5 or more records. Following all data edits described 33,371 early-life/pre-weaning weight records, 33,868 early-life/weaning weight records, 25,293 post-weaning weight records, 21,429 muscle depth records and 21,309 fat depth records remained across both countries (Table 1).

An international pedigree file was then produced for all animals in the original unedited dataset to allow all across-country links to be considered in the ensuing analyses. Breeding animals that had progeny with records in both Ireland and the UK were identified to confirm the presence of genetic links between the two countries. A total of 8,392 common ancestors were found, including 1,188 common sires.

Genetic Analysis

Combined data from Ireland and the UK were considered in a series of statistical analyses. Both carcass composition traits, namely muscle depth and fat depth, as well as post-weaning weight corresponded directly across the two countries. However, whilst the early-life body weight traits were similar in age range, they were not directly comparable between the two countries. Therefore, early-life weight as defined in the UK had to be combined separately with pre-weaning and weaning weight from Ireland. The following model was used for the statistical analyses:

$$\begin{aligned} Y = {} & CG + AFL + Parity + Dam\ age + Sex * Age + Birth\ type * Rearing\ type \\ & + Country + Animal + Dam + Litter + e \end{aligned}$$

Where Y = lamb live body weight or carcass composition record, CG=contemporary group of flock-by-week of weighing, AFL = age of the lamb's dam at first lambing, Parity = parity of the lamb's dam at lambing (Irish data only), Dam age = age of the lamb's dam at lambing (UK data only), Sex*Age = the interaction between the sex of the lamb and age of the lamb at recording, Birth type*Rearing type = the interaction between the birth type and rearing type of the lamb, Country = country of birth of the lamb, Animal = random additive genetic effect of the animal (lamb) including all pedigree available, Dam = random maternal effect of the lamb's dam, Litter = random common environmental effect among lambs in the same litter, and e= random residual effect.

The model was first applied to Irish and UK data, separately, after removing the country effect, to derive within-country estimates of variance components and animal breeding values of individual animals in each country. Subsequently, bivariate analyses were conducted on joint across-country data to estimate the genetic correlations between countries and breeding values of all animals in the combined dataset. In the latter analyses, all variance component estimates across-country were fixed to the previously calculated within-country estimates to allow for a direct comparison of estimated breeding values from within-country and across-country evaluations. Residual covariance estimates due to dam and litter effects as well as between countries were fixed to zero as no animal had phenotypic records in both countries. Estimated breeding values (EBVs) and accuracies of EBVs were derived for all animals and were expressed on the scale of each country.

All these analyses were conducted with the ASReml software (Gilmour et al., 2009).

Response to Selection

Predicted response to selection was calculated for each studied trait in each country, separately, using the following equation (Rendel and Robertson, 1950):

$$\Delta G = i * r * \sigma_a$$

Where ΔG = rate of genetic gain achieved per generation and trait; i = selection intensity; r = accuracy of genetic evaluation; and σ_α = additive genetic standard deviation for the trait in question.

This formula was used to derive the predicted response to the selection of sires based on EBVs from both across-country and within-country genetic evaluations. Different scenarios considered selection of the top 10 and 20 sires in each case. Only sires with a minimum EBV accuracy of 0.65 were considered in this step.

Results

Phenotypic description of the studied traits is given in Table 1. This Table portrays the individual traits as included pairwise in the across-country analyses. Overall, trait phenotypic results were relatively similar between the two countries; however, muscle depth and particularly fat depth were lower in the UK. This may be attributed to different techniques used in the two countries when measuring fat depth using the ultrasound scanning machine.

Genetic parameters from the univariate (within-country) and bivariate (across-country) analyses are also summarised in Table 1. For reasons that could not be determined, the bivariate analysis of muscle depth in the two countries failed to converge. Therefore, an approximate genetic correlation was derived in this case based on the correlation between EBVs of common sires calculated within-country and adjusted for EBV accuracy according to Calo et al. (1973).

Genetic correlation estimates between the two countries were stronger than 0.80 in all cases except when weaning weight from Ireland was combined with early life weight from the UK. In this case, the weak genetic correlation (0.38) suggests that the across-country evaluation for these traits would not be beneficial. Therefore, no further analyses were conducted for this trait combination. However, the other trait measured in Ireland at an early growth phase, pre-weaning weight, was highly correlated with UK early-life weight. In the latter case, as well as for all carcass traits the strong genetic correlation estimated between the two countries warrants possible benefits from a joint genetic evaluation. Strong genetic correlations between traits also indicate that limited re-ranking of sires would be expected between the two countries.

Response to selection

In order to further examine and quantify the benefit of across-country genetic evaluation, predicted response to sire selection within- and across-country was estimated for each trait separately (Tables 2-5). Two different selection scenarios were considered for illustration assuming selection of the top 10 and top 20 sires in each case. These numbers are generally reflective of the current selection practice in the two countries.

Difference between response to selection based on across- versus within-country evaluation would be expected to be mainly due to difference in EBV accuracy and selection intensity. Dependent on trait and country, average sire EBV accuracy ranged between 0.53 and 0.70 in both within- and across-country genetic analyses. Expectedly, selection intensity was always higher when sires were selected based on the wider pool of the across-country evaluations in comparison to selecting from the within-country evaluations.

After the minimum accuracy threshold of 0.65 was imposed there were between 119 to 369 sires remaining in the within-country analysis and 182-473 sires remaining for the across-country analysis, depending on the trait. Across-country evaluations were of benefit to both Ireland and the UK for all traits studied with a potential increase in predicted genetic gain between 2.59% (Table 2) and 19.63% (Table 3) in comparison to using within-country evaluations alone. The lowest predicted response to selection was for early-life body weight in the UK and the highest was for post-weaning weight in the UK. Overall, predicted response to selection using across-country genetic evaluations was of more benefit to the UK than Ireland for carcass traits although the opposite was true for live body weight in the early growth stage.

Discussion

International (across-country) genetic evaluations have already proven their worth in both the beef and dairy cattle industries with the development of Interbeef and Interbull, respectively. However, to date no international genetic evaluations have been conducted for sheep. Interbull provides genetic evaluations for a multitude of traits for dairy cattle including production, fertility, health and conformation traits (Mark, 2004; Mark, 2005). Interbeef provides international genetic evaluations for weaning weight and calving ease in beef (Pabiou et al., 2014; ICBF, 2020); additionally, further research has been conducted on the international evaluations for carcass traits demonstrating the benefits from across-country genetic selection in beef cattle (Englishby, 2018). The development of international genetic evaluations for sheep will be an important factor not only in improving the rate of genetic gain for growth and carcass traits but also in facilitating across-country trade of breeding stock. Therefore, in the present study we addressed this issue using Texel sheep data from Ireland and the UK by firstly determining the connectedness between the two countries and developing an international pedigree file. International EBVs were then produced for all animals and response to selection was estimated comparing the rate of genetic gain from the use of within-country evaluations in comparison to international (across-country) evaluations. Results from the present study show that across-country genetic evaluations would be of significant benefit to both Irish and UK sheep industries.

Connectedness

Connectedness among sheep populations in different countries is a key component in the feasibility of conducting international genetic evaluations. This is because bias in EBV estimation is reduced as connections between flocks and separate management units are increased (Hanocq et al., 1996; Kuehn et al., 2007; Kuehn et al., 2008). Connectedness was found to be relatively high between the Irish and UK Texel populations with 1,188 sires having progeny with records in both countries. Although the number of common sires is relatively high, the number of progeny per sire is relatively low when compared to dairy cattle, where artificial insemination (AI) is the norm in breeding programmes. Furthermore, in the case of sheep, progeny of the common sires appeared in relatively few flocks. Notably, the level of connectedness observed in the present study is only reflective of the true connectedness levels amongst flocks currently participating in performance recording schemes. In order to increase overall connectedness levels amongst populations, an increase in systematic performance recording of the entire population is required in addition to a higher uptake of data recording within pedigree flocks. Moreover, an increase in the use of AI in both pedigree and commercial breeding settings would create higher levels of connectedness amongst flocks both within and across-country. Further advances could also be made through the use of genomics due to the lack of depth in current pedigrees and missing relationship information associated with incorrect parentage in several breeds (Berry et al., 2019).

Genetic Parameters

In general heritability estimates derived in the present study were higher in Ireland than in the UK. There were substantial differences between heritability estimates for post-weaning weight and muscle depth between countries with Irish heritability estimates 10 to 12% higher than UK for these traits, respectively. These parameters are generally consistent, though, with the scientific literature (Safari and Fogarty, 2003).

The benefit of conducting international evaluations is dependent on the magnitude of the genetic correlation between countries for a trait (Mulder et al., 2005). Selection using across-country genetic evaluations will result in a higher rate of genetic gain than national genetic evaluations when the genetic correlation between traits across country is 0.70 or greater (Mulder et al., 2005). Genetic correlations between Ireland and the UK were strongly positive for all corresponding traits analysed with the strongest correlation seen for the post-weaning weight trait at 0.88. This is indicative of the similarity between the traits and production environments in both countries. Slightly stronger genetic correlation estimates were previously reported in across-country beef evaluations for carcass traits between Ireland and the UK, ranging from 0.95 to 0.99 (Englishby, 2018). The stronger correlations for beef cattle may be due to the traits that were chosen for the analysis. Beef carcass grading is standardised using the EUROP grading system in Europe so this trait definition may have led to the strong correlations than seen here (Jakobsen et al., 2009; Craigie et al., 2012). This may also be why, in the present study, post-weaning weight showed the strongest genetic correlation as this trait is almost identically defined in both countries. Although previous across-country carcass trait correlations reported by Englishby (2018) were stronger than those in the present study, other studies on across-country evaluations for weaning weight in Limousin cattle were weaker at 0.76 (Venot et al., 2007), although later studies estimated across-country genetic evaluations for the same trait in Limousin cattle to be 0.88 (Pabiou et al., 2014), which is similar to the present study. While no direct across-country genetic comparison has previously been completed for sheep, an earlier study produced across-country correlations for selection indices between Ireland and New Zealand, which ranged from 0.66 to 0.86 for terminal and maternal indices between countries, respectively (Santos et al., 2015).

Response to selection

When genetic correlations between countries are sufficiently strong, combined selection of animals across-country should always be on a par if not superior to within-country selection (Smith and Banos, 1991). This was also proven to be true for sheep in the present study, with selection using across-country evaluations proving to be superior to within-country selection alone for all traits in both Ireland and the UK. Expected benefit in carcass related traits (post-weaning weight, and muscle and fat depth) from across-country genetic evaluations tended to be higher for the UK than in Ireland with up to a 19.63% and 6.49% predicted increase in genetic gain achieved in the UK and Ireland, respectively. This result was also seen in previous international beef evaluations between the same countries although the extent of the benefit was greater for the latter, with predicted rates of genetic gain increasing by up to 34%

(Englishby, 2018). Previous studies for dairy cattle have also reported similar predicted responses to selection from international evaluations with predicted benefits of up to 17% reported by Lohuis and Dekkers (1998).

Pooling data from different countries and combining in an international dataset gives rise to a greater number of selection candidates, thus increasing selection intensity. As accuracy levels remained relatively stable in within- and across-country genetic evaluations, selection intensity was deemed to be one of the most influential factors in increasing the rate of genetic gain achieved per year.

Predicted response to selection derived in the present study demonstrates the benefits for individual traits separately. At a practical level, sires are selected based on overall selection indices rather than individual trait EBV estimates. As the gain differs according to the different traits, when all growth and carcass trait EBVs are combined it is unlikely that the expected increase in genetic gain predicted on a single trait basis would be realised, whether this is operated within- or across-country selection. This is an area that should be explored in future work.

Conclusion

Strong links and genetic correlations between Ireland and the UK were found which would facilitate a joint genetic evaluation for Texel sheep across the two countries. Through the combination of data and pedigree records across-country the present study has demonstrated that a considerable improvement can be achieved in the rate of genetic gain through the informed selection of breeding stock regardless of the country of origin.

Declaration of Interest

None

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Table 1 Number of records (n), trait mean (µ) and standard deviation (SD), the corresponding mean age of lambs, and estimates of heritability (h^2) with standard error (SE) by country and trait, and genetic correlation of traits between countries.

Trait	Country	n	µ (SD)	Age	h^2 (SE)	Genetic correlation
Pre-weaning weight (kg)	Ireland	11,891	20.86 (4.70)	46.59	0.19 (0.03)	0.82
Early-life weight (kg)	UK	21,480	27.16 (6.48)	65.53	0.18 (0.03)	
Weaning weight (kg)	Ireland	12,388	36.69 (7.63)	96.92	0.30 (0.03)	0.38
Early-life weight (kg)	UK	21,480	27.16 (6.48)	65.53	0.18 (0.03)	
Post-weaning weight (kg)	Ireland	12,074	48.70 (9.47)	144.76	0.32 (0.03)	0.88
	UK	13,219	49.00 (9.24)	146.70	0.22 (0.03)	
Muscle depth (mm)	Ireland	8,810	32.59 (4.09)	146.57	0.31 (0.03)	0.85
	UK	12,619	28.69 (4.05)	146.80	0.19 (0.03)	
Fat depth (mm)	Ireland	8,782	6.10 (2.70)	146.63	0.20 (0.03)	0.85
	UK	12,527	2.45 (1.26)	146.80	0.18 (0.03)	

Table 2 Predicted response (*ΔG*) to top sire selection based on within- and across-country genetic evaluation for early-life body weight; i=intensity of selection, r=average accuracy of selection candidate EBVs, σ=genetic standard deviation of trait; % ΔG achievable within-compared to across-country selection.

Selection Scenario	No. of Sires	Proportion Selected	*i*	*r*	*σ*	*ΔG*	%
Within-country -Ireland							
Top 10 Sires	192	5.21	2.063	0.74	1.39	2.12	95.19
Top 20 Sires	192	10.42	1.755	0.74	1.39	1.81	93.51
Within-country - UK							
Top 10 Sires	194	5.15	2.063	0.76	1.78	2.79	97.41
Top 20 Sires	194	10.31	1.755	0.76	1.78	2.37	95.52
Across-country - Ireland							
Top 10 Sires	276	3.62	2.197	0.73	1.39	2.23	100
Top 20 Sires	276	7.25	1.9025	0.73	1.39	1.93	100
Across-country - UK							
Top 10 Sires	260	3.85	2.175	0.74	1.78	2.87	100
Top 20 Sires	260	7.69	1.887	0.74	1.78	2.49	100

Table 3 Predicted response (*ΔG*) to top sire selection based on within- and across-country genetic evaluation for post-weaning weight; i=intensity of selection, r=average accuracy of selection candidate EBVs, σ=genetic standard deviation of trait; % ΔG achievable within-compared to across-country selection.

Selection Scenario	No. of Sires	Proportion Selected	*i*	*r*	*σ*	*ΔG*	%
Within-country - Ireland							
Top 10 Sires	369	2.71	2.309	0.76	3.46	6.06	97.35
Top 20 Sires	369	5.42	2.023	0.76	3.46	5.31	96.02
Within-country - UK							
Top 10 Sires	137	7.3	1.887	0.77	2.82	4.1	85.89
Top 20 Sires	137	14.59	1.554	0.77	2.82	3.38	80.37
Across country - Ireland							
Top 10 Sires	473	2.11	2.4035	0.75	3.46	6.23	100
Top 20 Sires	473	4.23	2.135	0.75	3.46	5.53	100
Across-country - UK							
Top 10 Sires	325	3.08	2.2555	0.75	2.82	4.77	100
Top 20 Sires	325	6.15	1.985	0.75	2.82	4.2	100

Table 4 Predicted response (*ΔG*) to top sire selection based on within- and across-country genetic evaluation for muscle depth; i=intensity of selection, r=average accuracy of selection candidate EBVs, σ=genetic standard deviation of trait; % ΔG achievable within- compared to across-country selection.

Selection Scenario	No. of Sires	Proportion Selected	*i*	*r*	*σ*	*ΔG*	%
Within-country - Ireland							
Top 10 Sires	279	3.58	2.197	0.76	1.66	2.77	97.00
Top 20 Sires	279	7.17	1.918	0.76	1.66	2.42	96.07
Within-country - UK							
Top 10 Sires	125	8	1.858	0.75	1.3	1.81	87.42
Top 20 Sires	125	16	1.521	0.75	1.3	1.49	82.97
Across-country - Ireland							
Top 10 Sires	348	2.87	2.295	0.75	1.66	2.86	100
Top 20 Sires	348	5.75	2.023	0.75	1.66	2.52	100
Across-country - UK							
Top 10 Sires	246	4.07	2.154	0.74	1.3	2.08	100
Top 20 Sires	246	8.13	1.858	0.74	1.3	1.79	100

Table 5 Predicted response (*ΔG*) to top sire selection based on within- and across-country genetic evaluation for fat depth; i=intensity of selection, r=average accuracy of selection candidate EBVs, σ=genetic standard deviation of trait; % ΔG achievable within- compared to across-country selection.

Selection Scenario	No. of Sires	Proportion Selected	*i*	*r*	*σ*	*ΔG*	%
Within-country - Ireland							
Top 10 Sires	165	6.06	1.985	0.74	0.1	0.15	93.80
Top 20 Sires	165	12.12	1.667	0.74	0.1	0.13	93.67
Within-country - UK							
Top 10 Sires	119	8.4	1.831	0.75	0.42	0.57	92.99
Top 20 Sires	119	16.81	1.489	0.75	0.42	0.47	89.51
Across-country - Ireland							
Top 10 Sires	228	4.39	2.116	0.73	0.1	0.16	100
Top 20 Sires	228	8.77	1.804	0.73	0.1	0.14	100
Across-country - UK							
Top 10 Sires	182	5.49	2.023	0.73	0.42	0.62	100
Top 20 Sires	182	10.99	1.709	0.73	0.42	0.52	100

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Submitted article inserted below

Genetic Characterization and Population Connectedness of North American and European Dairy Goats

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Keywords: dairy goats, genetic diversity, population structure, small ruminants, Alpine goats, Saanen goats

Abstract

Genomic prediction of breeding values is routinely performed in several livestock breeding programs around the world. Nevertheless, the size of the training populations and the genetic structure of populations evaluated have, in many instances, limited the increase in the accuracy of genomic estimated breeding values. Combining phenotypic, pedigree, and genomic data from genetically-related populations can be a feasible strategy to overcome this limitation. However, the success of across-population genetic evaluations depends on the pedigree connectedness and genetic relationship among individuals from different populations. In this context, this study aimed to evaluate the genetic connectedness and population structure of Alpine and Saanen dairy goats from four countries involved in the European project SMARTER (Small Ruminants Breeding for Efficiency and Resilience), including Canada, France, Italy, and Switzerland. These analyses are paramount for assessing the potential feasibility of an across-country genomic evaluation in dairy goats. Approximately 9,855 genotyped individuals (with 51% French genotyped animals) and 6,435,189 animals included in the pedigree files were available across all four populations. The pedigree analyses indicated that the exchange of breeding animals were mainly unilateral with flows from France to the other three countries. Italy has also imported breeding animals from Switzerland. Principal component analyses (PCA), admixture, and consistency of gametic phase revealed that French and Italian populations are more genetically related compared to the other dairy goat population pairs. Canadian dairy goats showed the largest within-breed heterogeneity as well as genetic differences with the European populations. The genetic diversity and population connectedness between the studied populations indicate that an international genomic evaluation may be more feasible, especially for French and Italian goats. Further studies will investigate the accuracy of genomic breeding values when combining the datasets from these four populations.

Introduction

Genomic prediction of breeding values are routinely performed in several livestock species, including dairy and beef cattle, dairy sheep, and dairy goats (Boichard et al., 2012; Carillier et al., 2013; Baloche et al., 2014; Ibanez-Escriche and Simianer, 2016; Rupp et al., 2016). Genomic selection has become possible due to the availability of a large enough training populations (individuals with both genotypes and phenotypes for the traits of interest) genotyped for thousands of genomic markers. However, the success of these genomic predictions depends on population specific parameters, including the effective population size, level of linkage disequilibrium (LD), genetic relationship between the training and target populations, pedigree connectedness, and trait heritability (Misztal et al., 2020; van den Berg et al., 2020; VanRaden, 2020). For instance, a single nucleotide polymorphism (SNP) chip panel of enough SNP density is required to capture the LD between quantitative trait loci (QTL) and surrounding markers and thus, accurately estimate the SNP effects (de Roos et al., 2008;

Lund et al., 2011). The size of the training populations and the pedigree connectedness also play a major role in the accuracy of genomic predictions (Lund et al., 2011; VanRaden, 2020) and lower-heritability traits require an even larger training population (Pszczola et al., 2012).

Combining data from genetically-related populations can be an efficient strategy for enlarging training populations for genomic predictions (Berry et al., 2014; Cardoso et al., 2021). For instance, this has been done in European dairy cattle populations through the Eurogenomics Consortium (www.eurogenomics.com/), which maintains a training population of ~40,000 genotyped bulls and provides genomic estimated breeding values (GEBVs) for 11 countries. More recently, international genomic evaluations have also been implemented in beef cattle populations (Bonifazi et al., 2020). In general, the method chosen to conduct these analyses are multi-trait single-step Genomic Best Linear Unbiased Prediction [ssGBLUP; (Bonifazi et al., 2020)], in which the same trait measured across countries are considered as different, but genetically correlated, traits. International genomic evaluations have been successfully implemented in international beef and dairy cattle populations. However, the success of across-population genomic evaluations requires a close collaboration between the partners as well as close population structure and genetic connectedness among the involved populations. For instance, the level of genetic connectedness (as a consequence of exchange of genetic material) between the different populations need to be sufficient to obtain accurate genomic prediction (Weigel et al., 2000; Fouilloux et al., 2006). Furthermore, combining data from several populations is only feasible if they are genetically related (Lund et al., 2014; Rezende et al., 2020). However, recent studies in Norwegian and New Zealand sheep with similar development history, but reduced recent exchange of genetic material, reported that collaborative genomic analyses could still be feasible (Oliveira et al., 2020, 2022).

Currently, genomic evaluations have been implemented in dairy goats in France (Carillier et al., 2013) and tested in Canada (Massender et al., 2022) for both Alpine and Saanen breeds. GEBVs are more accurate than pedigree-based EBVs (Carillier et al., 2013, 2014; Massender et al., 2022) but the observed gains in accuracy are still lower compared to dairy cattle. This is likely due to specific population characteristics such as the smaller size of the training populations and higher genetic diversity in dairy goats (Carillier et al., 2013; Brito et al., 2015). Combining data from different countries could contribute to improving the accuracy of genomic predictions by increasing the size of the training populations for economically-important traits. Furthermore, across-country genomic predictions could be even more beneficial to countries that do not currently carry it out genomic evaluations, such as Italy and Switzerland. Therefore, there is a need to assess the genetic connectedness and population structure of dairy goats from France, Italy, Canada, and Switzerland to evaluate the feasibility of an across-country genomic evaluation. In this context, the main objectives of this study were: 1) to investigate the historical exchanges of genetic material between these four countries based on pedigree recording (genetic connectedness), and 2) to evaluate the genomic relatedness of these four populations based on genome-wide levels of LD, consistency of gametic phase across population pairs, principal component analysis (PCA), and population admixture analyses. These analyses are paramount for assessing the potential feasibility of an across-country genomic evaluation in dairy goats.

Materials and Methods

Pedigree and genomic datasets

This study was carried out in the framework of the "Practical selection tools to benefit from international harmonisation and cooperation" work package of the SMARTER project (www.smarterproject.eu/). Four countries (Canada, France, Italy, and Switzerland) have shared 9,941 raw genotypes and pedigree information from Alpine and Saanen dairy goat populations. The animal identification (ID) was standardized in each country partner and was formed based on four components: three letters indicating the breed of the animal (ALP for Alpine and SAA for Saanen) + three letters indicating the country of origin (CAN, FRA, ITA, and CHE representing Canada, France, Italy, and Switzerland, respectively) + one letter indicating the sex of the animal (F for female and M for male) + 16 characters with the animal identifier (including the animal birth country code in two letters and the remaining characters after adding the animal ID completed on the left side by as many 0 as needed). For instance, the final identification of an Alpine female with local ID 5248383, born in France, and raised in Switzerland would be ALPCHEF0000000FR5248383. Imported animals may have multiple identifiers (one from the country of origin and another one in the importing country). Therefore, up to three aliases could be provided by the partners in addition to the ID of the animal. This identification is important to enable tracing the origin of the curated data but also useful for finding the connections between the different pedigrees.

Table 1. Number of animals, after the quality control, per breed (Alpine and Saanen) included in the pedigree and genotype files shared by each country (Canada, France, Italy, and Switzerland).

	Alpine		**Saanen**			
Country	**Pedigree**	**Genotypes**	**Pedigree**	**Genotypes**	**Total Pedigree**	**Total Genotype**
Canada	56,601	793	36,741	903	93,342	1,696
France	3,518,473	2,968	2,527,443	2,009	6,045,916	4,977
Italy	107,566	1,061	131,376	338	238,942	1,399
Switzerland	28,083	1,280	28,906	503	56,989	1,783
Total	**3,710,723**	**6,102**	**2,724,466**	**3,753**	**6,435,189**	**9,855**

Various quality control filters were implemented in these datasets. First, the format of each animal's identification included in the pedigree files were verified for consistency, including checking that all the animals present as sires or dams were also registered as individuals in the pedigree. After removing or correcting these inconsistencies, 6,435,189 animals remained in the pedigree files (Table 1). The pedigree file had 86%, 89%, 91%, and 94% females in Canada, Switzerland, France, and Italy, respectively, which were born between 1944 and 2020. The males were born from 1936 to 2020.

All the individuals were genotyped using the same SNP chip panel, i.e. Goat SNP50 BeadChip (Illumina Inc., San Diego, CA, USA). There are currently two versions of this SNP chip panel, but 90% of the genotyping was performed based on the first version that contains 53,347 SNPs. Genotypes were exchanged in TOP/BOT format and based on the ARS1 reference genome. As more than 90% of the genotyping was carried out based on the first version of the SNP chip panel, and all SNPs included in the version 1 (n = 53,347) were also present in version 2, only the SNPs from version 1 were considered for further analyses. Duplicated genotypes were filtered out based on animal call rate, in which the genotype sample with higher call rate was kept in the dataset. SNPs with minor allele frequency (MAF) lower than 0.01 and call rate lower than 0.90 were filtered out. Furthermore, animals with sample call rate lower than 0.90 were also removed from the analyses (n = 86). Quality control was performed within breed and country, but also after merging the four datasets. The quality control analyses were performed using the PLINK 1.9 software (Purcell et al., 2007). After the quality control, 9,855 animals and 50,578 SNPs remained for further analyses (Table 1).

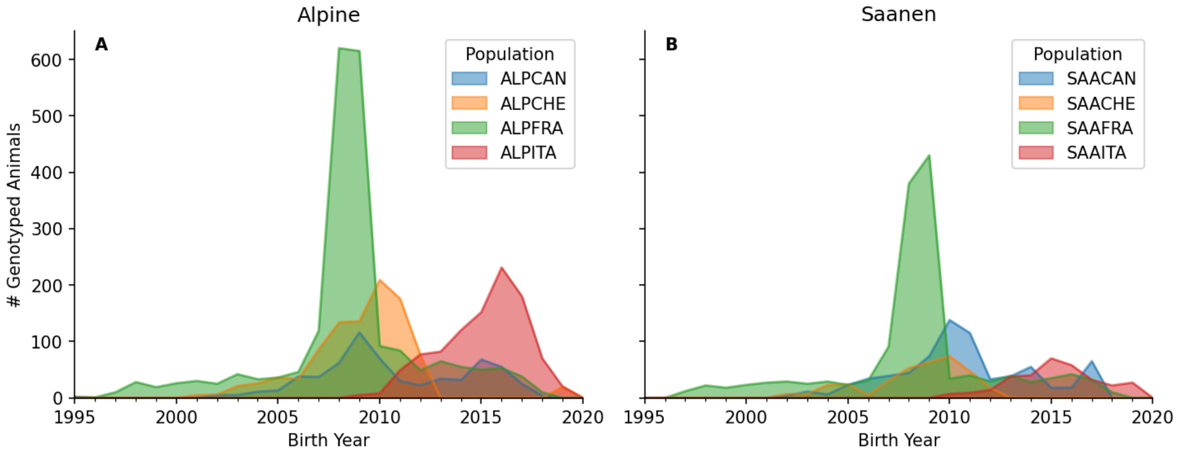

Figure 1. Number of genotyped animals according to birth year for Alpine (A) and Saanen (B) breeds in each country (France, Canada, Italy, and Switzerland). The legend represents the breed (ALP for Alpine and SAA for Saanen) and country (CAN for Canada, CHE for Switzerland, FRA for France, and ITA for Italy).

Figure 1 shows a density plots of the birth years of Alpine and Saanen genotyped animals in each country. An important point to highlight is that the genotyping activities did not start at the same time across partners. The oldest genotyped animals were born in 1997, 2000, 2001, and 2009 for French, Swiss, Canadian, and Italian goats.

Pedigree connectedness

The pedigree connection evaluations were done by pairs of countries, comparing a source pedigree and a target pedigree. The goal was to extract animals from the source country in the target pedigree and seek to find them in the source pedigree (for example, French animals from the Swiss pedigree were found in the French pedigree). In total, 12 comparisons were made to find all the connections. These analyses were done using Python scripts prepared by the authors.

The standardization of animal identification facilitated the extraction of foreign animals present in the other pedigree files. Several strategies were developed to retrieve the pedigrees of these animals. The simplest approach was to compare the identifiers (and aliases) of these animals with the source pedigree (e.g., France). This step was easily automated, but not sufficient to find all the pedigree connections. For instance, considering the Swiss dairy goat pedigree, some French animals were registered in Switzerland with only the last digits of the French identifiers. For these animals, we used the fuzzy string-matching approaches (with the fuzzywuzzy library in Python; https://pypi.org/project/fuzzywuzzy/) to find the matches between the two pedigrees. The verification of proposed animal matches based on this approach was done manually. This approach enabled the identification of animals with typos at the time of registration.

Characterization of genetic diversity

Linkage disequilibrium

The extent of LD was calculated for each breed both within each country and also with merged datasets. This was done based on the -r2 option implemented in the PLINK 1.9 software (Purcell et al., 2007). The r^2 statistic was calculated as $\frac{(p_{AB}-p_A p_B)^2}{pA(1-p_1)p_b(1-p_B)}$ where p_A and p_B are the respective frequencies of alleles A and B (two different loci) and p_{AB} the frequency of the haplotype AB, as proposed by Hill and Robertson (1968). The LD between markers was measured for each pair of SNPs within a chromosome. The distance between two SNPs ranging from 0 to 1Mb was categorized into 50 classes of 20kb. The average LD was obtained by calculating the average r^2 for each class. In the Results and Discussion sections, each class was named based on the median distance in each interval. The LD decay plots were also created for each breed within country.

Consistency of gametic phase

The calculation of consistency of gametic phase was done following Oliveira et al. (2020), by first calculating the square roots of the r^2 statistic and then adding the sign of the D-value obtained with the dprime-signed option of the PLINK 1.9 software (Purcell et al., 2007). The consistency of gametic phase was obtained as the Pearson correlation coefficient calculated between the signed-squared-root values of each country pair within breed, and between the signed-squared-root values across the two breeds within-country when grouping the two breeds together. The consistency of gametic phase was also calculated for nine categories of SNPs according to their distance: (0kb, 1kb], (1kb, 10kb], (10kb, 20kb], (20kb, 40kb], (40kb, 60kb], (60kb, 100kb], (100kb, 200kb], (200kb, 500kb], and (500kb, 1,000kb]. We used the same interval classes as those presented by Mdladla et al. (2016).

Genetic relatedness and population structure analyses

The study of the genetic similarity and structure of the eight populations (two breeds x four countries) was performed based on two methods: Principal Component Analysis (PCA) and genetic admixture analysis. To comply with the data independence assumption for performing PCA, the genotypes were pruned using the default parameter of the option -indep implemented in the PLINK 1.9 software (Purcell et al., 2007). A total of 31,951 SNPs was retained for the PCA analyses. PCA was performed using the -pca option of the PLINK 1.9 software (Purcell et al., 2007). The PCA was applied to the matrix of genomic relationships calculated as in Yang et al. (2011). The same pruned dataset was used to perform the admixture analysis using the Admixture software (Alexander et al., 2009). This software clusters individuals into k predefined groups according to allele frequencies (Oliveira et al., 2020). We tested k values ranging from 2 to 8 as it would be a more representative value of the expected number of subpopulations in our dataset. Only results with a k equal to 4 will be presented because it yielded the lowest cross-validation error.

Results

Pedigree connectedness

Table 2 describes the animals registered in several pedigrees for pairwise pedigree comparisons based on the animals' country of origin. Some animals could be identified as belonging to a country but their pedigrees were not found in the country of origin. This scenario corresponds to the row "Missing in local pedigree" in Table 2. We observed that only French and Swiss animals were found in several pedigree files. French animals were found in all pedigrees (Canada, France, Italy, and Switzerland), indicating that France exported animals to all country partners of the project. However, France did not import any animals from these countries. In contrast, Italian and Canadian animals were not exported to any other country based on available recording. Italy was the only country that imported animals from both France (9,037 animals) and Switzerland (1,095 animals). In Italy, 1,863 French animals were not found in the French pedigree. This number corresponds to 309 for French animals in Switzerland and 495 for Swiss animals in Italy.

Table 2. Pedigree connectedness for Alpine and Saanen populations between pairs of fout countries. Countries abbreviations are CAN for Canada, CHE for Switzerland, FRA for France, and ITA for Italy.

		Pairwise Pedigree Comparisons					
Status	**Local origin of animal**	**CAN–FRA**	**CAN–ITA**	**CAN–CHE**	**FRA–ITA**	**FRA–CHE**	**CHE–ITA**
Found in local pedigree	CHE	0	0	0	0	0	1,095
	FRA	180	135	34	9,037	322	223
Missing in local pedigree	CHE	0	0	0	0	0	495
	FRA	0	0	0	1,863	309	0
	All	180	135	34	10,900	631	1,813

Since the majority of animal exchanges occurred between France and the other three countries, we have identified Canadian, Italian, and Swiss animals with French parents to estimate the importance of their descendants in the host country. Table 3 presents the number of Canadian, Italian, and Swiss animals with a French sire. In total, 17,137 Italian animals had a French sire, which represented 7.2% of the Italian pedigree. This proportion was lower for the Canadian (5.8%) and Swiss (1.2%) populations. For animals with a French dam, we observed lower numbers: 3,932 (1.6%) Italian animals, 101 (0.1%) Swiss animals, and 1 (0.0%) Canadian animals.

Table 3. Number of Canadian (CAN), Italian (ITA), and Swiss (CHE) animals with a French (FRA) sire for the Alpine (ALP) and Saanen (SAA) breeds according to the sex of the animals (M for male and F for female).

French SIRE	**ALP F**	**ALP M**	**SAA F**	**SAA M**	**Total**
ITA	5,396	1,821	8,216	1,704	17,137

CHE	374	107	305	93	879
CAN	276	167	69	30	542
Total	**6,046**	**2,095**	**8,590**	**1,827**	**18,558**

Linkage disequilibrium

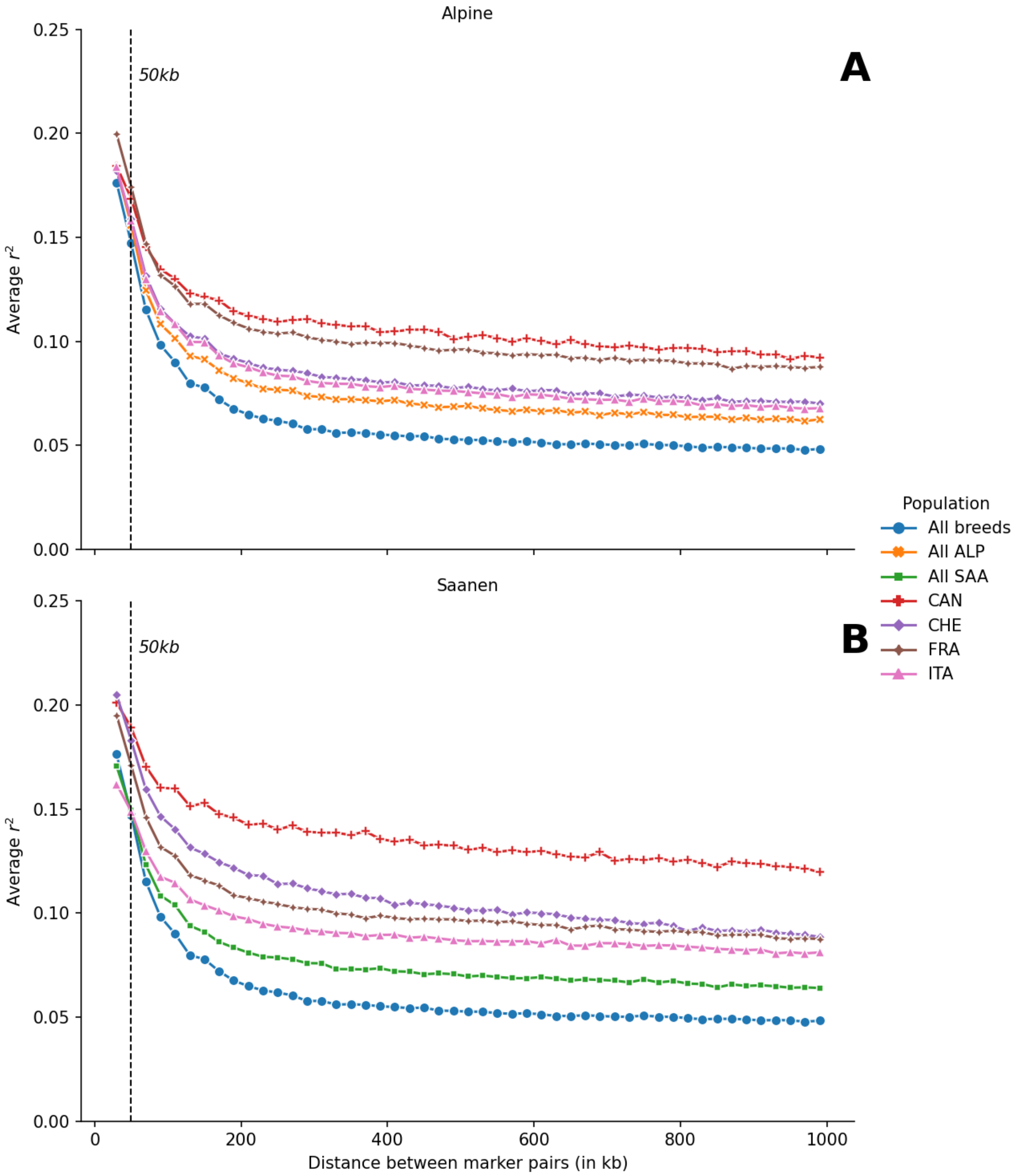

Figure 2. Average linkage disequilibrium (LD) in A) Alpine (ALP) and B) Saanen (SAA) breeds according to the distance between SNPs for each country evaluated: Canada (CAN), Switzerland (CHE), France (FRA), Italy (ITA), Saanen from the four countries together (All SAA), Alpine from the four countries together (All ALP), and both Saanen and Alpine goats from the four countries (All animals).

The average LD calculated in Alpine (A) and Saanen (B), for each country separately, and for multiple countries (ALP or SAA) or multiple breeds (All breeds) as a function of the SNP distance are presented in Figure 2. For both Alpine and Saanen, the average LD was higher in Canadian than in the other goat populations. The average LD at 50kb was 0.17 for Alpine and 0.19 for Saanen. The differences of LD values between Canada and the other countries was higher for the Saanen breed. For the Alpine breed, the average LD at 50kb ranged between 0.16 (Italy) and 0.17 (France and Canada). The average LD were quite close between Canada and France regardless of the distance between SNPs and the r^2 values stabilized around 0.10 to 1 Mb. The average LD for the Swiss and Italian populations were also very similar and stabilized around 0.07 to 1 Mb.

For the Saanen breed, the range of LD values at 50kb was wider than in the Alpine breed, with an average LD at 50kb between 0.15 (Italy) and 0.19 (Canada). Canadian populations had a higher LD than in the other countries regardless of the distance between SNPs. For short distances, LD values for Canadian and Swiss populations were close (0.18 and 0.19 at 50kb, respectively) before differentiating for distances greater than 90kb. The maximum difference was observed at 810 kb with an average LD of 0.09 in Swiss and 0.12 in Canadian goats.

Consistency of gametic phase

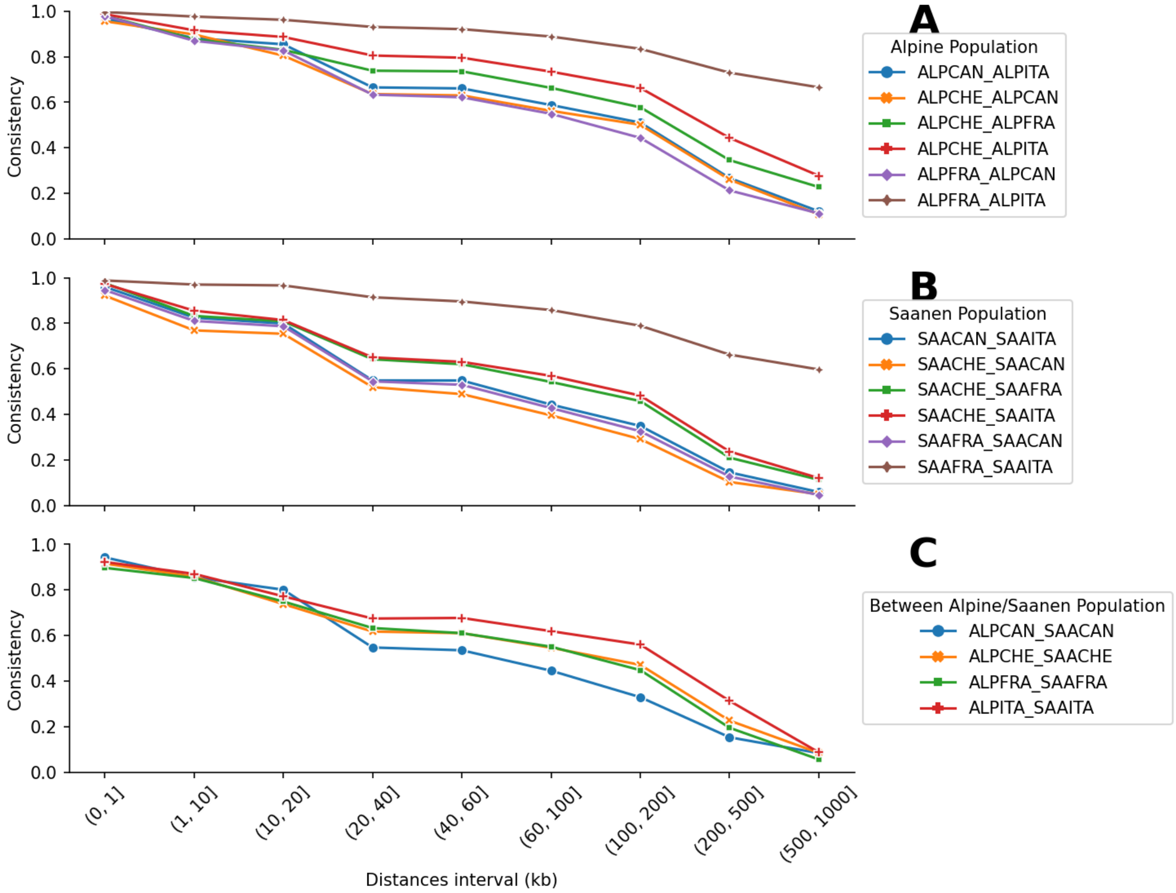

Figure 3. Comparison of the consistency of gametic phase for nine classes of distances between SNPs with comparison between Alpine populations (A), Saanen populations (B), and Alpine and Saanen from the same country (C). Breeds are represented by Alpine (ALP) and Saanen (SAA) while countries are represented by Canada (CAN), Switzerland (CHE), France (FRA), and Italy (ITA).

The consistency of gametic phase according to nine classes of distances between SNPs are shown in Figure 3. Figures 3.A and 3.B present the consistency of gametic phase between pairs of countries within the Alpine (A) and Saanen (B) breeds. Figure 3.C presents consistency of gametic phase between the Alpine and Saanen breeds within each country. Within the Alpine breed (Figure 3.A), consistency of the gametic phase values were the highest between France and Italy, and ranged from 1 (distance of (0, 1 kb]) to 0.67 (distance (500, 1000 kb]). The lowest values were obtained when comparing Canadian and European populations (ALPCAN_ALPITA, ALPCHE_ALPCAN, ALPFRA_ALPCAN). In this case, the consistency was on average 0.97 for a distance of [0, 1 kb] and dropped to 0.11 for a distance of [500, 1,000 kb]. Intermediate consistency of gametic phase were obtained when comparing Switzerland to France or Italy (ALPCHE_ALPFRA and ALPCHE_ALPITA) with an average consistency of 0.97 for a distance of (0, 1 kb] and a drop to 0.17 for a distance of (500, 1,000 kb].

The trends observed in Alpine were also found in the Saanen breed (Figure 3.B) but with slightly lower values than in the Alpine breed. Between France and Italy, the consistency of gametic phases varied between 0.99 for a distance of (0, 1 kb] and 0.60 for a distance of (500, 1,000 kb]. For a distance of (500, 1,000 kb], the consistency of the gametic phase values for all pairs of countries ranged between 0.06 and 0.60, while in Alpine these values ranged from 0.11 to 0.67.

Figure 3.C shows the consistency of gametic phase within-country when comparing Alpine and Saanen populations. The consistency of gametic phase is similar for all countries for short distances with an average consistency of 0.92 for (0kb, 1kb], 0.86 for (1kb, 10kb] and 0.77 for (10kb, 20kb]. Then, consistency between French and Swiss goat populations is similar across all distance intervals with an average difference of 0.01. The highest differences were observed between Canadian and Italian populations with an average difference of 0.10 across all distance intervals.

Principal Component Analysis

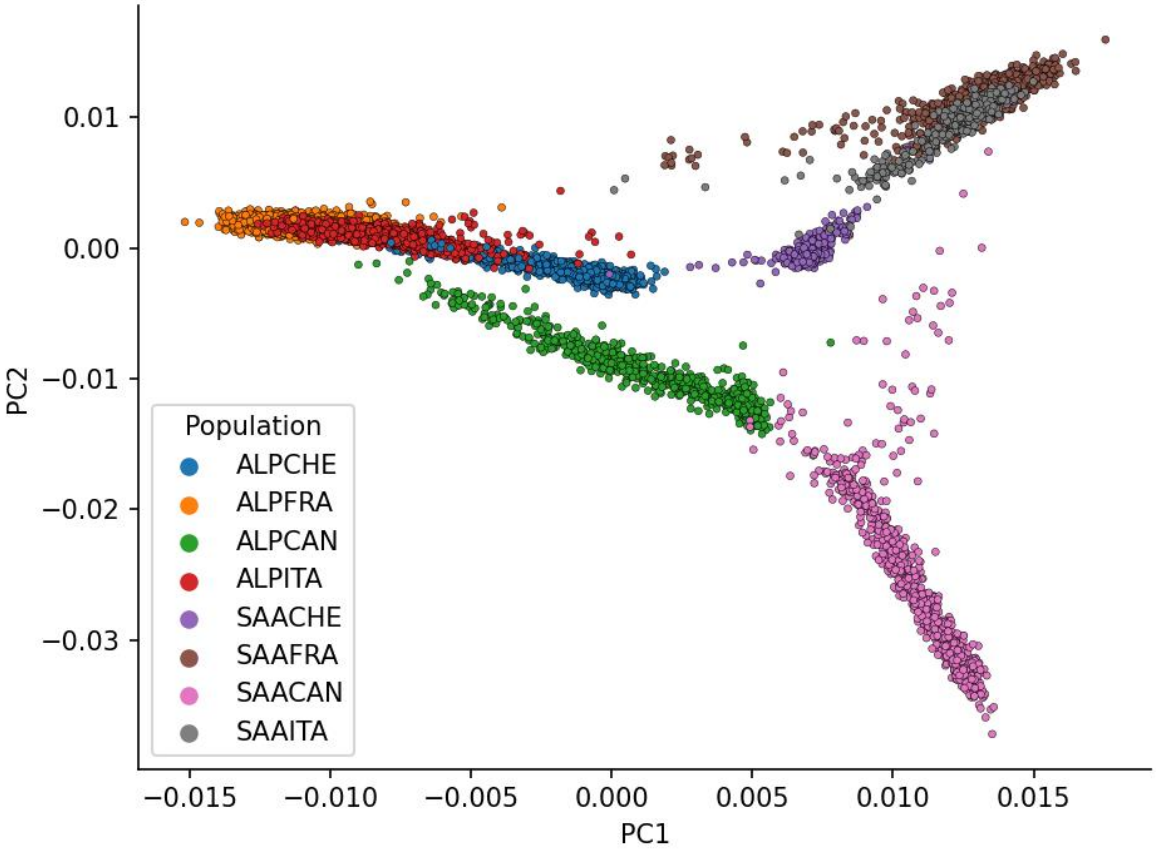

Figure 4. Principal Component Analysis (PCA) with all genotypes for each breed (ALP: Alpine, SAA: Saanen) and country (CAN: Canada, FRA: France, ITA: Italy, CHE: Switzerland) on the three first PCA components (PC1 to PC3).

Figure 4 presents the projection of each individual on the first two principal components of the PCA (PC1 and PC2). The first two components allow separate individuals according to their breed (PC1 3.26%), with the Alpine animals on the left and the Saanen on the right, and according to their country (PC2 2.32%), with the Canadian populations at the bottom and the European populations at the top. The French and Italian populations largely overlap and are indistinguishable for both breeds. The Canadian Saanen population is the most differentiated and does not group with the other Saanen populations. The few individuals present between the Canadian Saanen and the European populations are in fact animals with at least one French parent. The Swiss Saanen population is also more differentiated from the other European Saanen populations than the Alpine. Indeed, for the Alpine, there is an overlap of individuals for France, Italy, and Switzerland which is not the case in Saanen with a more homogeneous cluster.

3.1 Admixture

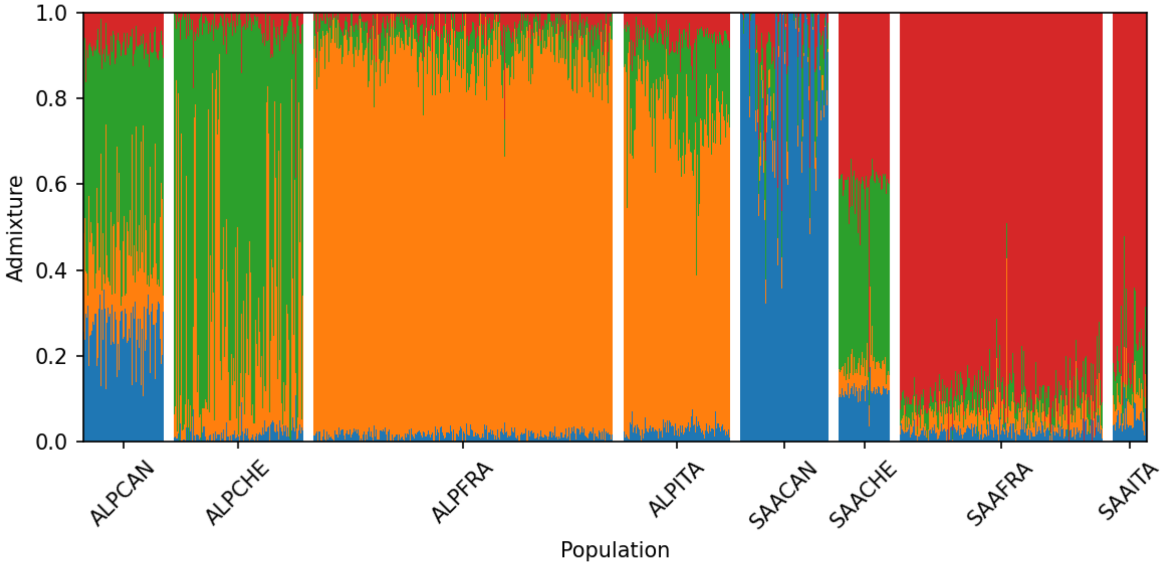

Figure 5. Breed composition per animal for each breed-country population estimated by the Admixture software, when considering k = 4. (ALP: Alpine, SAA: Saanen, CAN: Canada, FRA: France, ITA: Italy, CHE: Switzerland).

The breed composition for each animal calculated with the Admixture software is shown in Figure 5. This analysis determines, for a given genotype, the proportion originating from each k ancestral cluster. The lowest cross-validation errors were observed when k was equal to 4. It was observed that the French and Italian populations have close and similar genetic background. For Alpine, on average, 0.89 of the genome of French goats and 0.72 of the genome of Italian goats comes from the same ancestral cluster (orange color in Figure 5). This cluster is present to a lesser extent in the Canadian (0.19) and Swiss (0.26) populations. On the other hand, there is very little present in Saanen (less than 0.10 for all populations). A second ancestral cluster (red color in Figure 5) is predominant in Saanen for French (0.88) and Italian (0.79) goats. This cluster is present at 0.41 in Switzerland for Saanen but is almost absent in Canadian Saanen (0.06).

The Canadian Saanen population seems to be largely different from the other Saanen groups. Indeed, the main ancestral cluster in Canadian Saanen (blue color in Figure 5) covers 0.82 of the genome while it represents, on average, 0.11 for Swiss animals, 0.02 for French, and 0.04 for Italian animals. This blue cluster is also strongly represented (0.30) in the Canadian Alpine population. Another ancestral cluster (green color in Figure 5) also seems to be widely shared between Swiss Alpine (0.69), Canadian Alpine (0.46), and Swiss Saanen (0.41).

Discussion

Pedigree connectedness

The connections between populations coming from the four different countries based on their pedigree information is an essential parameter for a successful international genetic evaluation, especially when using the single-step GBLUP method. On the other hand, to simplify the creation of a unified pedigree, it is important to have a unique identifier for each animal, which did not exist in goat populations in this study (and which is also rarely the case for cattle and sheep breeds). Here, some of the pedigree connections have been found, but there is still work to be done because some original pedigree of foreign animals are still untraceable. The importance and difficulty of exhaustive research of pedigrees has been discussed in previous studies, such as in beef cattle for Interbeef (Venot et al., 2007), dogs (Wang, 2018), and race horses (Viklund et al., 2015).

We also have disproportional datasets with larger amounts of data in France in comparison to the other countries. This situation has also been reported in the framework of Interbeef for the Limousin cattle breed (Bonifazi et al., 2020), in which the numbers of French animals (2,942,297 animals) were higher than in the other countries (between 30,843 and 172,229 animals). The authors evaluated the within-country rankings of the top 100 animals for age-adjusted weaning weight (AWW) for both international and national evaluations. They observed that the majority of the animals in the top 100 were French (between 84% and 100%) for the international evaluations while they vary between 19% and 77% (100% being obtained in France) for the national evaluations. This is a situation that can potentially be reproduced in the international for dairy goat evaluations and could encourage the disproportional use of French breeding stock. Moreover, trade between countries has been mostly one-sided with France exporting to all partner countries. Therefore, more research needs to be done to elucidate the best options for short and long term international and national genomic evaluation for the partner countries to maximize the benefits of the collaboration.

Linkage disequilibrium and consistency of gametic phase

Population parameters such as LD and consistency of gametic phase have implications for the design of across-population genomic evaluations. For a multi-population (here multi-country) genetic evaluation to be effective, there should be equivalent LD between SNPs and QTLs in each country and a relatively high consistency of gametic phases between populations from different countries (Rahimi et al., 2020). For the French Saanen breed, the LD at 50kb estimated in this study (0.19) is slightly higher than the one observed in the study of Carillier et al. (2013) (0.17). In contrast, for Alpine, similar estimates were obtained (0.17 at 50kb). The difference observed for Saanen can be explained by the difference in the numbers of animals used to calculate the LD values, which could impact the accuracy of the estimates. In the study of Carillier et al. (2013), the calculation of LD was done for the Alpine breed on 470 Alpine genotypes compared to 2,968 in our study. For the Saanen breed, our study is based on 2,009 genotyped animals compared to 355 in Carillier et al. (2013). For Canada, the study by Brito et al. (2015) estimated the LD at 55kb around 0.14 for both breeds. We obtained higher values with 0.17 for Alpine and 0.19 for Saanen, which are identical to the estimates found for these breeds in France. Several factors can explain these differences in the estimates. The number of genotyped animals has increased substantially (403 vs 793 Alpine and 318 vs 903 Saanen), which contributes to obtaining more accurate estimates. On the other hand, although in both studies LD was estimated based on the r^2 metric, the bins used to group the SNPs are different. Between 10kb and 100kb, Brito et al. (2015) created intervals of 10kb while we used wider intervals of 20kb. To the best of our knowledge, no study has investigated the LD in Italy and Switzerland goat populations. Our study shows that, Saanen populations from these countries have similar levels of LD in comparison to the French Saanen population. For the Alpine breed, the LD in Italian and Swiss populations is lower than in French Alpine. In any case, the level of LD is very close at 50kb between populations and sufficient to consider genomic evaluation as it was demonstrated by Carillier et al. (2014). However, this level of LD will likely require larger training populations in comparison to less genetically-diverse populations to obtain similar GEBV accuracies.

The consistency of gametic phase is a key parameter for determining the effectiveness of a multi-population genetic evaluation (Biegelmeyer et al., 2016; Deng et al., 2019). This is the first time, to our knowledge, that the consistency of gametic phases is estimated between North American and European dairy goat populations. We observed that the French and Italian populations (Alpine and Saanen) have very high consistency of gametic phase up to large distances between SNP pairs, indicating that a joint genomic evaluation might be feasible for these two countries. The consistency of gametic phase values are lower when comparing the Canadian population with the European populations. This is also the case for Swiss when compared to French and Italian populations. This may make it more difficult to implement an international genetic evaluation across all the four countries. Deng et al. (2019) suggested that using a higher density SNP chip panel could be an alternative for increasing the consistency of gametic phase between SNP pairs (especially at shorter distances between SNPs). However, there are no high-density SNP chip panels available for goats. The availability of a second version of the Goat SNP50 BeadChip did not add enough SNP to get a significantly higher density of SNPs across all the goat genome.

The consistency of gametic phase in Alpine and Saanen breeds is similar within countries until the SNP distance of (10,20kb] with a decrease from about 0.92 to 0.62. After this distance the decrease of consistency of gametic phase shows different trends with a higher level for Italian, a lower level for Canadian and an intermediate level for Swiss and French populations. For French animals, these results are in accordance with those of Carillier et al. (2013), with a decrease from 0.88 to 0.56 for marker distance < 50kb, vs 0.89 to 0.63 in our study. For Canadian populations, Brito et al. (2015) reported a Pearson correlation of 0.69 at 20kb between Alpine and Saanen breeds, which is also consistent with our study. Carillier et al. (2014) have shown that in the case of the French populations, multi-breed or single-breed genomic evaluations yielded similar GEBV accuracies. However, the number of genotyped animals was significantly smaller in their study. In the context of an international genomic evaluation, the interest of a multi-breed multi-country genomic evaluation will have to be evaluated in comparison to a single-breed multi-country evaluation, which could significantly increase the training population size per breed. However, the current genotypes provided by the partners are both unbalanced in number and in the years of birth of the animals. In particular, between Italy and Switzerland for both breeds, there is almost no overlap in birth year of the genotyped animals. This study is, in fact, the first one carried out on such data for these two countries. Further analyses should be performed with larger genotyped populations to confirm our findings.

PCA and Admixture

The results of the PCA and Admixture analyses contribute to determining the genetic relationship of the animals, including breed and country of origin. The only populations with no clear distinction are French and Italian goat populations for both breeds. Italy is the country that imports the most animals from France, which may explain the genetic proximity between these two populations. In contrast, the Canadian and European populations are more genetically distant. This might be explained by the little exchange of animals and the geographical distance that separates Canada and the European countries. Finally, these results are consistent with the results observed on the connections between countries based on pedigree information.

Several genetic diversity studies have been conducted in goats. In France, the study of Oget et al., 2019) was conducted on eight French goat populations, but it included few genotypes of Alpine (45) and Saanen (38) animals. Our results, with more genotyped animals, confirm what has been previously shown for these two breeds. The French Alpine and Saanen populations are genetically different. A second study performed by Brito et al. (2015) compared genotypes from Alpine (403 animals) and Saanen (318 animals) from Canada and found that these two populations are genetically different.

The comparison of Alpine and Saanen genotypes within one country is more documented than international comparisons of these breeds. Denoyelle et al. (2021) is one of the few examples of an international comparison, which was done as part of the VarGoats project (www.goatgenome.org/vargoats.html). This project sequenced goats of different breeds from all over the world including Alpine and Saanen from France, Italy, and Switzerland. They studied the phylogeny of these breeds using a Neighbor-Joining tree constructed with 100,000 SNPs. For the Italian, Swiss, and French population, our results are in agreement with their study where a close relationship between France and Italy (for both Alpine and Saanen) and a greater distance with the Swiss goat population was observed.

Implications of the results and next steps

This work aimed to combine and analyze pedigree information and genomic data from four countries. Our analyses showed that an international evaluation would be most beneficial to the European populations that are genetically closer. However, it is necessary to verify the impact of Canadian data into international genomic evaluations, especially if other European dairy goat populations are added such as Yorkshire dairy goats (Mucha et al., 2015). Yorkshire goats represent a composite population potentially more similar with Canadian dairy goats due to more similar crossbreeding events. Pedigree connectedness and genotype analysis remains the first step before implementing an international genomic evaluation. The next steps will be to combine and analyze the phenotypes commonly recorded among the different country partners of the project. The joint analysis of phenotypes, pedigree, and genotypes will enable the estimation of genetic and genomic parameters between breeds/countries that will be potentially used in future genomic evaluations.

Conclusions

The genetic diversity and pedigree analyses performed in this study showed that the French and Italian populations are both the most genetically connected and more genomically similar. On the other hand, for the Swiss and Canadian dairy goat populations, the genetic connections are limited to the importation of few French animals. Besides, they are genomically more distant than the other populations. The genetic diversity and population connectedness between the studied populations indicate that an international genomic evaluation might be more feasible for French and Italian goats. Further studies will investigate the accuracy of genomic breeding values when combining the datasets from these four populations.

Author Contributions

HL, LFB, and CRG designed the study. MT analyzed the data, wrote all Python scripts and drafted the first version of the manuscript. LFB, FSS, HL, GB, and BB provided the datasets and information on the current genetic evaluations in their respective countries. MT, HL, LFB, FSS, and CRG interpreted the results and improved the manuscript. All authors read and approved the final manuscript. The authors declare they do not have any competing interests

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7.4 Paper “Genetic parameters across four countries in Alpine and Saanen goat breeds for milk production and type traits” to be submitted to Journal of Dairy Science Communications

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Soon-submitted article inserted below (MUST BE CONSIDERED AS A DRAFT) – The final version will lead to an update of the deliverable

GENETIC PARAMETERS ACROSS NORTH AMERICAN AND EUROPEAN IN ALPINE AND SAANEN GOAT BREEDS FOR MILK PRODUCTION AND TYPE TRAITS

Short running title: genetic correlations across dairy goat populations

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Abstract

The development of an international genomic evaluation may represent an interesting opportunity for small ruminant populations, especially to increase the size of their reference population. In this perspective, four countries, Canada, France, Italy, and Switzerland, have decided to evaluate the feasibility of an international caprine genomic evaluation in Alpine and Saanen breeds for milk production traits and type traits. For this purpose, these countries shared their phenotypes, genotypes and pedigrees. The amount of data was very different according trait, and from one country to another. In addition, the traits could be common to two, three or four countries. The variance-covariance components analysis were performed, with pedigree information alone or adding genomic information, in order to estimate heritabilities and across countries genetic correlations for three representative traits, milk yield, fat content and rear udder attachment. The heritabilities were accurately estimated and were coherent with previous estimations. The genetic correlations were high for rear udder attachment ranging from 0.75 to 0.92 and for fat content ranging from 0.75 to 0.78. However, they were only estimable between France and Italy for milk yield, with moderate values of 0.45 in Alpine breed with and without genomic information, and of 0.22 and 0.26 in Saanen breed with and without genomic information respectively. The results for the first two traits are encouraging. However, the results for milk yield need to be further investigated.

MAIN BODY

International genetic evaluations have been developed for dairy cattle, and then for beef cattle, for many years. Indeed, in these species, the intensification of genetic material exchanges has led importing countries to better know which bulls to import for their population and environment, and exporting countries to seek markets for their bulls (Nilforooshan and Jorjani, 2022). The more judicious choice of breeding stock can leads to an increase in genetic progress (Smith and Banos, 1991). In the genomic context this can be enhanced, as the across countries evaluations allow to increase the reference population and thus the reliability of genomic predictions (Brøndum et al., 2011).

In small ruminants, this type of evaluation has not been developed although, on a more modest scale than in cattle, exchanges of genetic materials exist between countries. Moreover, in these species, some countries have developed genomic evaluations (Carillier et al., 2013; Rupp et al., 2016; Teissier et al., 2019; Massender et al., 2022). However, the size of the reference populations is often small and combining them between countries would increase the reliability of genomic prediction, especially for traits of low heritability or difficult and/or costly to phenotype, as well as giving some countries access to genomic selection.

In dairy goats, France, Italy, Switzerland and Canada shared their phenotypes, genotypes and pedigrees, within the H2020 Smarter project, to evaluate the feasibility of an international caprine genomic evaluation for the Saanen and Alpine breeds. A first study has shown that exchanges of genetic material exist between these countries but that they are mainly limited from France to the other three countries (Teissier et al, submitted). Genotypes analysis has shown that European populations, and in particular French and Italian, are very close genetically while Canadian populations are further apart.

The further study is to estimate the variance components across these countries for common traits currently under selection. Genetic correlations if less than 1 indicate possible GXE interactions whether biological or statistical in origin (Nilforooshan and Jorjani, 2022). High genetic correlations (generally greater than 0.7) between countries are a prerequisite to ensure reliable and comparable genetic values for each country (Mulder and Bijma, 2006).

The objective of our study is therefore to estimate, in the Alpine and Saanen breeds, the variance components between the four countries, for two milk production traits, milk yield (MYI) and milk fat content (FCO), as well as for an udder type trait, rear udder attachment (RUA). These traits are representative of the situations encountered according to: the type of trait, milk production vs. morphology; the number of countries involved, 2, 3 or 4 countries for respectively FCO, RUA and MYI; and with different level of heritability.

The four countries share the MYI trait, Switzerland does not phenotype RUA which is common to the 3 other countries, and finally Italy and France share FCO. Table I present all records shared by each country in Alpine and Saanen breeds. We have chosen to consider the phenotypes as they are currently used by each country for their genetic evaluation. However, in order to reduce the amount of data we have retain for milk production traits the phenotypes of goats born between 2000 and 2010 for France and between 2002 and 2015 for Italy. Even so, France, in both breeds, has the highest number of phenotypes recorded both for milk production (1,882,056 in Alpine and 1,464,961 in Saanen for MYI) and for the udder type trait (326,423 in Alpine and 203,668 in Saanen). Italy is the second country to provide data for milk production traits followed by Switzerland, and finally Canada with 7,414 phenotypes in Alpine breed and 3,947 in Saanen breed for MYI. The RUA trait is recorded in the three concerned countries according to a scale from 1 to 9. The mean of this score is close between Canada and Italy and a little weaker in France in Alpine as in Saanen breeds. Moreover, the Italian scoring grid is very close to the French grid. For FCO, France expresses it in g/kg of milk and Italy in dg/kg of milk, the means of this trait in the 2 countries are close but are a little higher in France in Alpine as in Saanen breed. In contrast, the mean of MYI in kg is not similar across the 4 countries. Indeed, in France the total quantity of milk yield is calculated for a reference lactation duration of 250 days. Canada, usually using a test-day model, has recalculated a 305-day lactation and it can be observed that the mean of this trait in both breeds is higher in Canada than in France. Switzerland from a test-day model derives 2 quantities of milk: from 1 to 100 days of lactation and from 101 to 200 days of lactation. We have therefore summed up these two quantities. Italy, like France, corrects lactations for duration and extrapolates incomplete lactations, but then Italy uses a multiplicative pre-adjustment for parity, age and number of kids. Italy and Switzerland have lower lactation MYI levels than the other two countries: 524.02 and

565.74 kg respectively in the Alpine breed, and 549.15 and 614.51 respectively in the Saanen breed (Table 1).

The amount of pedigrees shared by each country is logically proportional to the number of phenotypes with in decreasing order France then Italy, Switzerland and finally Canada (Table 1). The four countries also shared the genotypes of their animals carry out with the Goat SNP50 BeadChip (Illumina Inc., San Diego, CA, USA). A quality control was performed on these genotypes with PLINK 1.9 software (Purcell et al., 2007) within breed and country and then by merging the genotypes of the 4 countries. It consisted in excluding SNPs with minor allele frequency (MAF) lower than 0.01 and a call rate lower than 0.90, as well as genotypes with a sample call rate lower than 0.90. Finally, 9,855 animals and 50,578 SNPs were kept. The genotypes of French animals represent about 50% of the total amount of genotypes in both breeds. Swiss genotyped animals constitute 21% and 8% of Alpine and Saanen animals respectively. This proportions are of the same order for Italian animals (18% and 8%) but is reversed between the two breeds for Canadian animals which represent 13% and 25% respectively of the genotyped Alpine and Saanen animals.

Variance-covariance components were computed via Gibbs sampling, with the gibbs1f90 software (Misztal et al., 2002), using pedigree information alone or combined with SNPs information. In each breed and for each trait, a multi-trait animal model was used where each country was considered as a different trait and for which the model was the one used in routine genetic evaluation. For milk production traits, the models included the random animal genetic and permanent environment effects, as well as the effects: for France: herd*year*parity (1,2,3+), age at kidding*parity*year*area(4), month of kidding*parity(1,2+)*year*area(4), length of dry period*parity(1,2,3+)*year*area(4); for Italy : herd-year-season of calving ; for Switzerland: lactation, year*season, herd (random); and for Canada: herd, lactation and birth . For RUA, models contained a random genetic animal effect as well as the environmental effects: for France: herd*year*parity, age at scoring*year, lactation stage at scoring*year; for Italy: DIM*parity, classifier, herd-season of classification, age (linear + quadratic); for Canada: herd*year*classifier (random), breed, parity, age, DIM.

Figure 1 shows for each trait the average of the heritability estimates obtained in 2-by-2 multi-country models with SNPs information. Estimation of variance components were close for a specific country whatever the two countries analyzed, so all heritability estimates for a country have a low standard deviation (presented on Figure 1). Elemental estimates of heritability had SE on average of 0.01 with a minimum of 0.00 and a maximum of 0.04. For the same trait and breed, averaged heritabilities were very close among countries and to those obtained with pedigree information alone. For France, the heritability estimates for both Alpine and Saanen breeds are close to the estimates used in the genetic evaluations, except for milk, with a slightly lower heritability, of about 0.21 compared to 0.30 in the French evaluations. For Italy, the estimates of heritabilities for RUA are of the same order of magnitude as those used in the genetic evaluation (0.18 vs. 0.16 in the Alpine evaluations and 0.16 vs. 0.10 in Saanen). In this country, FCO has relatively low heritabilities of about 0.23 for the two breeds whereas a heritability of 0.44 is used in genetic evaluation in Alpine breed. Similarly, for MYI the estimated heritabilities are around 0.13 while they are 0.25 for the evaluations. For Canada, the heritabilities estimates are consistent with those used in the evaluation for MYI around 0.30 in both breeds. They are lower for RUA, 0.20 against 0.45 in evaluation. For Switzerland, MYI has a low heritability of about 0.11 relatively close to the heritability used in evaluation, about 0.15. Overall, MYI has low heritabilities of 0.11 in Switzerland to moderate 0.30 in Canada. FCO has high heritabilities in France (around 0.49) and moderate in Italy (around 0.23). RUA shows comparable heritabilities between Canada (around 0.20) and Italy (around 0.17) and twice as high in France (around 0.40).

Estimates of variance-covariance and correlations between countries in the Alpine breed using pedigree information alone or with genomic information are presented in Table 2. For MYI, only the estimates between France and Italy are presented, due to important differences in the definition of the phenotypes and the small number of records of the two other countries.

For RUA, the correlations in Alpine breed with genomic or pedigree information are very close and are very strong ranging from 0.76 between France and Italy to 0.92 between France and Canada with genomic information. In the Saanen breed these estimates are similar and range from 0.78 to 0.95 between the same countries. For all these estimates the SE were ranged between 0.00 and 0.05 except between Canada and Italy, in the Saanen breed, for which SE reach 0.43. For FCO the correlation between France and Italy is 0.75 (SE 0.02) with pedigree information and 0.78 (SE 0.01) adding molecular information. In Saanen breed this correlation is 0.76 (SE 0.03) with pedigree information and 0.77 (SE 0.01) for genomic estimation. For MYI, the correlation between Italy and France is moderate and is the same in Alpine breed with or without genomic information: 0.45 (SE 0.10) (Table 2). In Saanen breed this correlation is low: 0.22 (SE 0.04) and 0.26 (SE 0.09) with and without genomic information respectively. For the MYI it was not possible to estimate correlations across the 4 countries. Variance estimates were accurate and consistent between the different tests performed: 2 by 2 or 3 by 3 or 4 by 4 countries, with or without genomic information. However, the covariance estimates were not consistent between the different tests and showed large SE.

These results show that for RUA, the very similar definition of phenotypes as well as the close analysis models are probably at the origin of the very strong correlations between countries. However, the high standard error for the correlation between Canada and Italy in Saanen breed suggests that the small amount of data for these countries combined with a low level of genetic connection between them do not allow us to accurately estimate this correlation.

The lower correlations for FCO than for RUA may be due to a different way of calculating phenotypes between Italy and France. Milk quality was assess in these countries according two different protocols. In Italy, a part sampling within an AC milk-recording design with two or three samplings per year is performed on the first two parities. In France, a standard A AT or AZ milk-recording design is applied with sampling intervals of four or five weeks along the lactations and for all parities. Moreover, the fixed effects including in the genetic models used by the two countries (described above) are very different.

Contrary to what could be expected, it is quite surprising that for MYI, a trait common to all 4 countries, it was not possible to correctly calculate covariances between countries, except between France and Italy. It seems that for this trait, the estimation of the variance components suffered from the combination of several factors. First, a weak genetic connection between countries except between France and Italy; then, a very marked imbalance amount of data: France contributing 88% and 85% of the data in the Alpine and Saanen breeds respectively; and finally, a phenotype measured in a different way between the 4 countries, with very different heritabilities and analysis models. Only correlations between Italy and France could be estimated but they did not reach the level of those for FCO. There may be differences in climate and/or management between these two countries but it is reasonable to assume that differences in phenotype measurements and/or analysis models are at the origin of this GXE interaction.

All in all, the strong genetic correlations estimated between countries for RUA and FCO are encouraging for future international genomic evaluations in goats, especially between France and Italy. However, as milk production is an important part of the selection objectives in goats, it will be necessary to work upstream on the standardization of phenotypes to be considered in such an international genomic evaluation.

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Country	Breed	Trait	# pedigree	# genotype	# phenotype	Mean	SD	CV
FRA	ALP	FCO	806,877	2,968	1,878,616	37.05	5.17	0.14
ITA	ALP	FCO	63,617	1,061	150,162	339.78	54.31	0.16
CAN	ALP	MYI	8,007	793	7,414	949.47	284.43	0.30
CHE	ALP	MYI	25,497	1,280	66,794	565.74	222.62	0.39
FRA	ALP	MYI	807,534	2,968	1,882,056	872.53	262.72	0.30
ITA	ALP	MYI	71,276	1,061	170,932	524.02	203.95	0.39
CAN	ALP	RUA	9,434	793	5,235	5.49	1.43	0.26
FRA	ALP	RUA	474,963	2,968	326,423	4.50	1.50	0.33
ITA	ALP	RUA	29,721	1,061	22,757	5.59	1.56	0.28
FRA	SAA	FCO	665,202	2,009	1,463,568	35.08	5.02	0.14
ITA	SAA	FCO	76,741	338	161,92	325.45	54.13	0.17
CAN	SAA	MYI	4,238	903	3,947	1,118.93	427.15	0.38
CHE	SAA	MYI	25,857	503	64,376	614.51	242.26	0.39
FRA	SAA	MYI	665,538	2,009	1,464,961	874.66	277.03	0.32
ITA	SAA	MYI	85,633	338	189,395	549.15	215.61	0.39
CAN	SAA	RUA	4,796	903	2,443	5.82	1.41	0.24
FRA	SAA	RUA	303,709	2,009	203,668	4.84	1.67	0.34
ITA	SAA	RUA	34,288	338	26,548	5.90	1.71	0.29

Table 1: Summary of data used for analyses. ALP: Alpine breed; SAA: Saanen breed; CAN: Canada; FRA: France; ITA: Italy; CHE: Switzerland; FCO: fat content; MYI: milk yield; RUA: rear udder attachment; SD: Standard deviation; CV: coefficient of variation.

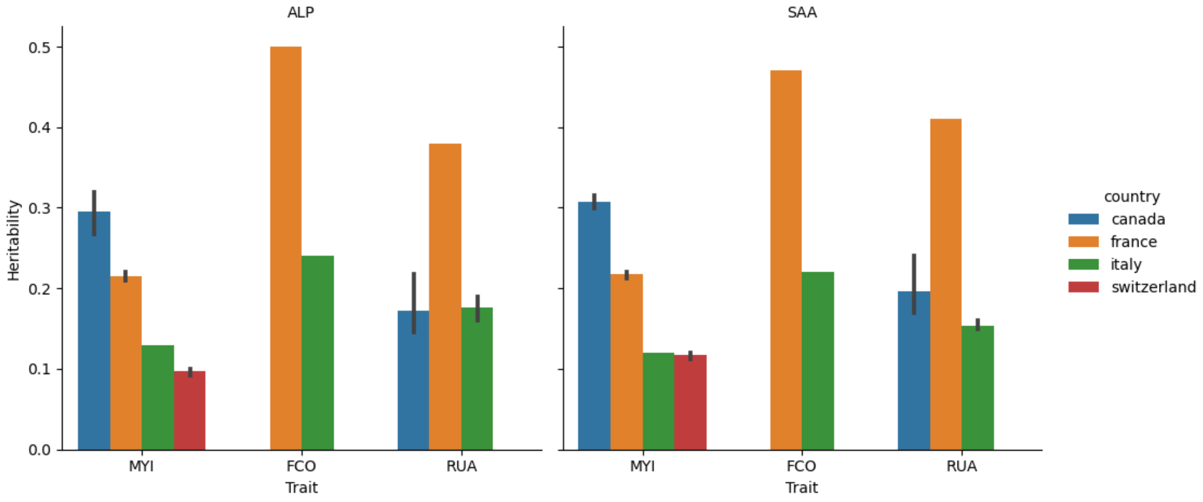

Figure 1: Average heritability of estimates obtained in 2-by-2 multi-country models with SNPs information for milk yield (MYI), fat content (FCO) and rear udder attachment (RUA) in Alpine (ALP) and Saanen (SAA) breeds (vertical lines indicate the standard deviation of the estimates).

Trait	Country	CAN	FRA	ITA
MYI	FRA		**9142 / 9180**	**2063 / 2098**
	ITA		*0.45 / 0.45*	**2320 / 2389**
FCO	FRA		**9.22 / 9.21**	**46.98 / 46.91**
	ITA		*0.75 / 0.78*	**425.78 / 450.15**
RUA	CAN	**0.27 / 0.25**	**0.40 / 0.39**	**0.21 / 0.20**
	FRA	*0.91 / 0.92*	**0.72 / 0.72**	**0.32 / 0.33**
	ITA	*0.81 / 0.78*	*0.75 / 0.76*	**0.25 / 0.26**

Table 2: Variances/Covariances (upper and bold) and correlation (lower and italic) for milk yield (MYI), milk fat content (FCO) and rear udder attachment (RUA) in Alpine breed with pedigree analyses (left number) and genomic analyses (right number).