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TOWARDS IMPROVEMENT OF **RUMI**NANT BREEDING THROUGH **GEN**OMIC AND EPIGENOMIC APPROACHES

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Effects of genomic selection on gain, diversity and drift

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1. Summary

Cattle breeds have many desirable characteristics, some of which have been developed and selected in order to adapt to specific environments throughout the centuries. With selection we aim to improve some of these characteristics (i.e., traits) without deteriorating other functional ones. Moreover, we aim at not losing genetic diversity since this would jeopardise future selection and genetic gains.

The introduction of genomic selection has largely impacted cattle breeding. Genomic data offer also new opportunities to assess the level and trend in genetic diversity of selected livestock populations throughout the genome. In cattle, previous studies showed that the implementation of genomic selection has led to increases in rates of inbreeding per year and per generation for different breeds such as Holstein, Jersey, and Ayrshire. On the other hand, the introduction of genomic selection did not lead to such increases in other breeds such as Normande, Mont-Beliard , and Aberdeen Angus. Thus, with genomic selection being increasingly implemented in large and small local cattle breeds, it is relevant to assess if and how much genomic selection has impacted on the genetic diversity of such (local) cattle breeds.

The objective of this deliverable was to investigate the effect of genomic selection on changes in genetic gain, diversity, and drift. We assessed the impact of five or more years of genomic selection on genetic trend, diversity, and genetic drift in five small local dairy cattle breeds from three European countries: the Abondance (ABO), Tarentaise (TAR), and Vosgienne (VOS) breeds in France, the Meuse, Rhine and Yssel (MRY) breed in the Netherlands, and the Norwegian Red Cattle (NRD) in Norway. Moreover, we researched changes in the breeds' population structure and management which may play a role on the observed changes in gain, diversity, and drift.

We computed pedigree-based and genomic-based measures of genetic diversity to investigate changes before and after the introduction of genomic selection in each of the five breeds and evaluated changes due to selection and drift. We computed rates of inbreeding per year and generation (i.e., rates adjusted for changes in the parents' generation interval) in each of the five breeds, based on either pedigree-based or genomic-based measures of inbreeding, and with such rates being a proxy for expected changes also due to drift. For genomic based measures, a common definition of runs of homozygosity was used for the five breeds analysed. Moreover, we investigated changes in population structure through populations statistics measures which aid to identify changes in the population structure and breed management due to the implementation of genomic breeding programs and better help in explaining observed changes in genetic diversity. The computed population structure metrics were: i) the generation intervals (trends) for sires, dams, and for both parents; ii) the number of males and females becoming sires and dams in each year, respectively; iii) the number of sires and number of calves per sires used in each year; iv) the contribution of the top 10 sires to the total number of offspring born in each year. Finally, we evaluated changes in the total merit index (TMI) of each breed to explore changes in genetic gains due to genomic selection in each breed.

Results showed that the introduction of genomic selection had a different impact on genetic diversity and drift depending on the breed. Indeed, inbreeding rates increased in MRY and TAR breeds, while it remained overall stable in NRD, and decreased in ABO and VOS. Moreover, results showed that after the introduction of genomic selection, genetic gains remained similar or increased in NRD, ABO, TAR and VOS, or slightly reduced in MRY, likely due to changes in the underlying composition of the TMI. Finally, insights obtained on the population structure of the five breeds showed changes due to the implantation of genomic selection. Overall, results showed that genomic selection resulted in shorter generation intervals, especially for sires. Moreover, the implantation of genomic selection resulted in a reduction in the number of sires used at the population level due to the screening a higher number of selection candidates allowed by genomic data, and to the preselection of males for becoming sires. Overall, these results show that genetic management of local breeds is more important and has more impact on genetic diversity, gain and drift, than the implementation of genomic selection per se.

Teams involved:

The RUMIGEN partners involved and that contributed to this deliverable are: Wageningen Livestock Research (WR) with Jack J. Winding (as Task Leader) and Renzo Bonifazi, Norwegian University of Life Sciences (NMBU) with Theo Meuwissen, and Institut national de la recherche agronomique (INRAE) with Pascal Croiseau, Gwendal Restoux, and Stéphanie Minery.

An extension on the deliverable deadline was needed to allow collecting all necessary data and information required to perform analyses among all partners, and to further help in the interpretation of the results. More time was also needed to ensure that the same methodology was used by all partners, warranting more comparability across results of the different breeds analysed.

2. Introduction

Cattle breeds have many desirable characteristics, some of which have been developed and selected in order to adapt to specific environments throughout centuries. With selection we aim to improve some of these characteristics (i.e., traits) without deteriorating others that are functional to the breeds themselves, e.g., milk or meat production. Furthermore, in animal breeding we aim to not lose genetic diversity as this would jeopardise future selection opportunities and, in extreme cases, may result in loss of biodiversity. Genetic changes are indeed related to the amount of genetic diversity available for exploitation though selection. Consequently, increase in performance or adaptation to a changing environment by breeding will be difficult if genetic diversity is under pressure. Thus, maintaining genetic diversity is key to animal breeding.

The introduction of genomic selection has largely impacted cattle breeding, with genomic breeding programs being common practice in most popular cattle breeds. Moreover, local breeds started to, or are in the process of, introducing genomic selection in their breeding programs. In the pre-genomics era, pedigree-based inbreeding was the only tool to assess genetic diversity, genetic drift, and inbreeding. Nowadays, genomic data offers new tools to further evaluate and assess inbreeding in cattle populations throughout their genome. Genomic selection allow to better estimate mendelian sampling with the expectation that rates of inbreeding could be reduced under genomic selection due to the exploitation of Mendelian sampling variation reducing co-selection of family members (Daetwyler et al., 2007; Lillehammer et al., 2011). Nonetheless, results from previous studies across different cattle breeds showed that genetic diversity in cattle may be impacted by the implementation of genomic selection. In Holstein, the rates of inbreeding increased since the introduction of genomic selection in the USA (Forutan et al., 2018; Makanjuola et al., 2020), the Netherlands (Doekes et al., 2018), Poland (Topolski & Jagusiak, 2020), France (Doublet et al., 2019), Australia (Scott et al., 2021), and Italy (Ablondi et al., 2022). Similarly, Makanjuola et al. (2020) and Sarviaho et al. (2023) reported an increase of the rates of inbreeding after the introduction of genomic selection also in Jersey cattle and Finnish Ayrshire, respectively. The reported increases were not only for rates of inbreeding on a yearly basis, which was to be expected due to the shortening of the generation interval in genomic selection (Pryce & Daetwyler, 2012), but also on a generation basis. In contrast, a similar increase in rates of inbreeding was not observed in some other breeds where genomic selection has also been introduced; for example in Normande and Mont-Beliard (Doublet et al., 2019), and Aberdeen Angus (Lozada-Soto et al., 2023).

Following from the above, in this task we assessed the impact of five or more years of genomic selection on the genetic trend, diversity, and drift of five small local dairy cattle breeds from three European countries: the Abondance, Tarentaise, and Vosgienne breeds in France, the Meuse, Rhine and Yssel (MRY) breed in the Netherlands, and the Norwegian Red Cattle breed in Norway.

Data available

The MRY is a Dutch dual-purpose cattle breed that originates from the central region of the Netherlands between the rivers Meuse, Rhine and Yssel, from which it is named after, and that can be considered a small population (Stoop et al., 2017). In the Dutch MRY population, genomic selection began in late 2018 (CRV). Based on the breed composition, purebred MRY genotyped animals at ~50K SNPs were analysed.

Norwegian Red (NRD), also known as Norsk Rødt Fe, originates in Norway around the ‘30s. For NRD, individual genotypes were available at a density of 777K SNPs. A subset of 50K SNPs were used for further analyses. NRD was the largest population among all analysed as indicated by the number of calves per year Table 1.

Three French breed were analysed and they are described below. For FRA breeds, individual genotypes at 50K, or imputed to 50K, were available.

Abondance (ABO) is the 4th French dairy cattle in terms of population size with 55,000 animals even if it represents only 1.3% of the total French dairy cattle population. It originates from the French

Alps where it uses to graze on pasture, it is well adapted to altitude (>2,000m). ABO is mainly a free-range breed even if it is raised indoor during the winter season due to the rigorous conditions in the mountains. It produces about 6,000kg of milk per year per cow. The mean herd size for this breed is about 20 cows. Reproduction is almost exclusively conducted with artificial insemination (AI). The selection nucleus consists in 1,261 farms and 21,000 cows (38% of the total population). Each year about 20 AI sires are selected. ABO was the largest among the three French breeds analysed. Finally, genomic selection has started in 2014 in this ABO.

Tarentaise (TAR) is a French dairy cattle breed originating from the Alps where it also grazes. It is often found in the same area than the Abondance breed. TAR is raised under the same conditions as of ABO, mainly free-range except during winter. As for ABO, feeding mainly relies on hay when indoor and silage is usually not used. It produces about 4,800kg of milk per year per cow. Its population size is only 13,500 animals, with a selection nucleus of 424 farms including 7,700 cows (59% of the total population). Each year 18 AI sires are selected. In TAR, genomic selection has started in 2014.

Vosigenne (VOS) is a dual-purpose breed selected for milk and meat. It produces about 4,200 kg of milk per year per cow. VOS is a very small French cattle population located in the eastern Vosges massif. Like the other mountainous local French breeds, it is raised free-range except during winter. It consists in 9,400 animals in total with only 4 to 6 AI sires selected each year. The selection nucleus consisted in 79 farms and 1,400 cows (15% of the total population). In VOS breed all animals are genotyped, making it the only breed in France to fall in such situation. Genomic selection has started in 2014 for this breed.

Based on the numbers of animals born per year, incomplete recent years were identified and discarded from the analyses. Table 1 reports an overview of the dataset analysed per each breed and the years analysed next to the year in which genomic selection was introduced.

Table 1. Summary of data available across breeds: number of calves per year, pedigree size, genotyped animals, years analysed, and year of introduction of genomic selection in each breed.

Breed	Calf/year	Pedigree	Genotypes	Years analysed	Introduction of genomic selection
MRY	5,053	205,934	4,645	1975-2021	2018
Norwegian Red	35,701	721,805	193,489	1975-2020	2016
Abondance	25,020	807,387	16,427	2000-2020	2014
Tarentaise	9,514	259,150	8,882	2000-2020	2014
Vosgienne	3,738	99,833	4,466	2000-2020	2014

Population statistics

We used Retriever v1.0 (Windig & Hulsegge, 2021) to explore population structure and statistics based on pedigree data. The average generation interval (L) per year, defined as the average age of the parent(s) at the time of birth of their offspring, was computed for: sires, dams, and both parents. Furthermore, we explored changes in the number of males and females becoming sires and dams, and in the number of sires used and number of calves per sires in each year. Finally, we explored changes in sires' contribution, looking at the contribution (expressed as percentages) of the ten most used sires in each year to the total number of offspring born in the same year.

Pedigree-based and genomic-based measures of genetic diversity

Different pedigree-based measures of genetic diversity were computed in Retriever v1.0 (Windig & Hulsegge, 2021). These measures used the whole pedigree and were averaged per year. Inbreeding coefficients for each animal in the pedigree (F_{PED_ALL}) were calculated following

Meuwissen and Lou (1992). Kinship coefficients (f_{PED}) between each animal and all other animals born in the same year were calculated following Sargolzai et al. (2005). Moreover, f_{PED} was computed without self-kinship (with self-kinship being equal to $(1 + F)/2$) for all animals in the pedigree, sires, dams, and both parents.

For genotyped animals, genomic inbreeding (F_{ROH}) was calculated based on runs of homozygosity (ROH) detected using Plink v1.9 (Chang et al., 2015) and analysed using the detectRUNS R package (Biscarini F et al., 2019). Plink parameters were: *--homozyg-window-snp 15, --homozyg-gap 150, --homozyg-snp 15, --homozyg-density 75, homozyg-kb 1000*. Thus, ROH were defined using a scanning window of 15 homozygotes SNP. ROH must have had a maximum gap between two SNPs of 150 kb, a minimum of 15 SNP, a minimum of one SNP per 75 kb, and a minimum length of 1,000 kb.

Based on observed trends in pedigree-based inbreeding, specific periods were defined for each breed to calculate annual and generation rates of inbreeding. For MRY these periods were 1975-2000, 2000-2013, 2013-2019, and 2019-2021. For NRD the defined periods were 1975-2000, 2000-2010, 2010-2016, and 2016-2020. For ABO, TAR, and VOS the defined periods were 2000-2014, and 2014-2020.

Annual rates of inbreeding (Δ) of F_{PED_ALL} and F_{ROH} coefficients were computed following Pérez-Enciso (1995), i.e., as the opposite of the slope of the regression of the $ln(1 - \bar{x})$ on the year of birth, with $\bar{x}$ being the average year value of either F_{PED_ALL} or F_{ROH}. Rates of inbreeding were computed for specific intervals of years based on observed trends in inbreeding. Inbreeding rates per generation (Δ_{gen}) were then obtained by multiplying the annual rates of inbreeding by the average generation interval of both parents in the years considered. Rates are hereafter expressed as percentages.

Genetic trends and gains

To estimate the impact of GS on genetic gains, we investigated changes in trends and gains on the total merit index (TMI), which is the aggregated breeding index composed of traits related to production as well as other traits (e.g., health, fertility). As such, negative impacts of inbreeding on genetic gains would be reflected into trends and rates in TMI genetic gains. Genetic gains were defined as the slope of the regression of the average TMI in an interval of years on the corresponding years.

3. Results

Population structure

MRY

Figure 1 reports the number of males becoming sires and of female becoming dams in MRY, while Figure 3 shows the number of sires used in each year, the number of litters, and the number of calves per sire. Overall, there has been a reduction over time of the number of sires and dams for MRY (Figure 1). Values close to zero for the years 2020 and 2021 are due to male and females being too young to give birth to offspring yet. The highest number of females becoming cows was in 1999 with 1,799 individuals, remaining around or above 1,500 until 2015 when the number started to decrease over time. The number of males becoming sires started reducing from 1975 onwards, with 367 sires in 1975, 187 sires in 2020, and 85 sires in 2018 (Figure 1). Similarly, Figure 3 shows that the number of sires used in each year decreased over time, going from 607 in 1975 to 356 in 2021. On the other hand, the number of litters and the number of calves per sires increased from 1975 to 2015-2016. These results suggest an increased sires' contribution over time, but from fewer sires.

Figure 5 shows the sires' contribution for the top 10 MRY sires in each year. On average across the interval 1975-2021, the top 10 MRY sires contributed to 35.86% of the offspring born each year,

with the top sire contributing on average 8.5% of the offspring born each year. Overall, the top 10 sires' contribution was around 30% for the period 1975-1993 and increase further around 40% up to 2013 (Figure 5). In more recent years (i.e., 2014-2021) the top 10 sires' contribution reduced back to around 30%

NRD

Figure 2 reports the number of males becoming sires and of female becoming dams in NRD, while Figure 4 shows the number of sires used in each year, the number of litters, and the number of calves per sire. In 1975, there were 246 males becoming sires, which remained around 200 over the period 1975-2008, except for a peak in 2000 (number of males becoming sires increased to 287). Finally, from 2013 onwards the number of males becoming sires started to reduce (Figure 2). The number of females becoming steadily increased from 1975 onwards, moving from 5,076 in 1975 to 22,225 in 2015. An inversion of trends was observed from 2015 onwards, with the number of females becoming dams reducing over time (13,853 in 2019 and 5,269 in 2020, although this last year may be not complete due to young animals not having offspring yet, as explained above) (Figure 2). Figure 4 also shows a reduction in the number of sires used in each year from 2015 onwards (from 562 in 1975 and 537 in 2015 to 228 in 2020), while, at the same time, the number of calves per sire increased (from 6.98 in 1975 and 26.15 in 2015 to 150.62 in 2020). This pattern is likely due to the implementation of genomic selection which allows to screen more animals reducing the number of sires used.

Figure 6 shows the sires' contribution for the top 10 NRD sires in each year. Overall, the top 10 sires contribution increased over time from 1975 to 2000 (average of 29.58% in the 1975-2000 period, moving from 20.1%in 1975 to 38.9% in 1999). The top 10 sires contribution kept increasing in the period 2000-2016 with an average value of 51.06%. From 2017 onwards the contribution of the top 10 sires started to reduce: average of 33.25% for 2017-2020. This reduction in the contribution of the top 10 sires after the implementation of genomic selection, despite the observed reduction in the number of sires during the same period, is likely related to a more balanced contribution of sires' usage in the population achieved through management practices when implementing genomic selection in the breeding program.

ABO, TAR, VOS

Figure 2 reports the number of males becoming sires and of female becoming dams per year in each of the three French breeds. ABO is the biggest breed as shown by the number of sires and dams, followed by TAR, and VOS. In all of the three French breeds, the number of females becoming dams was steadily increasing over time up to or close to the year of introduction of genomic selection, i.e., around 2014 and 2015 (Figure 2): the number of females moved from 5,898, 2,135, 390 in 2000 to 7,417, 2,770, 626, in 2014 for ABO, TAR, and VOS, respectively. Short after the introduction of genomic selection, the number of females becoming dams started to reduce in all the three breeds: 4,342, 1,739, and 410, in 2018 for ABO, TAR, and VOS, respectively. For ABO, the number of males becoming sires was rather stable and slightly increased over time (from 137 in 2000 to 183 in 2014), but staring to reduce around 2017 (n = 145) (Figure 2). For TAR, there were some fluctuations in number of males becoming sires (Figure 2), while a reducing trend was present from 2012 onwards (except for the year 2017): from an average of 56.27 sires for the period 2000-2014 to an average of 50 for the period 2015-2018. VOS was the breed showing the most variation in the number of males becoming sires in each year which was likely due to its small population size (Figure 2). The average number of males becoming sires for VOS was 16.2 for the period 2000-2014 and 22.5 for the period 2015-2018, therefore showing a slight increase. As mentioned above, values close to zero for the years 2019 and 2020 are due to male and females being too young to give birth to offspring yet.

Figure 4 shows the number of sires used in each year, the number of litters, and the number of calves per sire in each of the three French breeds. Overall, there was a positive trend for all the three breeds, with the number of sires used each year increasing over time, also after genomic selection, and moving from 288, 122, and 44 in 2000 to 437, 177, and 69 in 2014, and to 449, 168, and 100 in

2020 for ABO, TAR, and VOS, respectively. The number of calves per sire remained overall stable over time (Figure 4), with average values of 61.66, 54.56, and 26.01 for ABO, TAR, and VOS, respectively in the period 2000-2020.

Figure 6 shows the sires' contribution for the top 10 sires in each year and each of the three French breeds. For ABO, there was a high contribution of the top 10 sires despite being the largest French breed analysed, with an average top 10 sires contribution of 54.78% in the period 2000-2015. Reduction in the contribution of top 10 sires was observed in more recent years after the implementation of genomic selection: average top 10 sires contribution of to 29.56% in the period 2016-2020. For TAR, the top 10 sires contributed close to 50% in the period 2000-2016 (average of 50.86%), while the contribution reduced from 2016 onwards (average of 31.86% in 2016-2020). VOS was the breed showing the highest contribution of the top 10 sires, with values above 65% and close to 75% for the 2000-2011 period (average of 70.14%). From 2012 onwards, there was a reduction in the top 10 sires contribution for VOS, although values remained high and close to 50% (average of 53.6% for the 2012-2020 period). Such higher contribution of the top 10 sires for VOS was expected given the small population size and the small number of AI sires selected each year. The reductions observed for breeds such as ABO and TAR in more recent years after the implementation of genomic selection are likely related to achieving a more balanced sires' contribution and usage through management practices.

Figure 1. Number of females becoming dams (in orange, and on the left y-axis) and number of males becoming sires (in blue, and on the right y-axis) in each year for MRY breed (vertical blue line indicates the year of introduction of GS).

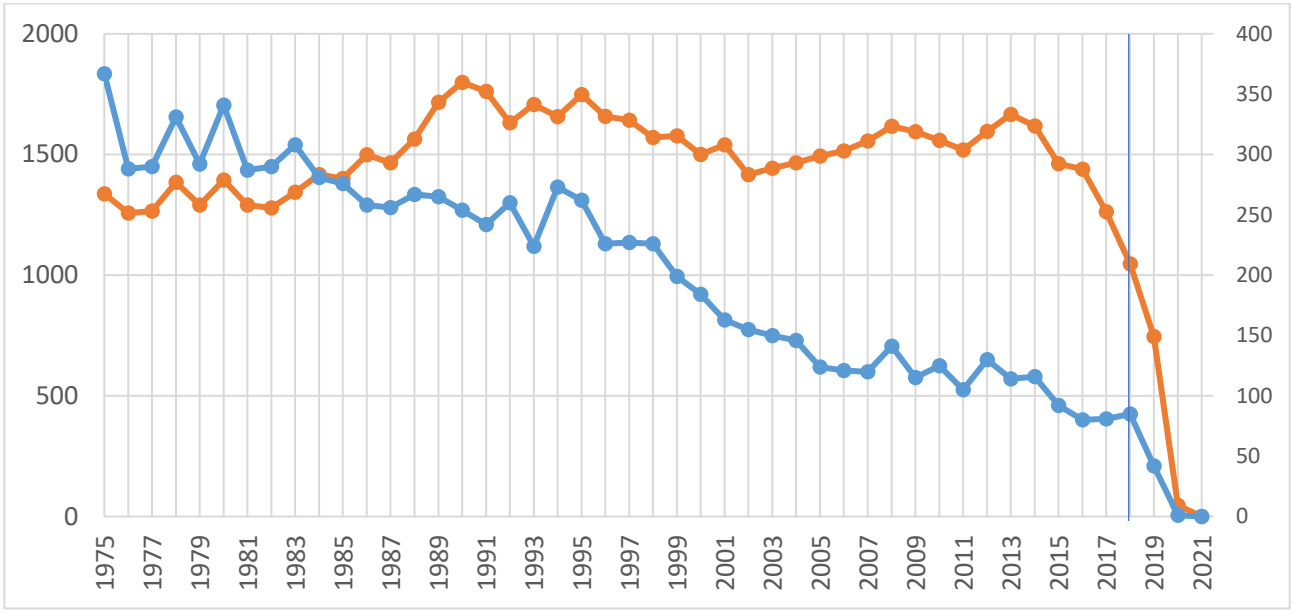


Figure 2. Number of females becoming dams and number of males becoming sires in each year for NRD, ABO, TAR, and VOS breeds (vertical blue line indicates the year of introduction of GS).

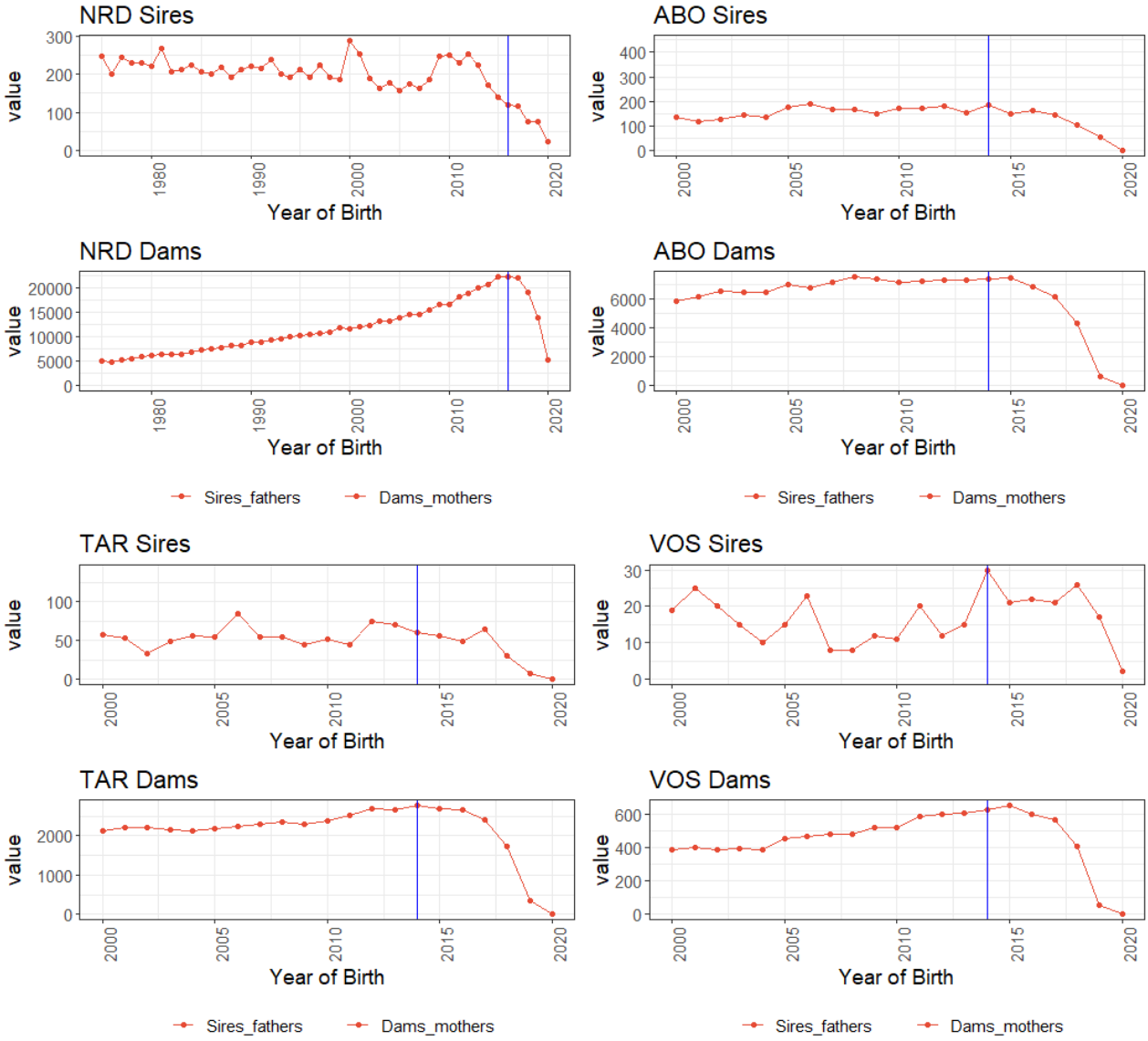


Figure 3. Number of sires used in each year (in grey), and number of litters (in blue) on the left y-axis, and number of calves per sires (in green) on the right y-axis per year for MRY (vertical blue line indicates the year of introduction of GS).

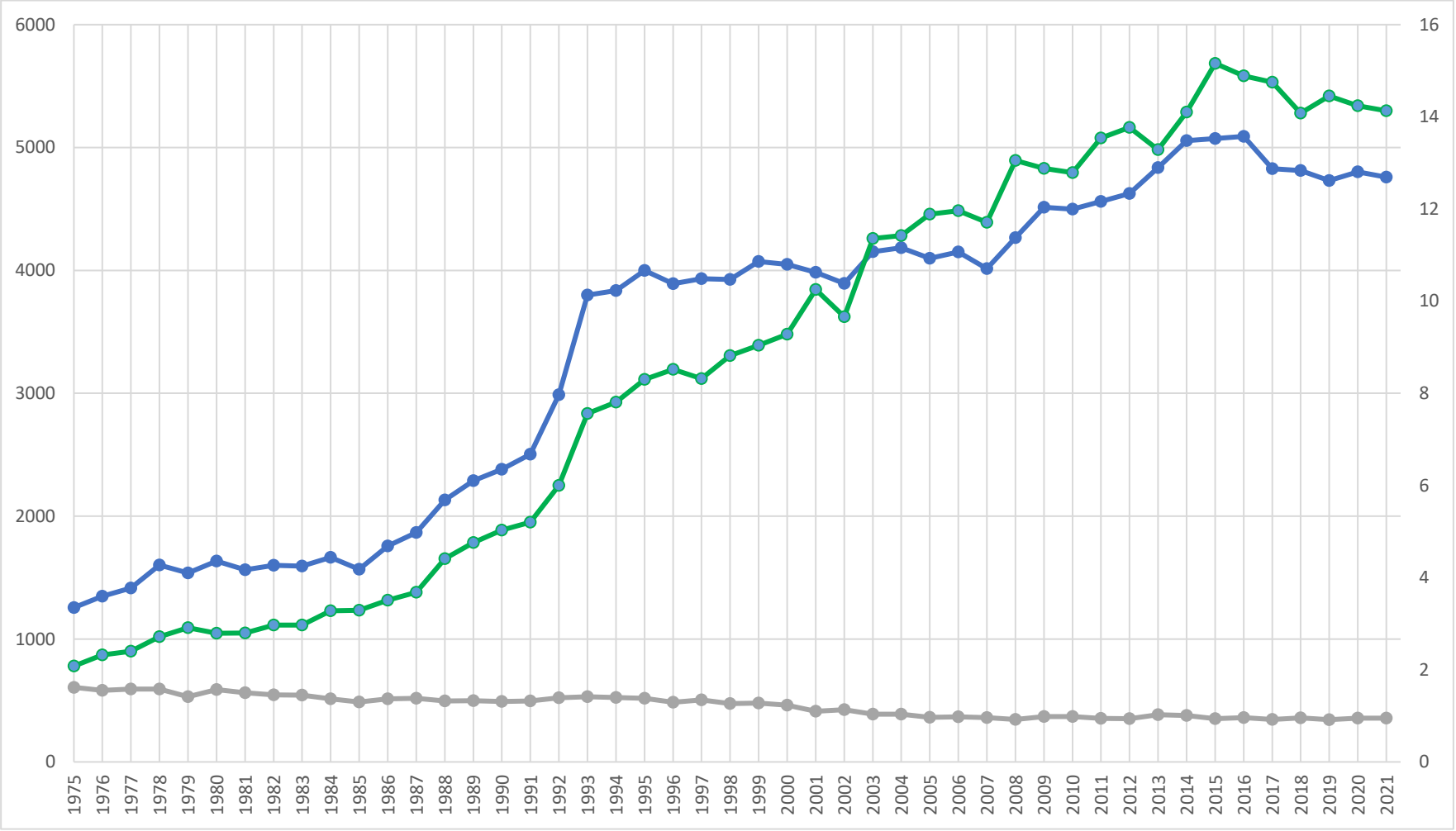


Figure 4. Number of sires (in green, "number_fathers"), number of litters per sires (in blue, "nests_per_father"), and number of calves per sires (in red, "calves_per_father") for NRD, ABO, TAR, and VOS (vertical blue line indicates the years of introduction of GS).

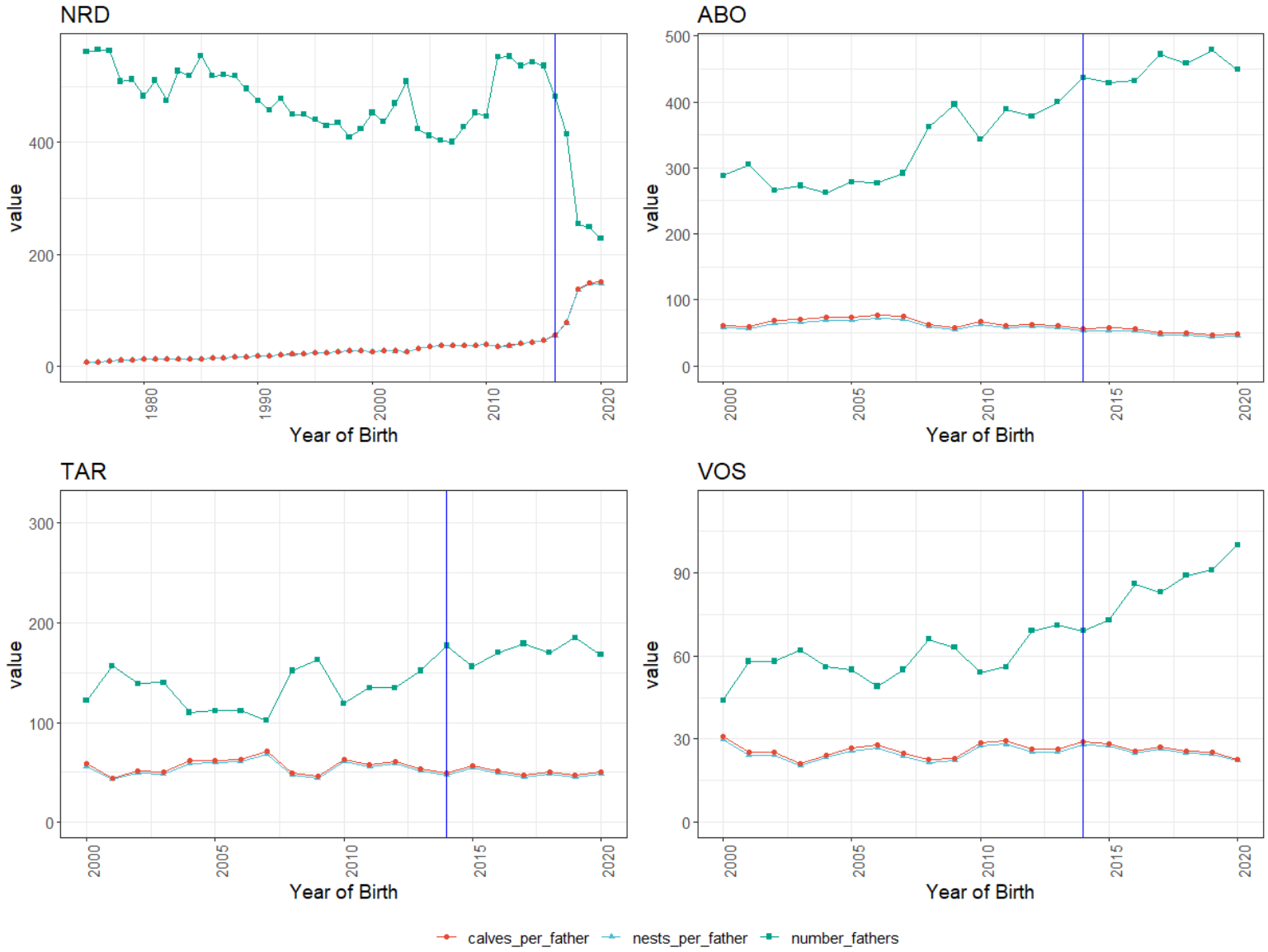


Figure 5. Contribution (in percentage) of the top ten MRY sires for animals born in each year (vertical blue line indicates the introduction of GS).

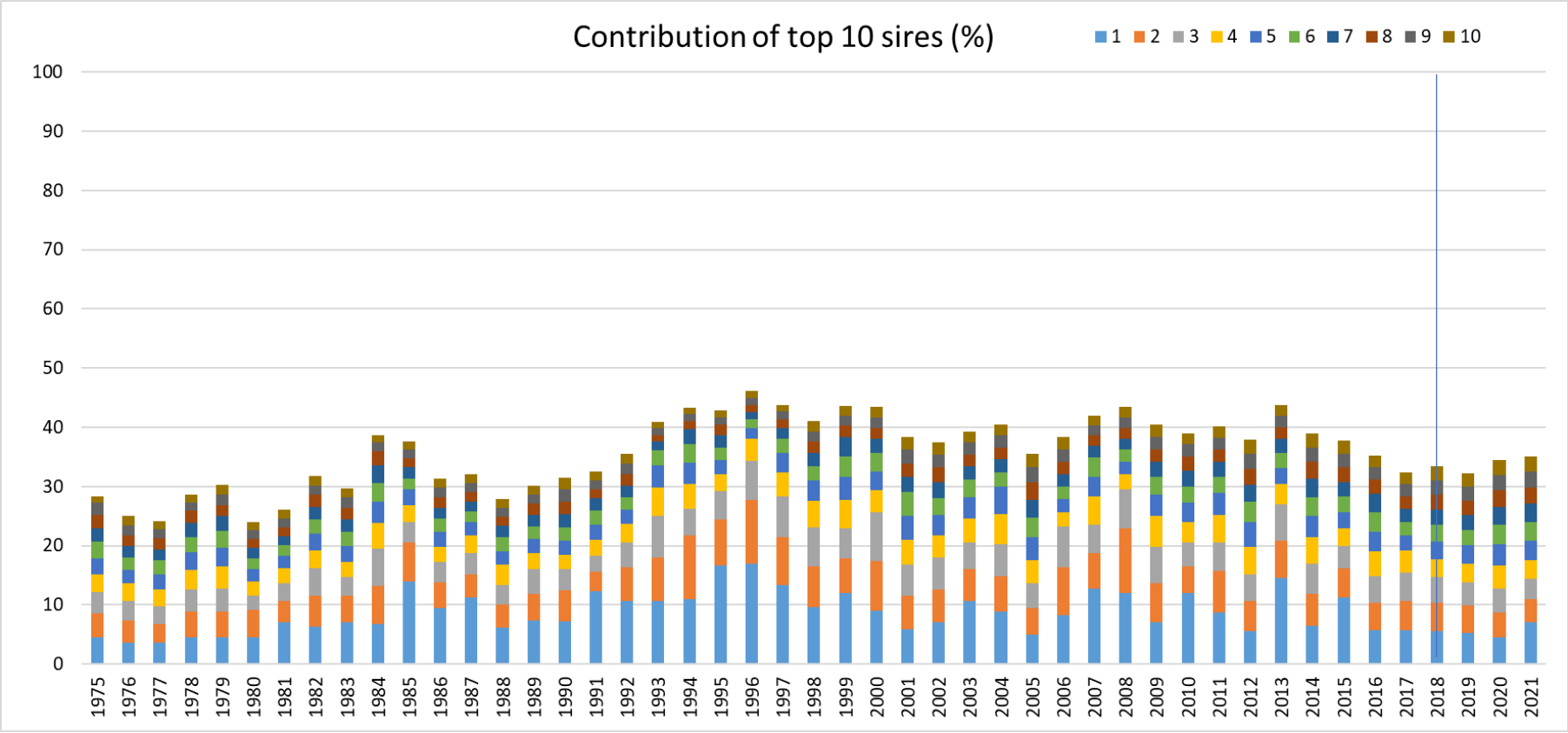
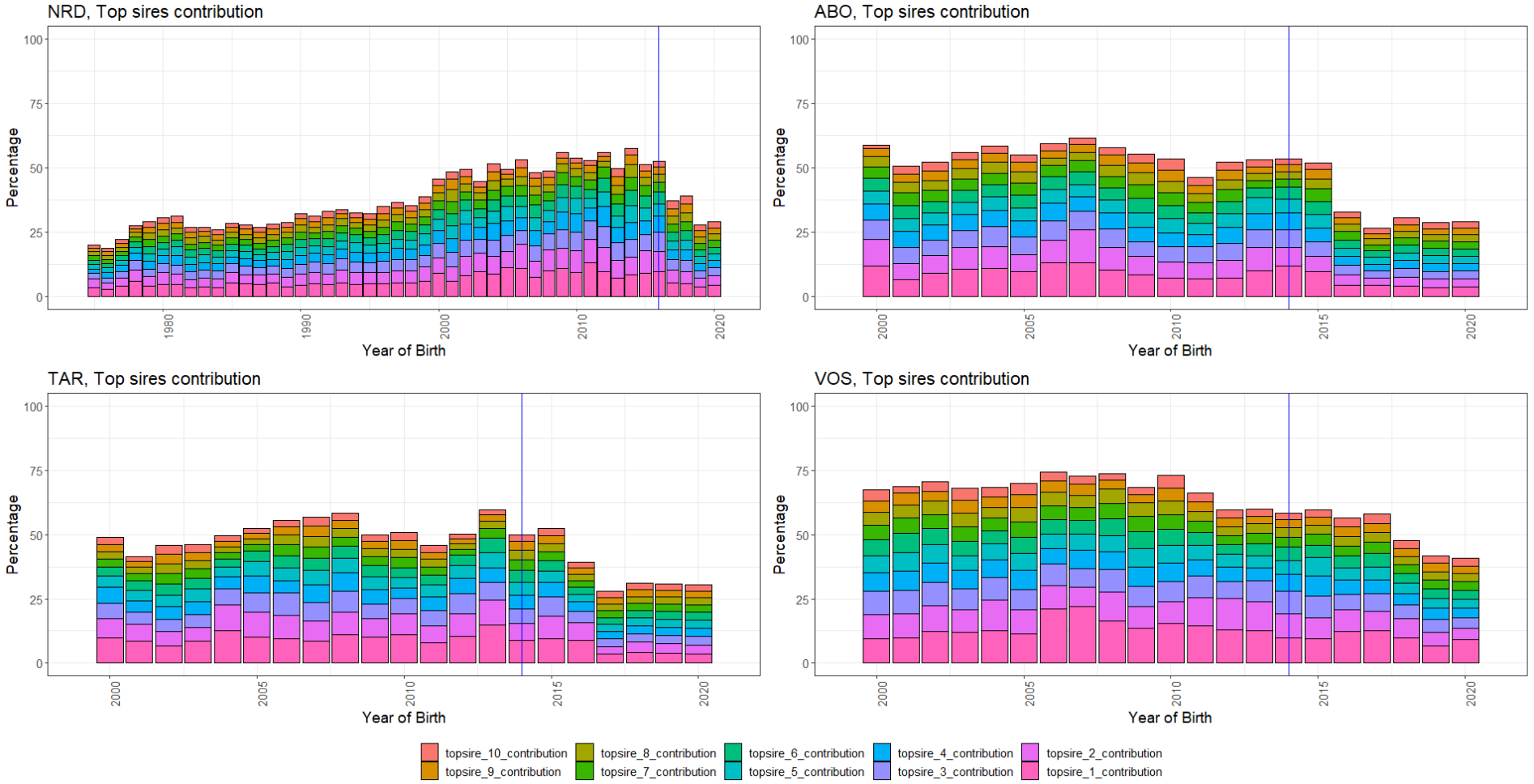


Figure 6. Contribution (in percentage) of the top ten sires for animals born in each year for NRD, ABO, TAR, and VOS (vertical blue lines indicates the year of introduction of GS).



Genetic diversity

MRY

For MRY, *L* computed across the whole pedigree was equal to 5.68 years for both parents, 6.64 for sires, and 4.72 for dams. Figure 7 reports *L* computed per year interval for the analysed period. For dams, *L* was stable at around 5 years across the whole 1975-2021 period. For sires, *L* was close to 5 around 1950 (results not shown) and, as expected, increased up to 8 in 1975-1980, fluctuating then around 6-7 from 1980 onwards depending on the period considered: *L*≈6 in 2000-2003 and 2015-2017, and *L*≈7 in 2004-2014 and 2018-2021). As *L* for dams was overall stable across the years analysed, changes in *L* for both parents followed mostly changes in *L* due to sires. Table 2 reports *L* for both parents in the different analysed periods for both all animals in the pedigree and genotyped animals only. Overall, longer generational intervals were observed for genotyped animals up to the period of 2000-2013,while from 2013 onwards *L* was larger for all animals in the pedigree compared to genotyped ones, likely due to changes in the breeding program and the shortening of generational intervals due to the usage of GS.

Trends in inbreeding and kinships for MRY are reported in Figure 8, while Table 2 reports rates of inbreeding per year and generation for the periods analysed. From 1975, both F_{PED_ALL} and kinship coefficients increased steadily up to 2013. After 2013, F_{PED_ALL} started to decrease up to 2019 and showed to increase again in 2020 and 2021. Similarly, kinship coefficients showed a decreasing trend from 2013 to 2017 and a slight increasing trend from 2017 to 2021. Kinship coefficients excluding self-kinship (f_{PED}) (Figure 8) were always smaller than F_{PED_ALL} until 2007. From 2007 kinship coefficients excluding self-kinship were larger than F_{PED_ALL}, especially in the period 2013-2021. Comparing kinship coefficients between parents showed that sires and dams had similar kinship until 1975-1980 (Figure 8). From this decade, both sires' and dams' kinships started to increase, although sires' kinship was always smaller than dams' kinship. Furthermore, comparing kinship coefficients for sires and dams with F_{PED} and f_{PED} showed that sires' kinship was always smaller than the average inbreeding per year, and that sires were recruited from animals that were less related than average (Figure 8). Instead, dams showed higher kinship coefficients than the average inbreeding per year from 2013 onwards, and a higher kinship than average animals from 2015 onwards. A smaller kinship for sires compared to dams was unexpected given the size of the MRY population, and could be due to selection schemes aiming to manage inbreeding in the population which may have focussed more on sires rather than on dams.

Table 2. MRY annual (Δ) and generation (Δ_{gen}) rates of pedigree-based inbreeding for all animals in the pedigree (F_{PED_ALL}) and genomic-based inbreeding for genotyped animals only (F_{ROH}), and average generation interval for both parents (L) in different periods for all animals in pedigree (ALL) and genotyped animals only.

	L		Δ		Δ_{gen}	
Years	***ALL***	***Genotyped***	F_{PED_ALL}	F_{ROH}	F_{PED_ALL}	F_{ROH}
1975-2000	5.84	6.85	0.10%	0.11%	0.61%	0.76%
2000-2013	5.61	6.21	0.08%	0.08%	0.46%	0.48%
2013-2019	5.64	5.28	-0.12%	-0.21%	-0.67%	-1.13%
2019-2021	5.81	5.40	0.09%	0.17%	0.51%	0.92%

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The average F_{ROH} for genotyped animals is reported in Figure 9 for the period 1975-2021. F_{ROH} increased steadily from 0.05 in 1975 up to 0.083 in 2001 and was then stable around 0.08 until 2013. F_{ROH} started to decrease in the period 2013-2019, with values of F_{ROH} of 0.069 in 2019. Finally, F_{ROH} showed a slight increase from 2019 onwards, which was also observed for F_{PED_ALL} (Figure 8). Similarly to F_{PED_ALL}, F_{ROH} suggest a slight decreasing trend in inbreeding in the period 2013-2019.

Inbreeding rates were always positive besides for the period 2013-2019 (Table 2). We observed an increasing inbreeding in recent years (2019-2021), which corresponded to inbreeding rates per generation of 0.92% based on F_{ROH} (Table 2). Furthermore, the corresponding F_{PED} using only a sub-population of MRY purebred animals was 1.56% (results not shown). The F_{ROH} for the 2019-2021 period was the only one showing inbreeding rates close or over the 1% recommended value by FAO (Table 2). Overall, inbreeding rates for the whole population were lower than for genotyped animals, but still showing a positive trend. These results suggest a possible increasing trend in inbreeding due to the onset of genomic selection in 2018. Increases in inbreeding could be due to changes in the population structure brought by the implementation of genomic selection rather than to genomic selection itself: for instance, shorter generation intervals due to the selection of younger bulls or a reduction in the number of bulls used. The average generation interval for the period 2019-2021 was not smaller than that of 2013-2019 (Table 2). Moreover, the number of sires in the period 2019-2021 remained quite stable relative to the last decade (Figure 3). However, the number of sires of genotyped animals started to decrease from 2016 (n=85) onwards which may have an impact on the observed inbreeding rates for the 2019-2021 period.

Figure 7. Generation interval trends for MRY (vertical blue line indicates the introduction of GS).

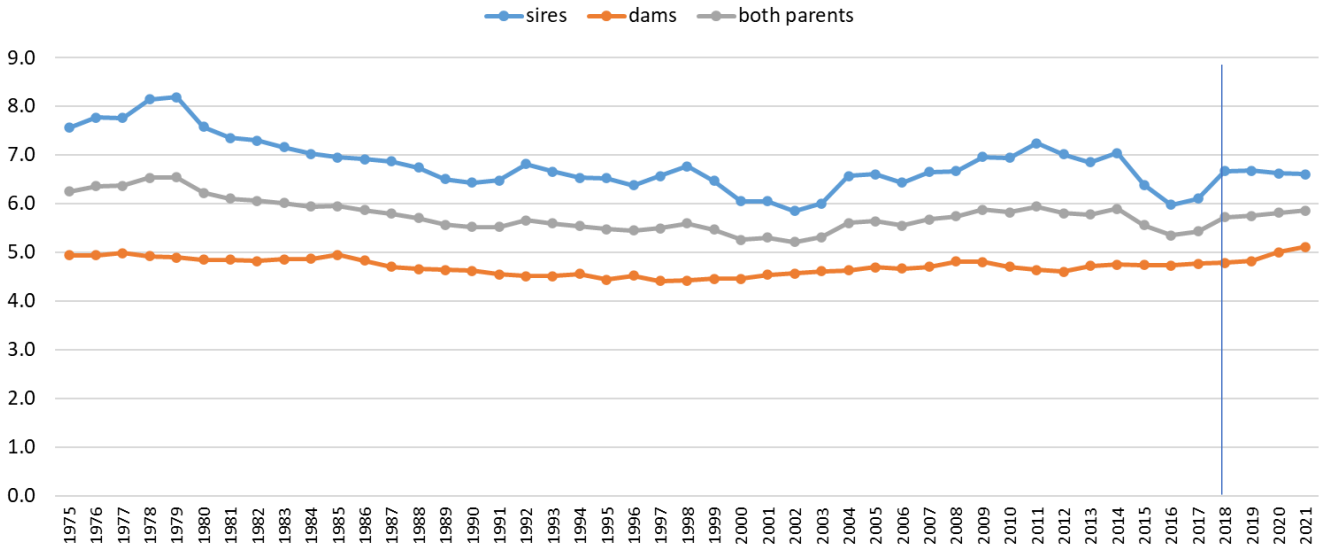


Figure 8. Breed = MRY. Yearly average of pedigree-based coefficients of inbreeding and kinship for all animals in the pedigree (vertical blue line indicates the introduction of GS).

F all animals: F_{PED_ALL}, f: kinship, f excl. self: kinship excluding self-kinship (f_{PED}).

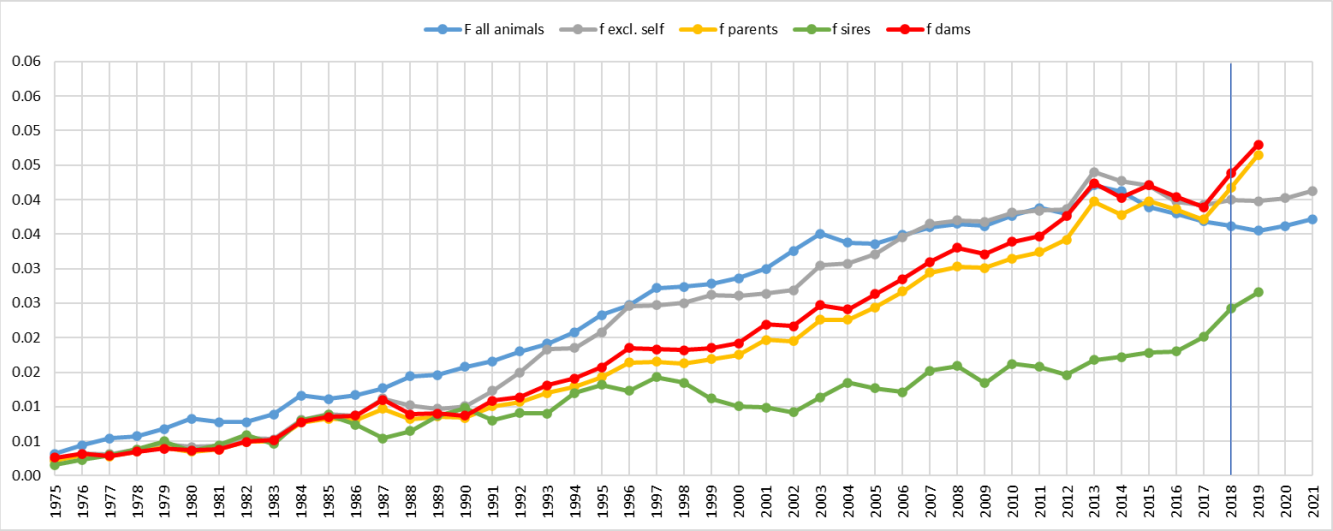
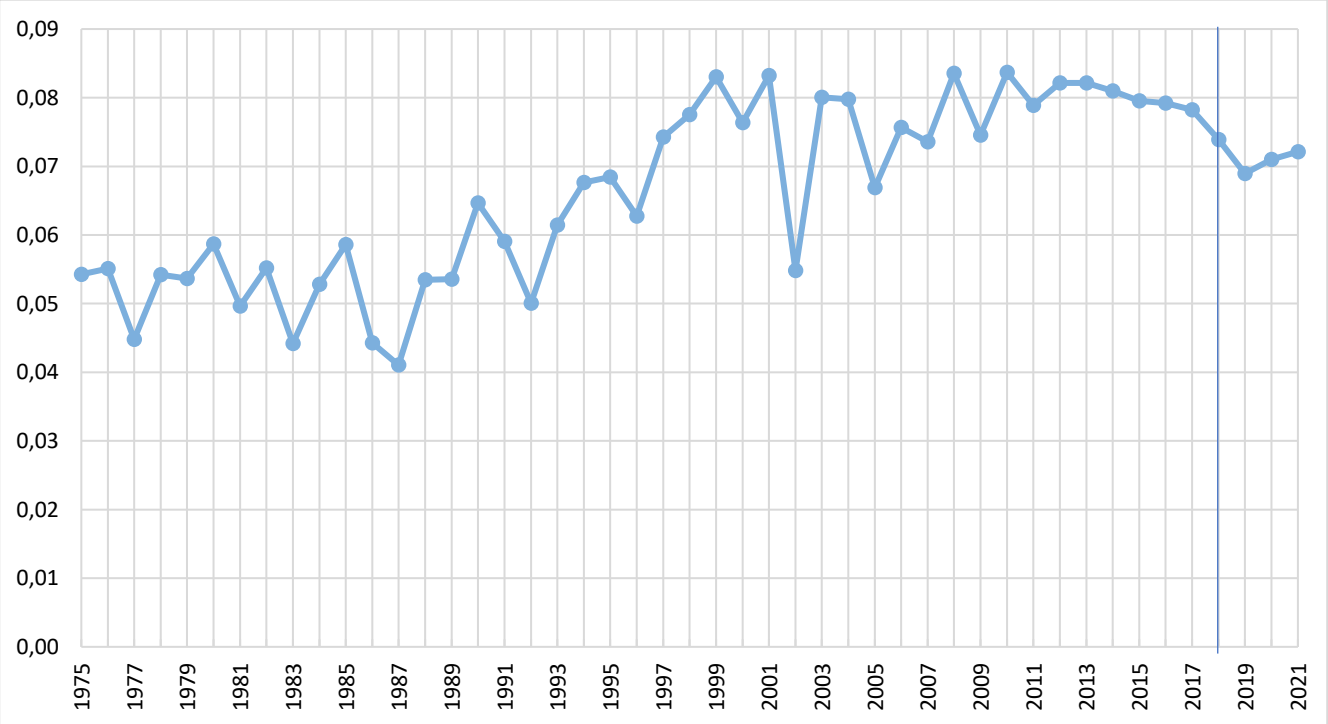


Figure 9. Breed = MRY. Yearly average of genomic-based coefficients of inbreeding for genotyped animals (F_{ROH}) (vertical blue line indicates the introduction of GS).



NRD

Figure 10 shows *L* computed per year for the whole period analysed, while Table 3 reports *L* for the different periods analysed. *L* was stable over time up to 2016, with values close of *L* close to 3.5 for dams and 6 for sires. From 2016 onwards, with the onset of genomic selection, a decrease in *L* was observed for sires with values being close to *L* = 3 from 2017 onwards (Figure 10). Similarly, a slight decrease in *L* was also observed for dams after 2016, with values of *L* closer to 3. The observed changes in *L* for both parents are mostly driven by changes in the generation interval of sires. Overall, similar generation intervals were observed for all animals in the pedigree and for genotyped animals (Table 3). The *L* for both parents reflected the reduction in generational interval after the implementation of genomic selection, with *L* reducing from 4.57 in the period 2010-2016 to 3.53 in the period 2016-2020 (Table 3).

Figure *11* shows inbreeding and kinship trends for NRD. Overall, F_{PED_ALL} showed an increasing trend in inbreeding from 1975 until the introduction of genomic selection in 2016: corresponding to an inbreeding rate per generation of 0.28% in the period 1975-2000, 0.22% in the period 2000-2010, and 0.32% in the period 2010-2016 (Table 3). After the introduction of genomic selection, inbreeding kept increasing, although with lower generational rates: rate of 0.30% in 2010-2016 (Table 3). Kinships in the population decreases from 2009 onwards and keep decreasing after the introduction of genomic selection (

Figure *11*). On the other hand, kinship for parents kept increasing over time diverging from the level of kinship in the whole population for both dams and sires from 2010 and 2016 onwards, respectively (

Figure *11*). F_{ROH} was generally stable over time and indicated an increase in inbreeding rates after the introduction of genomic selection (Figure 12, Table 3). Overall, generational rates of inbreeding for both F_{PED_ALL} and F_{ROH} were below the 1% threshold recommended by FAO, with F_{ROH} showing lower rates compared to F_{PED_ALL} (Table 3).

Table 3. NRD annual (Δ) and generation (Δ_{gen}) rates of pedigree-based inbreeding for all animals in the pedigree (F_{PED_ALL}) and genomic-based inbreeding for genotyped animals only (F_{ROH}), and average generation interval for both parents (L) in different periods for all animals in pedigree (ALL) and genotyped animals only.

	L		Δ		Δ_{gen}	
Years	***ALL***	***Genotyped***	F_{PED_ALL}	F_{ROH}	F_{PED_ALL}	F_{ROH}
1975-2000	4.78	4.79	0.06%	0.02%	0.28%	0.09%
2000-2010	4.65	4.65	0.05%	0.04%	0.22%	0.18%
2010-2016	4.57	4.55	0.07%	0.02%	0.32%	0.10%
2016-2020	3.53	3.51	0.08%	0.08%	0.30%	0.30%

ABO, TAR, VOS

Generation intervals for the three French breeds are reported in Figure 10 computed per each year for the whole period, while Table 4 shows the value of *L* computed for the specific intervals analysed. For all three breeds, *L* for dams was stable at around 5 years, with values slightly higher for VOS, which had values closer to about 5.5 (Figure 10). In ABO and TAR, *L* for sires reduced after the implementation of genomic selection in 2014. For ABO, *L* for sires showed a slight increasing trend in the period 2000 to 2014, with *L* = 7.44 in 2020 and *L* = 8.88 in 2014. After 2014, a reduction in *L* was observed for ABO sires with *L* getting closer to 5 (Figure 10; *L* for sires = 4.91 in 2020). For TAR, *L* for sires showed some fluctuations, with values overall above 7.5 in the period 2000-2015, with a maximum of *L* = 8.52 in 2010. *L* for TAR sires started to decrease from 2015 onwards, with values becoming smaller than 5 in the last three years (*L* = 4.16 in 2020). VOS showed an increasing *L* for sires over time, even after the implementation of genomic selection (Figure 10): *L* increased from 7.36 in 2000 to 10.44 in 2015. Similarly to the other breeds, VOS showed a reduction in *L* for sires after 2015, although less marked: *L* for 8.78 and 8.48 in 2019 and 2020, respectively. Overall, in all three French breeds, changes in generation intervals of both parents over time are driven by changes in the *L* for sires. *L* for both parents for the analysed periods for either all animals in the pedigree or genotype animals reflect the reduction in generation intervals for both ABO and TAR (Table 4). A possible explanation for the long generation intervals in VOS compared to ABO and TAR is that fewer AI sires are selected and available for breeding in this breed. Therefore, sires are being used for longer periods of time, increasing the sires' generation interval.

Figure *11* shows trends in pedigree inbreeding and kinships for all the three French breeds, while Figure 13 reports trends in genomic inbreeding (F_{ROH}). It should be noted that only three years of genomic data were available before the introduction of genomic selection (2012-2014) to compute rates of genomic inbreeding in the French breeds. Finally, the kinship values for years 2019 and 2020 were removed since animals born in these years are not yet parents due to their young age.

For ABO, both F_{PED_ALL} and all kinships computed are steadily increasing in the period 2000-2020 (

Figure *11*). F_{PED_ALL} inbreeding rates per generation are 1.19% in 2000-2014 and 0.99% in 2014-2020 (Table 4). Kinship for sires and dams was higher than kinship for all animals in pedigree, indicating that the recruited parents have a higher kinship than that of the population. F_{ROH} also showed increase in inbreeding (Figure 13) in the 2000-2020 period. Moreover, compared to F_{PED_ALL}, F_{ROH} showed a higher rate of inbreeding per generation before the introduction of genomic selection: 2.76% in 2000-2014 and 0.68% in 2014-2020. Thus, both F_{PED_ALL} and F_{ROH} suggest that rates of inbreeding reduced after the introduction of genomic selection in 2014. Finally, generational rates of inbreeding for both F_{PED_ALL} and F_{ROH} before genomic selection were overall close to or above the 1% threshold recommended by FAO.

For TAR, F_{PED_ALL} was stable until around 2008 and started increasing from this year onwards (

Figure *11*). F_{PED_ALL} generational rates of inbreeding were 0.35% in 2000-2014 and 0.93% in 2014-2020, indicating an increase in the rate of inbreeding after the implementation of genomic selection (Table 4). In a similar way, kinship levels also increased from 2010 onwards for both sires and dams (although with some fluctuations for sires) (

Figure *11*). Parents' kinships levels higher than those of all animals in pedigree indicates that recruited parents have higher kinship than that of the whole population (

Figure *11*). Finally, both F_{PED_ALL} and F_{ROH} showed that generational rates of inbreeding in TAR were below the 1% threshold recommended by FAO before the implementation of genomic selection, but became close to 1% after 2014 (Table 4).

For VOS, F_{PED_ALL} had the lowest level among all French breeds and showed a steady increase over time (

Figure *11*). Overall, kinship for dams increased up to 2018 to then decrease, while kinship for sires was stable in the 2000-2020 period albeit with fluctuations likely due to the small number of sires selected in this breed (

Figure *11*). As for other French breeds, in VOS, the recruited parents had higher kinship than that of the whole population (

Figure *11*). Similarly to F_{PED_ALL}, also F_{ROH} showed lower level of inbreeding in VOS breed compared to other French breeds (Figure 13). F_{PED_ALL} inbreeding rates per generation were 0.53% in 2000-2014 and 0.23% in 2014-2020, showing a decrease in inbreeding rates after the implementation of genomic selection (Table 4). Similarly, inbreeding rates per generation based on F_{ROH} showed decreasing rates of inbreeding after the implementation of genomic selection: 0.51% in 2000-2014 and 0.09% in 2014-2020 (Table 4). Finally, both F_{PED_ALL} and F_{ROH} showed that generational rates of inbreeding in VOS were lower than the 1% limit suggested by FAO.

Table 4. ABO, TAR, and VOS annual (Δ) and generation (Δ_{gen}) rates of pedigree-based inbreeding for all animals in the pedigree (F_{PED_ALL}) and genomic-based inbreeding for genotyped animals only (F_{ROH}), and average generation interval for both parents (L) in different periods for all animals in pedigree (ALL) and genotyped animals only.

	L		Δ		Δ_{gen}	
Years and breed	***ALL***	***Genotyped***	F_{PED_ALL}	F_{ROH}	F_{PED_ALL}	F_{ROH}
ABO						
2000-2014	6.67	6.59	0.18%	0.42%	1.19%	2.76%
2014-2020	5.89	5.87	0.17%	0.12%	0.99%	0.68%
TAR						
2000-2014	6.55	6.43	0.05%	0.10%	0.35%	0.64%
2014-2020	5.37	5.39	0.17%	0.18%	0.93%	0.96%
VOS						
2000-2014	7.12	6.98	0.07%	0.07%	0.53%	0.51%

2014-2020	7.77	7.61	0.03%	0.01%	0.23%	0.09%

Figure 10. Generation interval trends for NRD, ABO, TAR, and VOS (vertical blue line indicates the introduction of GS).

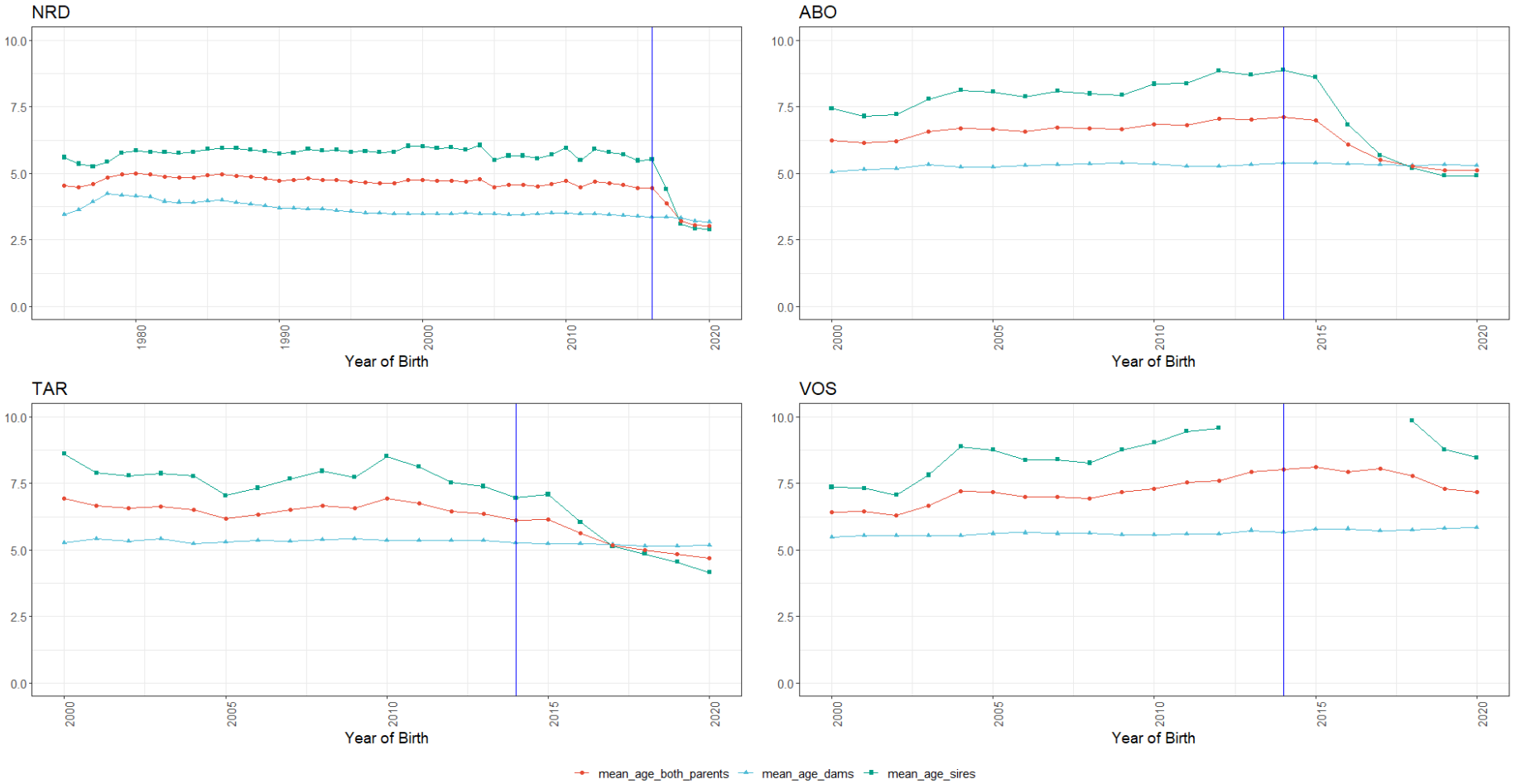


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Figure 11 Breeds = NRD, ABO, TAR, and VOS. Yearly average of pedigree-based coefficients of inbreeding and kinship for all animals in the pedigree (vertical blue line indicates the introduction of GS).

F_all_animals: F_{PED_ALL}, f: kinship, f_excl_self: kinship excluding self-kinship (f_{PED}).

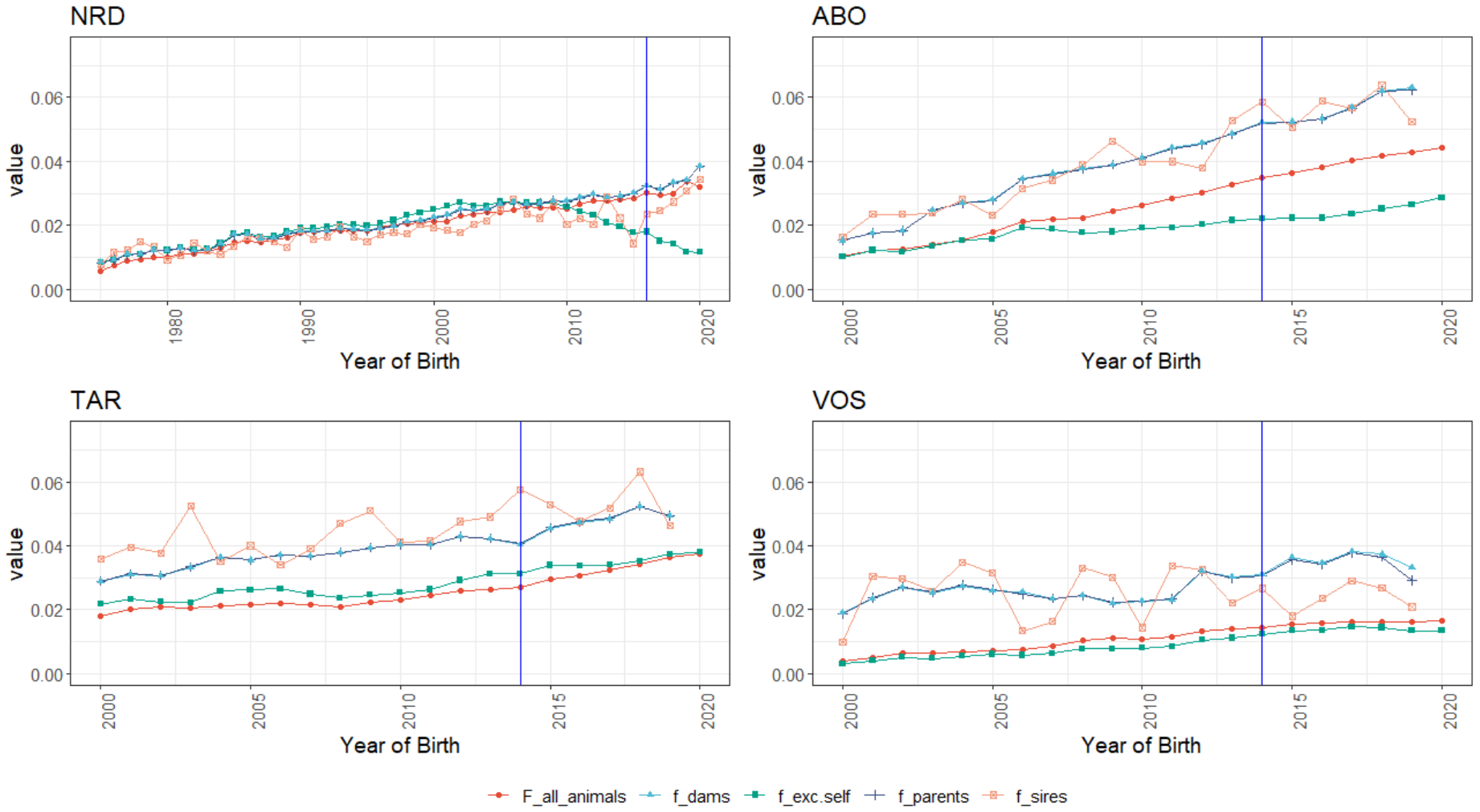


Figure 12. Breed = NRD. Yearly average of genomic-based coefficients of inbreeding for genotyped animals (F_{ROH}) (vertical blue line indicates the introduction of GS).

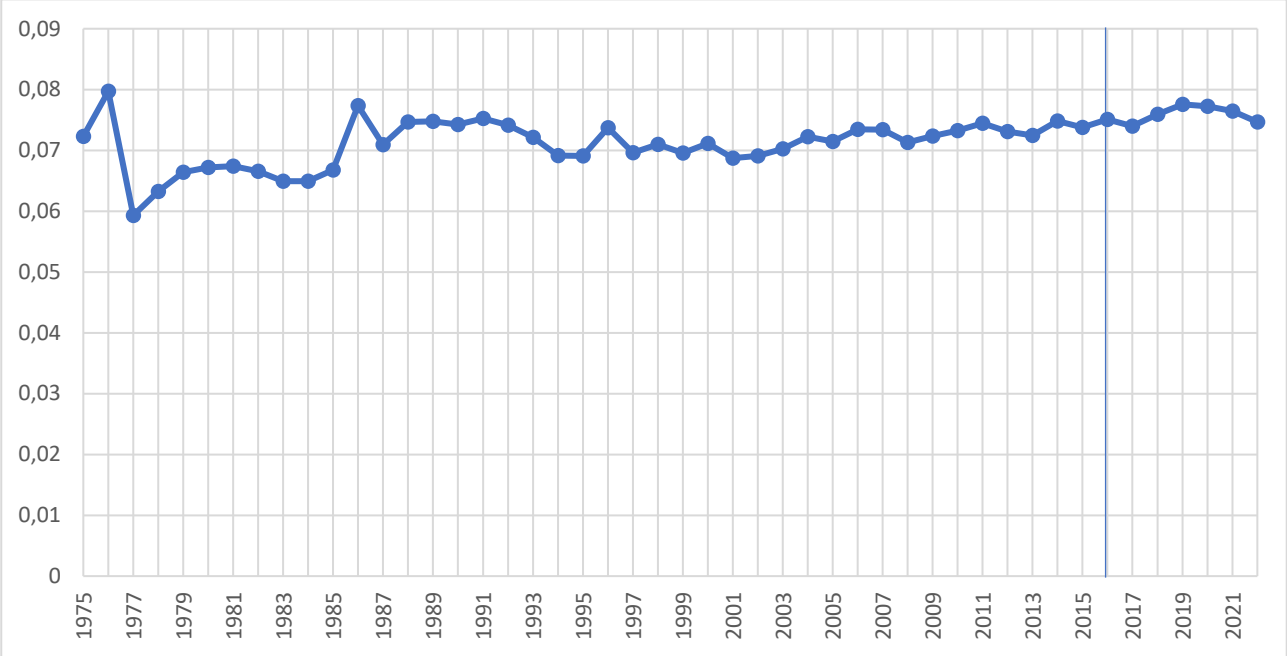
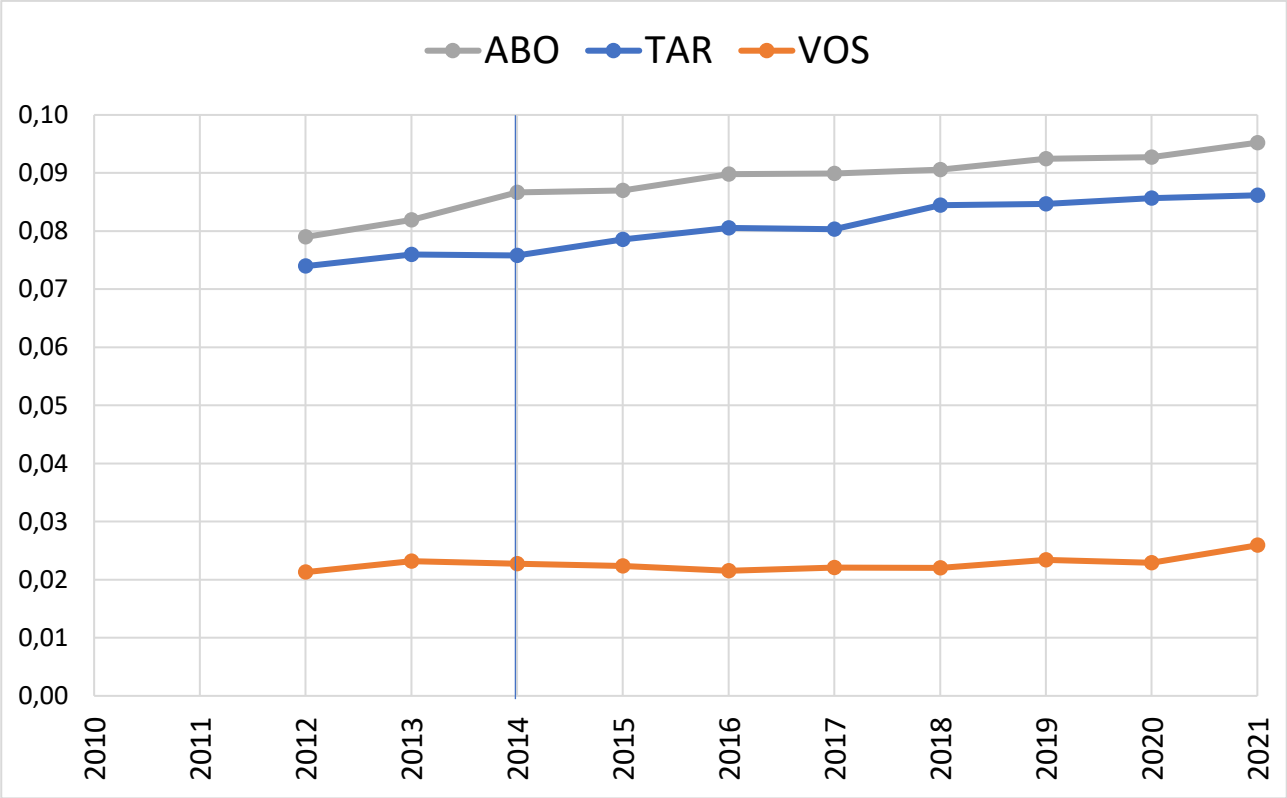


Figure 13. Breed = ABO, TAR, VOS. Yearly average of genomic-based coefficients of inbreeding for genotyped animals (F_{ROH}) (vertical blue line indicates the introduction of GS).



This project has received funding from the European Union's Horizon 2020 research and innovation programme under grant agreement N°101000226.

Genetic trends

Results on the TMI genetic trends for the analysed periods next to more recent years are reported below for each breed.

For MRY, overall, a positive genetic trend was observed for the period 2000-2020 (Figure 14). The genetic gain per year were: 9.55 for the period 2000-2013, 8.53 for 2013-2019, and 4.70 for 2019-2020. This slight reduction in the slope of the TMI genetic trend in the last 2 years is likely due to an incomplete set of observations for the year 2020. Upon further inspection of trait groups that compose the TMI for MRY, we observed that in the 2013-2019 period the genetic gains per year for production traits and lifespan reduced compared to 2000-2013, while the genetic gains for the udder health and fertility trait groups increased. This could explain why genetic gain for TMI slightly reduced in the period 2013-2019 compared to 2000-2013, with more emphasis being given to health traits over production trait in more recent years. Overall, we did not observe large impact on the TMI genetic trend before and after the implementation of GS in MRY.

A positive genetic trend was observed for NRD in the period 2001-2020 (Figure 15). Genetic gains for TMI were: 1.51 for the 2001-2010 period, 2.06 for 2010-2015, 2.92 for 2015-2020, and 3.44 for 2020-2022. Therefore, genetic gains kept increasing across the analysed year intervals. After the implementation of genomic selection, a higher genetic gain was observed compared to the previous period (2020-2022 *vs* 2015-2020).

For the French breeds, TMI data was available for males and females separately. For all three breeds a positive genetic trend was observed for TMI, with higher TMI genetic levels for males compared to females for all three breeds. For ABO, albeit with small fluctuations, genetic trends for male and females almost overlap before the introduction of genomic selection in 2014 (Figure 16). After 2014, there was an increase in genetic gain, especially for males compared to females. This is also detectable from the genetic gains in the analysed periods, with genetic gains being equal to 1.82 for males and 1.73 for females in 2000-2014, and 3.47 for males and 2.70 for females in 2014-2020. Thus, it seems that higher genetic gain was achieved with the introduction of genomic selection in ABO breed, with higher gains on males compared to females. For TAR, genetic gains were similar for males and females before 2014: genetic gain per year of 2.69 for males, and 2.35 for females in 2000-2014. Although the genetic level of males is still higher than that of females, an increase in the annual genetic gain was observed for females after the introduction of GS in 2014: genetic gain per year of 2.69 for males and 3.38 for females in 2014-2020 (Figure 17). For VOS, some fluctuations were present in the genetic trend for males (Figure 18), likely due to the small number of AI sires selected every year. For VOS, genetic gains per year were 1.48 for males and 2.11 for females in 2000-2014, and 2.65 for males and 2.03 for females in 2014-2020. For VOS, a high increase in genetic gain was detected in the period 2017/2018-2020 for milk production in both males and females, likely as a result of the onset of genomic selection a generation prior, i.e., in 2014. Thus, overall, in French breeds similar or higher genetic gains per year were observed after the introduction of genomic selection in 2014 compared to before.

Overall, the introduction of GS led to similar or higher genetic gains for TMI in all the breeds analysed and we did not observe any negative impact of genomic selection on TMI genetic gains in any of the five breeds.

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Figure 14. TMI genetic trend for MRY (vertical blue line indicates the introduction of GS).

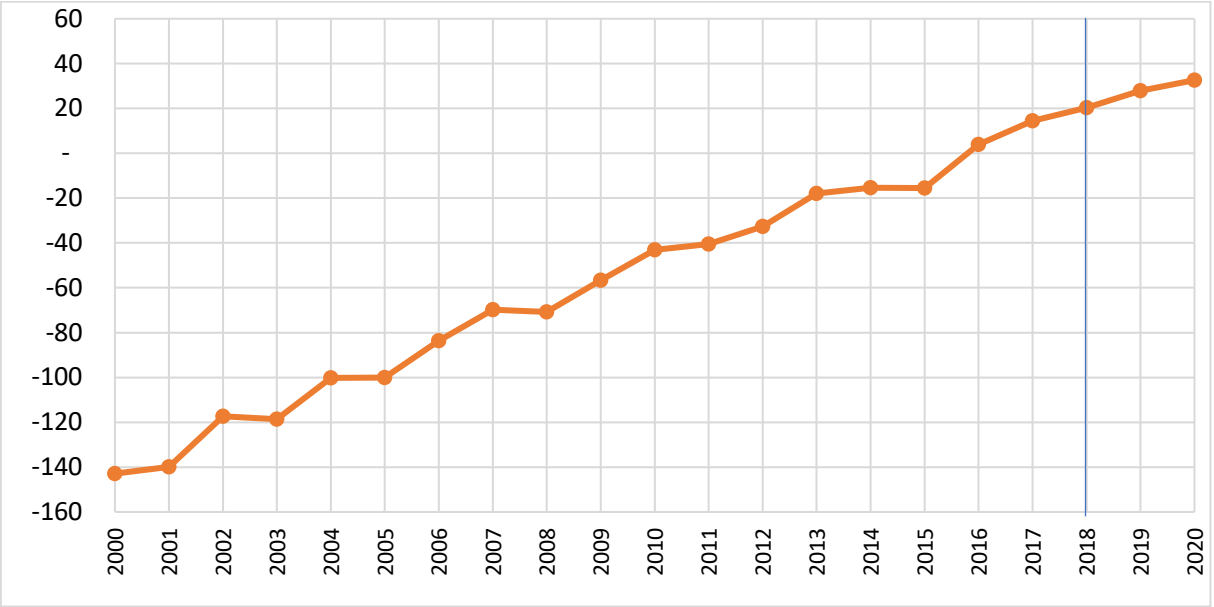


Figure 15. TMI genetic trend for NRD (vertical blue line indicates the introduction of GS).

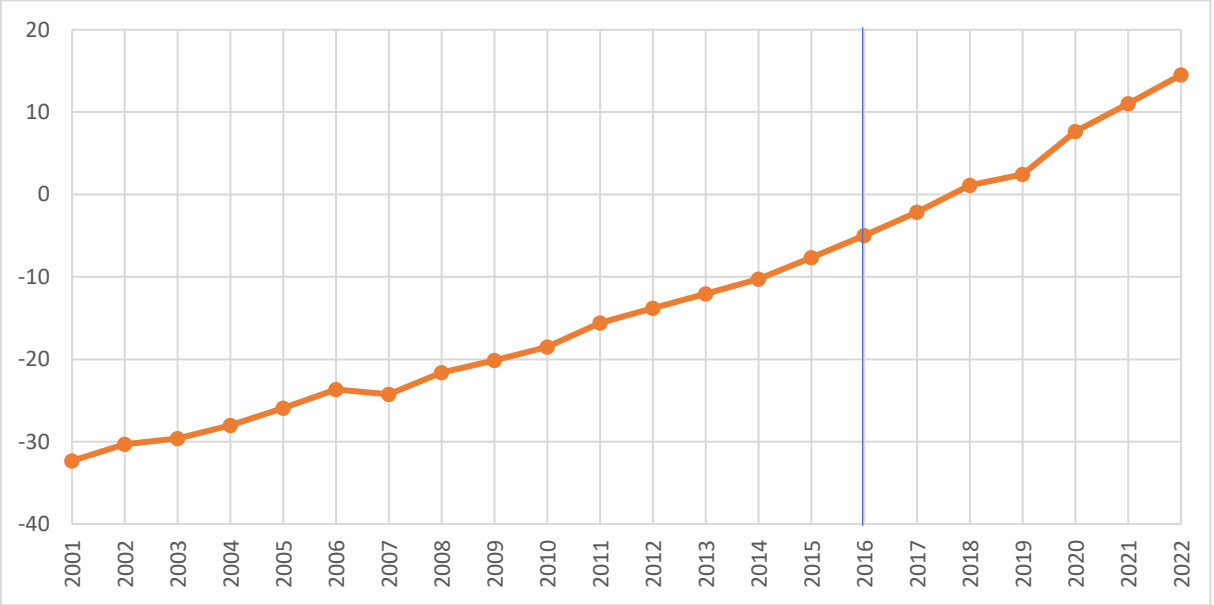


Figure 16. TMI genetic trend for ABO (vertical blue line indicates the introduction of GS).

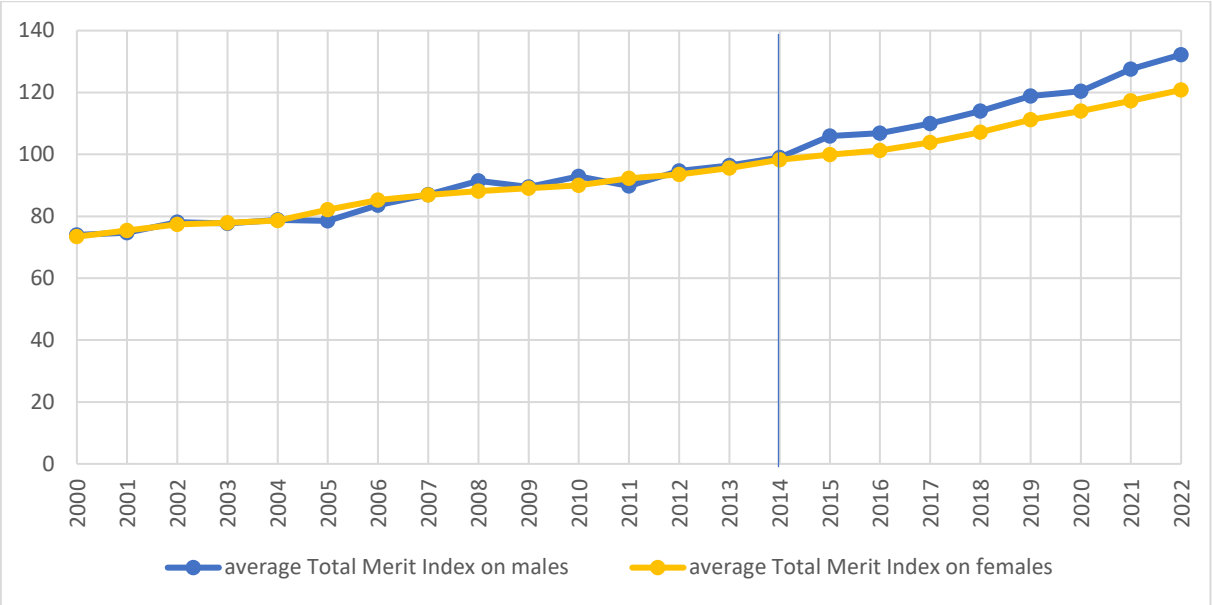


Figure 17. TMI genetic trend for TAR (vertical blue line indicates the introduction of GS).

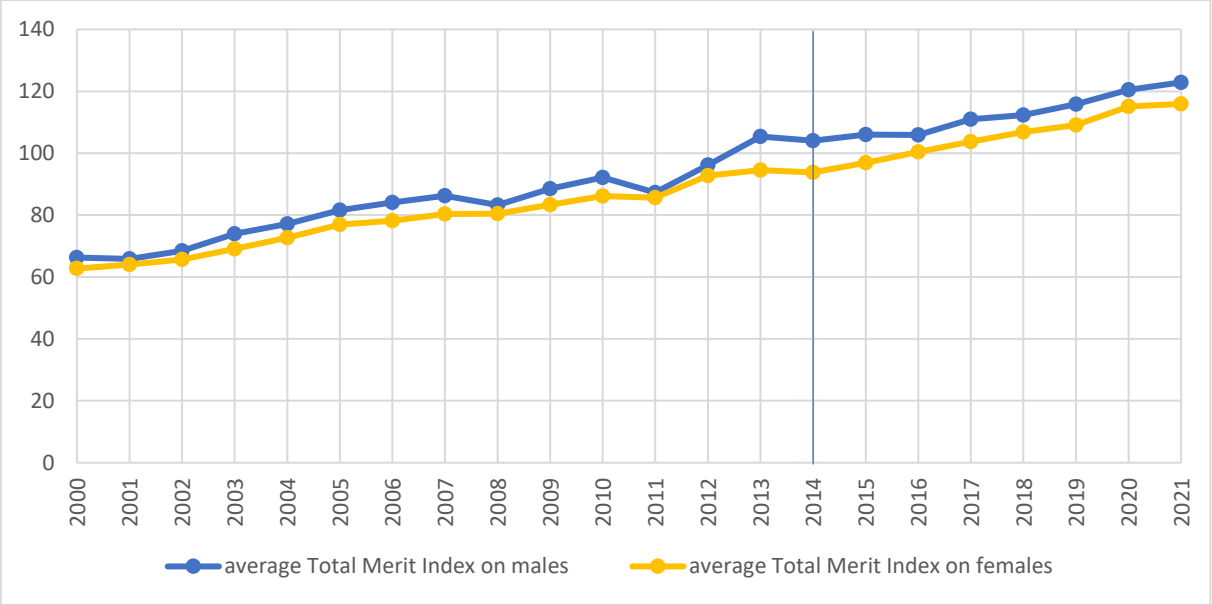
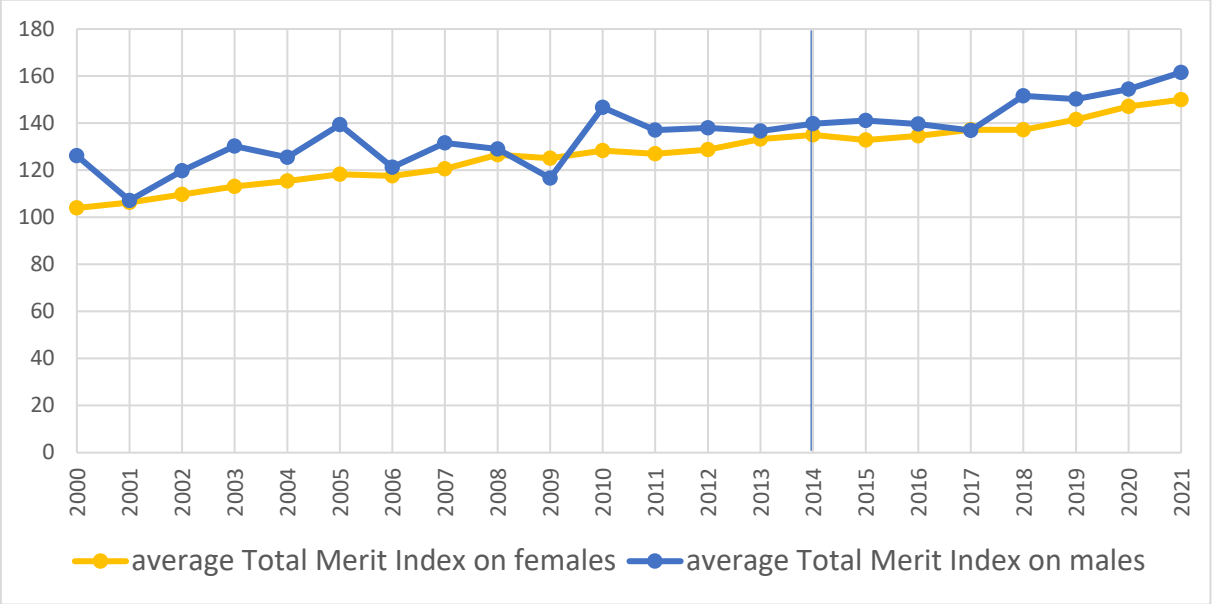


Figure 18. TMI genetic trend for VOS (vertical blue line indicates the introduction of GS).



4. Conclusion

In this deliverable we investigated the impact of genomic selection on gains, diversity, and drift in five local cattle breeds: MRY from the Netherlands, NRD from Norway, and ABO, TAR, and VOS from France. Results showed that the introduction of genomic selection had a different impact on genetic diversity and drift depending on the breed. Indeed, inbreeding rates per generation increased in MRY and TAR breeds, remained overall stable in NRD, and decreased in ABO and VOS. Moreover, results showed that after the introduction of genomic selection, genetic gains remained similar or increased in NRD, ABO, TAR and VOS, or slightly reduced in MRY, likely due to changes in the underlying composition of the total merit index. Finally, insights obtained on the population structure of the five breeds showed changes due to the implementation of genomic selection. Overall, results showed that genomic selection resulted in shorter generation intervals, especially for sires. Moreover, genomic selection resulted in a reduction in the number of sires used at the population level due to genomic selection enabling the screening of a higher number of selection candidates and the preselection of males to become sires. Overall, these results show that genetic management of local breeds is more important and has more impact on genetic diversity, gain and drift, than the implementation of genomic selection per se.

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6. Annex