

Conservation of local Red cattle breeds by collaboration with a mainstream Red dairy cattle breed

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ABSTRACT

- Genetic gain in a local cattle breed increases greatly by use of mainstream bulls.
- Inbreeding in a local cattle breed decreases greatly by use of mainstream bulls.
- Breed proportions of a local cattle breed dropped by use of mainstream bulls.
- Selection of local breeds needs to include proportion of native genes.

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ABSTRACT

Numerous Red cattle breeds exist all throughout Europe. Some Red cattle breeds are only used locally in certain regions and are smaller in population size, whereas other Red cattle breeds are used in multiple countries in mainstream production environments. Conservation of local Red breeds is necessary to maintain genetic diversity. Collaboration between local and mainstream Red cattle breeds can increase the genetic potential of the local breed and thereby the success of survival. The aim of this paper was to explore possibilities to increase the genetic potential of local Red cattle breeds by collaboration with a mainstream Red cattle breed, while at the same time conserve the local Red cattle breeds. Three breeds were included in this study; the mainstream Red dairy cattle breed from Denmark, Finland and Sweden (RDC) and two local Red cattle breeds, German Red and White dual-purpose cattle (RDN), and Lithuanian Red (LIR). Each simulation included the RDC breeding program and one local Red breeding program. Simulated time was 30 years, in which the first 20 years were used to build up reference populations and the last 10 years were used to run a genomic selection scheme with varying levels of collaboration between the local and the mainstream breeding program in the different scenarios. The maximum percentage of breeding bulls selected for breeding to the cows in the local breeding program that could originate from the RDC breeding program differed between scenarios, and could be either 0, 20, 50 or 100%. Results show that the maximum rate of genetic gain in the local breeds was reached in the scenarios where maximum 20, 50 or 100% of the breeding bulls could originate from the RDC breeding program. The highest rate of inbreeding was found in the scenario where no RDC bulls were selected in the local breeding programs. However, even with very restricted selection, the breed proportion of the local breeds dropped significantly after ten years of genomic selection. To really conserve a local breed such as RDN or LIR, a different selection strategy is needed.

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1. Introduction

Numerous Red cattle breeds exist all throughout Europe. Some Red cattle breeds are only used locally in certain regions and are smaller in population size, whereas other Red cattle breeds are used in multiple countries in mainstream production environments (Schmidtman, 2021). The Red dairy cattle populations from Denmark, Finland and Sweden (RDC) have a joint genetic evaluation and selection index, the Nordic Total Merit index (Sørensen et al., 2018). With 273,000 dairy cows spread over the three countries, the RDC form the largest red dairy cattle population in the world (Nordic Cattle Genetic Evaluation, n.d.). Mainstream Red breeds are genetically superior in milk production compared to local Red breeds, but local Red breeds may be better adapted to local environments. Moreover, local breeds form a source of genetic diversity (Medugorac et al., 2009). Increasing the genetic potential of local breeds may lead to larger utilization of the breed. Collaboration between local and mainstream Red cattle breeds can increase the genetic potential of the local breed and thereby the success of survival.

Different types of collaboration between dairy cattle populations are possible. Collaboration can be between populations of the same or similar breeds in the form of exchange of breeding animals. Schmidtman et al. (2021) studied collaboration between two different lines of European Red dairy cattle populations, a dairy type line and a dual-purpose type line. The degree in which the two lines collaborated was influenced by differences in genetic level of breeding goal traits. The degree of collaboration is also affected by the genetic correlation between breeding goals for different breeding programs (Cao et al., 2020; Mulder and Bijma, 2006; Slagboom et al., 2019). Collaboration can also mean the exchange of genotypes to form a combined reference population from related cattle breeds such as the Danish, Swedish, and Finnish Red dairy cattle populations (Brøndum et al., 2011). Potential benefits of collaboration for the local breeds are for example that the genomics of the mainstream population will capture information from the local breeds influencing the accuracy of the selection criterium. In addition, the selection intensity increases when bulls from the mainstream population are also candidates for selection. When offspring of bulls from local breeds appear in the mainstream population with phenotypic records, genomic reliabilities increase for prediction of breeding values in the local breed. Potential benefits of collaboration for the mainstream breeds are for example that the local breed will form a source of genetic diversity that is not present in the mainstream breed anymore. Collaboration might lead to an introduction of genetic material from the local breeds which have been lost or which have never been in the mainstream population. In the long run, the mainstream population might have benefits from introducing these new alleles, for example with changing environmental conditions (Ødegård et al., 2009). Genetic diversity provided by the smaller breed forms an insurance for the future. All of this will reduce the gap between local and mainstream breeds and enable conservation through utilization.

The aim of this paper is to explore possibilities to increase the genetic potential of local Red cattle breeds by collaboration with a mainstream Red cattle breed, while at the same time conserve the local Red cattle breeds.

2. Material and methods

In this study, one mainstream Red cattle breeding program and two smaller sized local Red cattle breeding programs were simulated with breed-specific genome data. Each simulation included the mainstream Red breeding program and one local Red breeding program.

2.1. Breeds

The mainstream Red breed was based on the population of the RDC. The two local breeds were chosen based on their relatedness to the RDC:

the Red and White dual-purpose cattle from Germany (RDN) is distantly related to the RDC and the Lithuanian Red breed (LIR) is closely related to the RDC (Li and Kantanen, 2010; Petrakova et al., 2012). The relatedness of the three breeds in this study is shown in the supplementary Figure. In addition, breeds differed slightly in linkage disequilibrium decay; LIR had the highest linkage disequilibrium and RDC the lowest. Data for the Meuse-Rhine-Yssel cattle from the Netherlands were added to RDN data since this breed is genetically essentially the same breed as the RDN (Schmidtman et al., 2021). Sequence data for each breed were collected in other work packages of the ReDiverse project (ERA-Net SusAn, 2017).

2.2. Scenarios

Simulated time was 30 years, in which the first 20 years were used to build up reference populations and the last 10 years were used to run a genomic selection scheme with varying levels of collaboration between the local and the mainstream breeding program in the different scenarios. Only the local breeding program was different in the different scenarios, the RDC breeding program was the same regardless of the scenario.

In scenario ‘Separate’, there was no exchange of breeding bulls between the local and the RDC breeding program.

In scenario ‘Restricted-20%’, 20% of the bulls selected for breeding to the cows in the local breeding program could originate from the RDC breeding program.

In scenario ‘Restricted-50%’, 50% of the bulls selected for breeding to the cows in the local breeding program could originate from the RDC breeding program.

In scenario ‘Unrestricted’, the number of bulls selected for breeding to the cows in the local breeding program that could originate from the RDC breeding program was unrestricted, i.e. all these bulls could originate from the RDC breeding program.

Each scenario was replicated 20 times, and separately for the RDN breeding program and the LIR breeding program.

2.3. Traits

All simulated scenarios included milk production and udder health, with heritabilities of 0.48 and 0.04 (Interbull, 2012, 2014). The genetic correlation between these two traits was -0.32 (Norberg et al., 2009). The correlation between each trait and the whole breeding goal (BG) was calculated with Eq. (1).

$$r_{i,j} = \frac{b_i' G b_j}{\sqrt{b_i' G b_i b_j' G b_j}} \quad (1)$$

where $r_{i,j}$ = the correlation between trait i and BG j (j = BG-LOCAL, BG-MAINSTREAM),

b_i = a vector containing a 1 for trait i and 0 for the other traits,

b_j = a vector containing the BG weights for BG j ,

G = a matrix containing the genetic correlations between BG traits.

The correlation between milk production and the mainstream BG was set to match the correlation of the milk production index with the Nordic Total Merit index (Sørensen et al., 2018) and was 0.75 in the mainstream BG. The correlation between health and the mainstream BG was 0.38. The two local breeding programs had the same BG, with a correlation between milk production and the whole BG of 0.64. The local BG was set to have more emphasis on health compared to the mainstream BG, with a correlation between health and the whole BG of 0.53.

2.4. Processing of genomic data

Sequence data were available for 38 RDN and MRIJ cattle, 40 LIR cattle, and 146 RDC from Sweden, Denmark and Finland. These data were reduced by retaining only SNPs available on the Illumina BovineSNP50v3 Beadchip (Illumina Inc., San Diego, USA). Quality control was performed using the PLINK v1.09 software (Purcell et al., 2007). Quality criteria included a call rate higher than 0.9 for each animal and SNPs with more than 10% missing data were discarded. Furthermore, filtration for minor allele frequency <0.05 was applied. The final dataset contained 48,708 SNPs. To reconstruct haplotypes, the quality-filtered dataset was split by chromosome and phased using SHAPEIT2 (Delaneau et al., 2013). For phasing, an average genome-wide recombination rate of 1cM/Mb was assumed. The obtained haplotype data were used as input for the simulations, where the haplotypes of RDN and RDC were combined into one datafile for the RDN-RDC simulations, and the haplotypes of LIR and RDC were combined into another datafile for the LIR-RDC simulations.

2.5. Simulation set-up

A full genomic simulation was set up in stochastic simulation program ADAM (Pedersen et al., 2009), adapted for breeding programs that include multiple breeds (Liu et al., 2022). The set-up of the simulation was similar to the set-up used in Thomasen et al. (2020). In the first 20 years of the simulation a progeny testing scheme was incorporated to build the reference population (Fig. 1). Each year 60 or 500 1-year old bulls were genotyped and tested within each breeding program, in which bulls that were progeny of bull dams had priority. Each test bull had 150 daughter yield deviations realized for milk yield and 135 daughter yield deviations for the health trait. These daughter yield deviations were observed when males were 4 years old. From the group of test bulls, each year 5 or 20 5 to 6-year-old proven bulls were selected for mating. In year 0–18, 150 or 1500 heifers of 1 to 3-year-old were selected as bull dams, and in year 19–20 this number was increased to provide enough male offspring from bull dams in the genomic selection scheme.

The last 10 years included a genomic selection scheme in both breeding programs (Fig. 2), meaning that animals were selected based on genotypes and the QTL effects estimated in the progeny testing scheme. Each year, 500 or 2000 1-year old bulls and heifers were selected based on parent average breeding values and genotyped. From the genotyped heifers, 50 or 500 were selected for embryo transfer and these heifers were mated twice, resulting in 3 progenies from each mating (6 offspring per selected heifer). Breeding bulls (1 to 6-year-old) were selected from genotyped bulls. In scenario ‘Separate’, bulls selected for breeding in the local breeding program could only originate from the

local breeding program. In scenarios ‘Restricted-20%’ and ‘Restricted-50%’, either two or five out of the ten bulls selected for breeding in the local breeding program could originate from the RDC breeding program. In scenario ‘Unrestricted’, there was no restriction as to which breeding program bulls originated from. Bulls selected for breeding in the RDC breeding program could always originate from both breeding programs. Phenotypic observations for both traits were realized at the age of 3.

Breeding values were estimated using the DMU package (Madsen and Jensen, 2013). All available information was included when estimating breeding values.

2.6. Statistical analysis

All statistical analysis of the simulation output were performed in R statistical software (R Core Team, 2021). Genetic level in each year for each breed in genetic standard deviation (σ_A) units was used to calculate genetic gain per year for 4 time periods: 1–10, 11–20, 21–25, and 26–30. Annual genetic gain in σ_A units was calculated per replicate and consequently averaged over replicates. Genetic gain in the aggregate genotype was calculated by multiplying annual genetic gain in σ_A units for each trait with its corresponding BG weight and summing this value for each trait. Genetic gain in the aggregate genotype was also expressed in standard deviation of the BG (σ_H) units. Inbreeding was calculated both by using pedigree and identity-by-descent markers in the same way as described in Thomasen et al. (2020). Genetic gain and inbreeding were compared between scenarios with an ANOVA test, followed by Tukey’s Honest Significant Differences test to find all pairwise differences, by use of the Agricolae package in R (Mendiburu, 2020).

In each breeding program, the percentage of selected bulls that originated from each breeding program was calculated, i.e. the percentage of native and foreign bulls. This was calculated for each scenario and per year, for the last 10 years of the simulation. In addition, the breed proportions of all dairy cows as well as each selected bull in each breeding program were calculated by tracing the pedigree to the base population by use of the OptiSel package (Wellmann 2021).

3. Results

3.1. Genetic gain

The genetic level in the aggregate genotype in σ_H -units increased steadily over time for all scenarios and breeding programs (Fig. 3). There was no difference in genetic levels between the different scenarios in the RDC breeding program. The genetic level in the aggregate genotype was the lowest in both the RDN and the LIR breeding programs in scenario ‘Separate’, where the level in year 30 was higher for LIR compared to RDN. From year 21 genetic gain in the aggregate genotype started

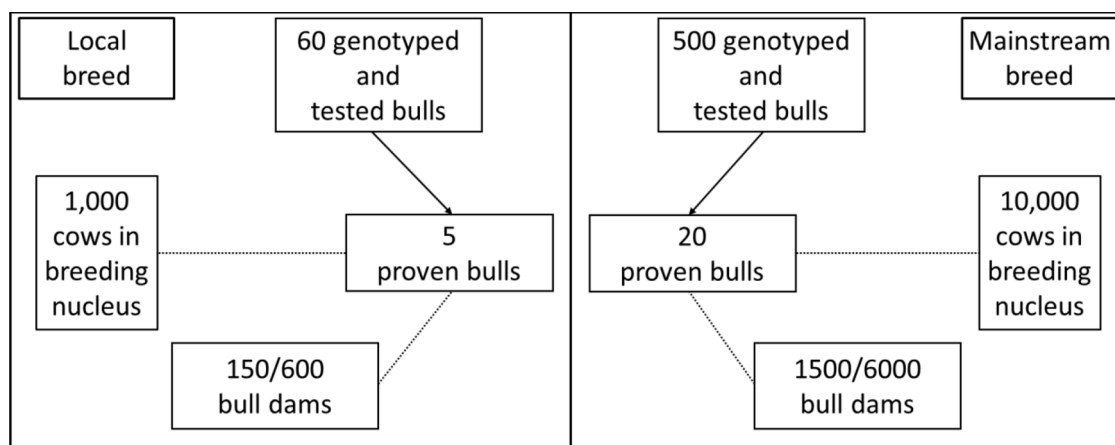


Fig. 1. Simulated breeding scheme in year 1–20. Arrows indicate that a group of animals was selected. Dotted lines indicate groups of animals being mated.

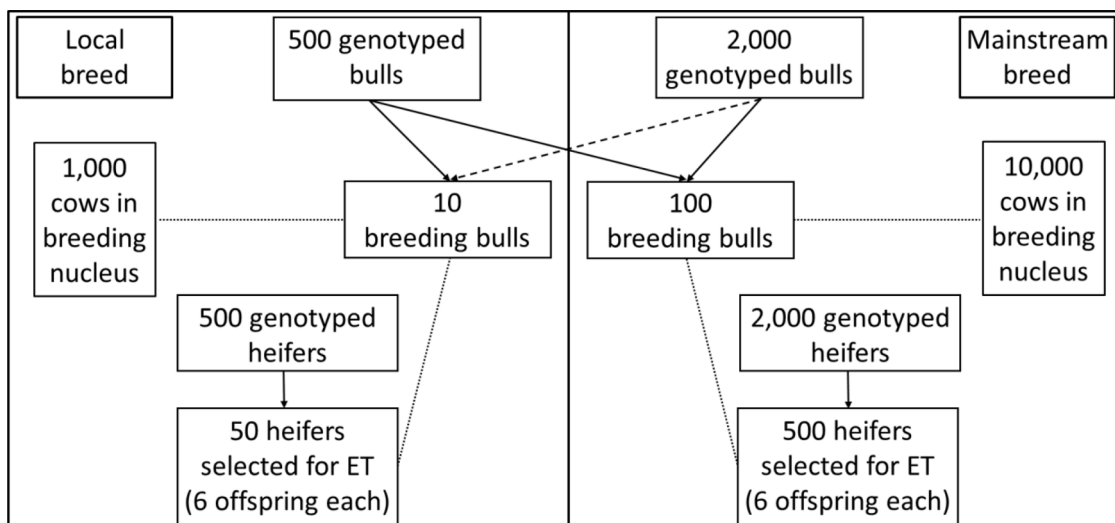


Fig. 2. Simulated breeding scheme in year 21–30. Arrows indicate that a group of animals was selected, where the striped line with an arrow only occurs in part of the scenarios. Dotted lines indicate groups of animals being mated. ET = Embryo transfer.

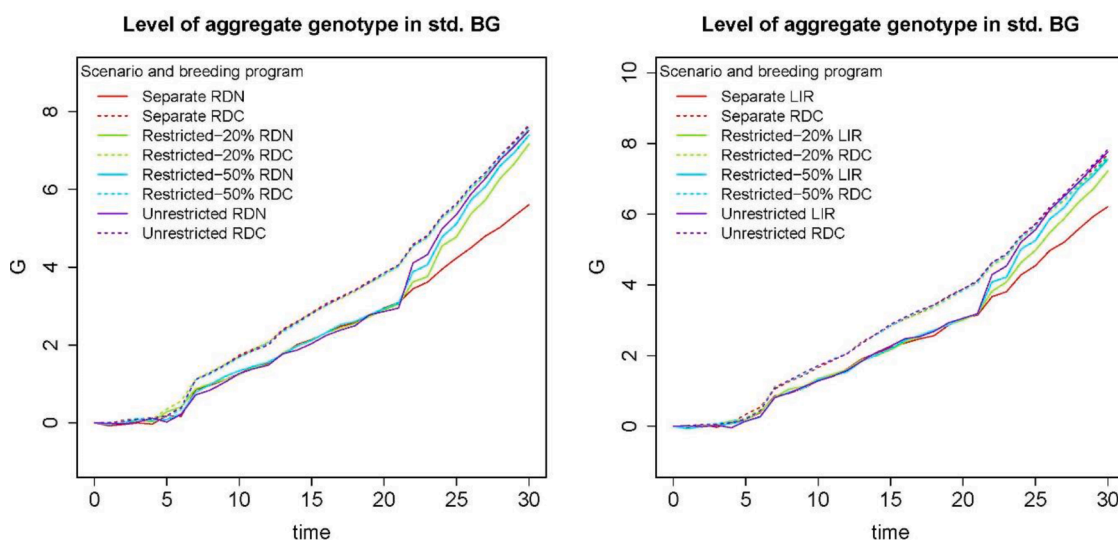


Fig. 3. Level of the aggregate genotype in standard deviation units of the breeding goal (std. BG), plotted over the years of the simulation, per scenario and breeding program: German Red and White dual-purpose cattle (RDN), Red dairy cattle breed from Denmark, Finland and Sweden (RDC) and Lithuanian Red (LIR).

increasing in the other scenarios. The level of the aggregate genotype was highest in scenario ‘Unrestricted’ in the RDN and LIR breeding programs.

Annual genetic gain in the aggregate genotype and per trait was not significantly different between scenarios in year 1–20 in any of the breeding programs (results not shown). In addition, there were no significant differences in annual genetic gain in year 21–25 and year 26–30 in the RDC breeding program in any of the two simulation set ups (results not shown). The highest genetic gain in the aggregate genotype in the RDN and in the LIR breeding program in year 26–30 was found in scenarios ‘Restricted-20%’, ‘Restricted-50%’, and ‘Unrestricted’ (Tables 1 and 2). There were no significant differences between these scenarios for genetic gain in the aggregate genotype and genetic gain per trait. Genetic gain in milk production in scenario ‘Separate’ was significantly lower in both the RDN and the LIR breeding program compared to the other scenarios, but genetic gain in health was not significantly lower from the other scenarios.

3.2. Inbreeding

Level of inbreeding increased steadily over time for all scenarios in the RDC breeding program, and for scenario ‘Separate’ in the RDN and LIR breeding programs (Fig. 4). The level in year 30 was higher for RDN compared to LIR. However, in scenarios ‘Restricted-50%’ and ‘Unrestricted’ in the RDN and LIR breeding programs there was a drop in inbreeding levels in year 21. In scenario ‘Restricted-20%’, there was a drop in inbreeding levels in year 24. Rate of inbreeding per generation was therefore negative in all scenarios apart from ‘Separate’ in the RDN and LIR breeding programs in year 21–25 (Tables 1 and 2). In year 26–30, rate of inbreeding per generation became positive again for all scenarios and was highest in scenario ‘Separate’ and lowest in scenario ‘Restricted-20%’.

3.3. Origin of breeding bulls

The percentage of breeding bulls that were born in each breeding program differed between scenarios (Fig. 5). The results for the LIR-RDC

Table 1

Rate of genetic gain per year and rate of inbreeding per generation, per scenario and time period in the RDN¹ breeding program.

	Separate	Restricted-20%	Restricted-50%	Unrestricted
Year 21–25				
Aggregate genotype (in std. BG)	0.28 ^a	0.44 ^b	0.50 ^b	0.57 ^c
Milk production	0.25 ^a	0.39 ^b	0.49 ^c	0.47 ^{bc}
Health	0.07 ^a	0.11 ^a	0.07 ^a	0.19 ^b
Rate of pedigree inbreeding	2.27% ^{a2}	−0.73% ^b	−1.25% ^c	−1.42% ^c
Rate of true inbreeding	2.78% ^a	−0.64% ^b	−1.14% ^{bc}	−1.36% ^c
Year 26–30				
Aggregate genotype (in std. BG)	0.27 ^a	0.45 ^b	0.42 ^b	0.41 ^b
Milk production	0.27 ^a	0.43 ^b	0.43 ^b	0.40 ^b
Health	0.04 ^a	0.08 ^a	0.04 ^a	0.06 ^a
Rate of pedigree inbreeding	1.85% ^a	0.36% ^c	1.06% ^b	0.74% ^{bc}
Rate of true inbreeding	2.69% ^a	0.68% ^c	1.49% ^b	1.12% ^{bc}

¹ German Red and White dual-purpose cattle.

² Subscripts with different letters indicate significant differences between estimates in the same row.

Table 2

Rate of genetic gain per year and rate of inbreeding per generation, per scenario and time period in the LIR¹ breeding program.

	Separate	Restricted-20%	Restricted-50%	Unrestricted
Year 21–25				
Aggregate genotype (in std. BG)	0.34 ^a	0.44 ^b	0.51 ^c	0.57 ^d
Milk production	0.30 ^a	0.39 ^b	0.46 ^c	0.46 ^c
Health	0.09 ^a	0.11 ^a	0.12 ^{ab}	0.19 ^b
Rate of pedigree inbreeding	2.05% ^{a2}	−0.69% ^b	−1.42% ^c	−1.54% ^c
Rate of true inbreeding	2.49% ^a	−0.60% ^b	−1.40% ^c	−1.51% ^c
Year 26–30				
Aggregate genotype (in std. BG)	0.32 ^a	0.43 ^b	0.43 ^b	0.41 ^b
Milk production	0.30 ^a	0.39 ^b	0.41 ^b	0.38 ^b
Health	0.06 ^a	0.10 ^a	0.08 ^a	0.08 ^a
Rate of pedigree inbreeding	1.46% ^a	0.52% ^b	0.78% ^b	0.68% ^b
Rate of true inbreeding	2.11% ^a	0.78% ^b	1.15% ^b	0.98% ^b

¹ Lithuanian Red cattle.

² Subscripts with different letters indicate significant differences between estimates in the same row.

scenarios are not shown because they were very similar to the RDN-RDC results. In scenario Separate, there was no selection of bulls from the other breeding program. In scenarios ‘Restricted-20%’ and ‘Restricted-50%’, maximum 20% or 50% of the bulls that were selected for breeding in the local breeding program could originate from the RDC breeding program. In the first years of the genomic selection scheme the maximum number of foreign bulls was selected for breeding in the local breed in these scenarios, and this percentage decreased slightly in later years (Fig. 5). Bulls selected for breeding in the RDC breeding program initially mostly originated from the RDC breeding program in all scenarios. However, at later years of the genomic selection scheme a small proportion of breeding bulls selected for breeding in the RDC breeding program originated from the local breeding programs. In scenario

‘Unrestricted’, both breeding programs mainly selected bulls that originated from the RDC breeding program in the first years of the genomic selection scheme. In later years, this proportion decreased and a percentage of up to 29% local bulls were selected for breeding.

The breed proportion of the local breed in bulls born in each local breeding program and selected for breeding in the local breeding program did not differ much between the RDN and the LIR breeding program (Table 3). The difference between scenarios was however very clear. In scenario ‘Separate’, the breed proportion of the local breed in bulls born in the local breeding program did not change over the years of the simulation. In the other scenarios, the breed proportion of the local breed in bulls born in the local breeding program decreased over the years of the genomic selection scheme. This decrease was the smallest in scenario ‘Restricted-20%’ and the largest in scenario ‘Unrestricted’.

3.4. Breed proportions

The breed proportion in dairy cows in each breeding program decreased less over the years of the simulation compared to the breed proportion in selected bulls (Table 4). There was a large difference between scenarios, but not between the two local breeds.

4. Discussion

In this study, different scenarios were simulated in order to compare genetic gain and inbreeding in local Red breeds while simultaneously maintain breed specific diversity. The aim of this paper was to explore possibilities to increase the genetic potential of local Red cattle breeds by collaboration with a mainstream Red cattle breed, while at the same time conserve the local Red cattle breeds.

4.1. Behavior of scenarios

The scenarios in this study differed in the origin of bulls selected as breeding bulls in two local breeds, RDN and LIR. The different scenarios caused large differences in trends for genetic gain and inbreeding in both local breeds. There were no clear differences in results for the two local breeds, except in scenario ‘Separate’, where the local breeding programs operated independently of the mainstream breeding program. In this scenario the consequences of running a separate breeding program for a small, local breed can be seen. Due to the limited population size, the rate of inbreeding was very high, and the rate of genetic gain was low. The rate of genetic gain was higher in year 30 in the LIR breeding program compared to the RDN breeding program and this was due to a higher accuracy of selection in the LIR breeding program (results not shown). The higher accuracy in this breeding program was likely due to the higher linkage disequilibrium in this breed compared to the other breeds and due to the higher relatedness with the RDC population.

Being able to select at least part of the breeding bulls from the RDC breeding program in scenarios ‘Restricted-20%’, ‘Restricted-50%’, and ‘Unrestricted’ drastically increased the pool of selection candidates and thus the selection intensity. In addition, these selection candidates had higher genetic merit compared to the bulls from the local breeding program. The number of foreign bulls that were selected in the first years of the genomic selection scheme was always equal to the maximum number that was allowed because the genetic merit of bulls originating from the RDC breeding program was higher (Fig. 5). The consequence of this change in the origin of breeding bulls from year 20 to year 21 was a drastic increase in genetic gain in all scenarios except for scenario ‘Separate’, even if only a small proportion of breeding bulls could originate from the RDC breeding program (Fig. 3). Thus, selecting mainstream bulls had a large impact on genetic gain in local breeding programs.

Interestingly, genetic gain in year 26–30 did not significantly differ between any of the scenarios except for scenario ‘Separate’ (Tables 1 and 2). This implies that the exact proportion of breeding bulls that

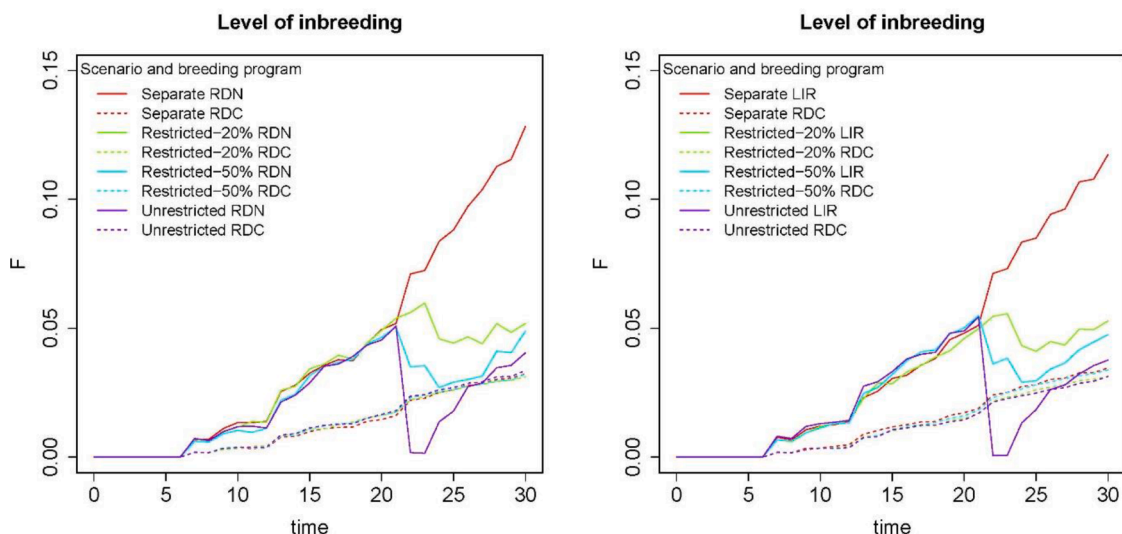


Fig. 4. Level of inbreeding plotted over the years of the simulation, per scenario and per breeding program: German Red and White dual-purpose cattle (RDN), Red dairy cattle breed from Denmark, Finland and Sweden (RDC) and Lithuanian Red (LIR).

originated from the RDC breeding program did not matter in terms of genetic gain if the possibility to select RDC bulls was there, when the breeding program was ran for at least 5 years. The reason for this can be found in the proportion of local breed in selected breeding bulls (Table 3). A large proportion of RDN or LIR genes caused a lower breeding value compared to a large proportion of RDC genes, considering the genetic superiority of RDC bulls at the start of the genomic selection scheme. Therefore, as the proportion of local breed decreased in bulls born in the local breeding programs, their breeding values increased. After just 5 years of genomic selection, the proportion of local breed in selected bulls already decreased to less than 50%. Due to the increased proportion of RDC in the local breeds, the effect of selecting mainstream bulls with higher breeding values to increase genetic gain decreased over time. Thus, even though bulls were born in the local breeding program, the proportion of the local breed was so low at the end of the simulation that these bulls were genetically not local anymore.

Inbreeding dropped massively in the local breeding programs in year 21 in scenario 'Unrestricted', where an unrestricted proportion of bulls selected for breeding in the local breeding program could originate from the RDC breeding program (Fig. 4). This drop in inbreeding was due to the large proportion of breeding bulls that originated from the RDC breeding program. In later years of the simulation the level of inbreeding stabilized again. In addition, there was a drop in inbreeding in scenario 'Restricted-50%', but this was not as profound as in the 'Unrestricted' scenario. The restriction on the proportion of breeding bulls that could originate from the RDC breeding program caused more balanced rates of inbreeding since bulls were selected from both breeding programs. However, in year 30 levels of inbreeding were comparable between all scenarios except for 'Separate'. For a longer time span, the effect of the different scenarios on inbreeding will probably be negligible.

4.2. Limitations of simulated breeding strategies

The aim of the set-up of the different scenarios was to find a breeding strategy that would increase the utility of the local breed while keeping at least part of the genetic diversity of the local breed. While it was not determined how large the conserved proportion of the small breed should be, the achieved proportion at the end of the simulation was not very large (Table 4). The maximum breed proportion of the local breed in dairy cows in any of the scenarios except for 'Separate' was 0.40 at the end of the simulation. Therefore, it would not be recommendable to apply any of the breeding strategies in this study for 10 years of genomic

selection. However, local cows in scenario 'Restricted-20%' still had a proportion of the local breed of 0.81 in year 25. In addition to the relatively high rate of genetic gain and low rate of inbreeding, applying this breeding strategy for a couple of years would be the most recommendable breeding strategy.

4.3. Longer time span

The simulated time was set at 30 years due to computational limits. If the simulation had run for a longer time, the expected breed proportion would most likely decrease even more. To study this, five replicates of scenario 'Restricted-20% RDN-RDC' were run for 40 years to see the effect of longer genomic selection on the results. In year 31–40, the breed proportion of RDN in RDN cows dropped further down to 0.19. This confirms the assumption that it is not recommendable to apply any of the breeding strategies in this study for a longer time span.

4.4. Introgression of foreign genes

Even though the current study used breed-specific haplotypes as input for the simulation, for the calculation of breed proportions we did not consider the starting level of native genes present in RDN or LIR. The RDN breed is characterized by a large amount of introgressed genes from the superior Red Holstein breed (Addo et al., 2019; Schmidtman, 2021). Similarly, a large number of Danish Red bulls have historically been used in the LIR breed (Petrankova et al., 2012). This introgression of genetic material should be viewed critically because it might lead to the loss of native genetic material, in the worst case to the extinction of breeds. Even small amounts of introgressed genetic material can quickly spread in a population. Recovering the native genetic background of a recipient breed is possible only in rare cases, such as when there is only a small amount of foreign introgression and maximum one to three generations of crossing (Amador et al., 2013). The results of this study need to be placed in a more conservative perspective that considers the native genetic material that is already lost in these local breeds. Therefore, the loss of local genes that is considered acceptable should be even lower.

4.5. Alternative selection methods

Using breed proportions in selection candidates instead of which breed the bulls is born into might be a better method of increasing the genetic potential of local breeds while conserving the local breed. Optimum contribution selection would be a good method for selecting the

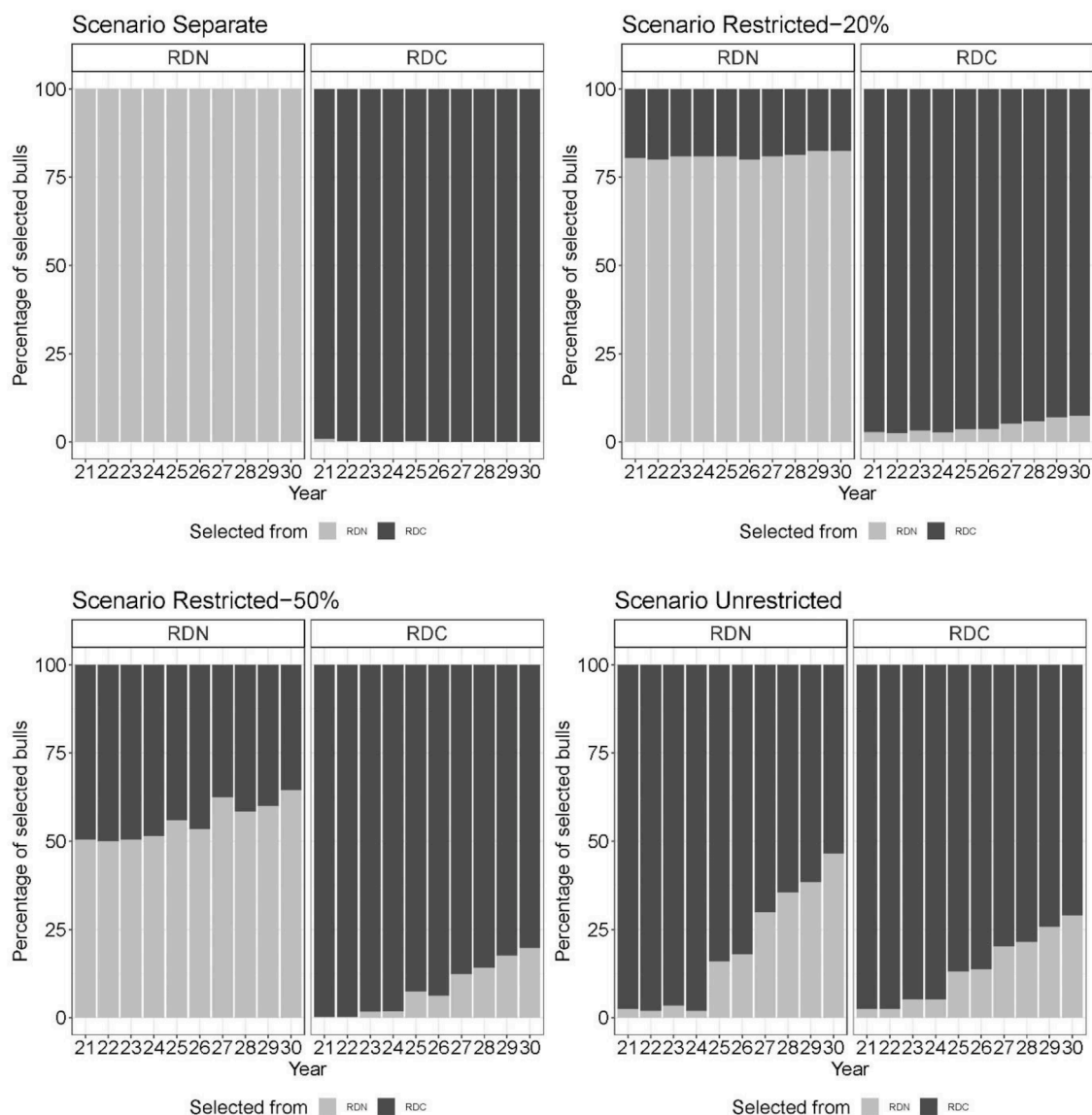


Fig. 5. Percentage of selected bulls that are selected from each breed, per scenario and per breeding program: German Red and White dual-purpose cattle (RDN) and Red dairy cattle breed from Denmark, Finland and Sweden (RDC).

Table 3

Proportion of the local breed in bulls born in the local breeding program and selected for breeding in the local breeding program, per year and per breeding program.

Yr	RDN breeding program ¹				LIR breeding program ²			
	Separate	Restricted-20%	Restricted-50%	Unrestricted	Separate	Restricted-20%	Restricted-50%	Unrestricted
21	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
22	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
23	1.00	0.57	0.56	0.50	1.00	0.59	0.55	0.57
24	1.00	0.55	0.54	0.75	1.00	0.57	0.53	0.53
25	1.00	0.42	0.29	0.27	1.00	0.45	0.35	0.28
26	1.00	0.38	0.28	0.26	1.00	0.43	0.32	0.26
27	1.00	0.34	0.24	0.18	1.00	0.36	0.25	0.18
28	1.00	0.30	0.23	0.16	1.00	0.33	0.24	0.18
29	1.00	0.26	0.19	0.12	1.00	0.30	0.20	0.14
30	1.00	0.24	0.17	0.12	1.00	0.28	0.21	0.11

¹ German Red and White dual-purpose cattle.

² Lithuanian Red cattle.

best candidates while minimizing inbreeding, which is especially important in small populations. In particular, advanced optimum contribution selection considers the historical migration of foreign genes in local breeds and aims to optimize inbreeding and genetic gain, but

also aims to preserve the native genetic background of a breed (Wang et al., 2017). This might be the best option to genetically improve and simultaneously conserve breeds such as RDN and LIR. This was however beyond the scope of this study.

Table 4

Proportion of the local breed in cows in the local breeding program, calculated per year and per breeding program.

Yr	RDN breeding program ¹				LIR breeding program ²			
	Separate	Restricted-20%	Restricted-50%	Unrestricted	Separate	Restricted-20%	Restricted-50%	Unrestricted
21	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
22	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
23	1.00	0.96	0.90	0.81	1.00	0.96	0.90	0.80
24	1.00	0.93	0.82	0.65	1.00	0.93	0.82	0.64
25	1.00	0.81	0.68	0.48	1.00	0.82	0.68	0.48
26	1.00	0.71	0.56	0.38	1.00	0.73	0.57	0.38
27	1.00	0.61	0.45	0.30	1.00	0.63	0.47	0.30
28	1.00	0.52	0.37	0.24	1.00	0.55	0.39	0.24
29	1.00	0.46	0.31	0.19	1.00	0.48	0.33	0.20
30	1.00	0.40	0.26	0.17	1.00	0.42	0.28	0.17

¹ German Red and White dual-purpose cattle.² Lithuanian Red cattle.

5. Conclusion

This study aimed to explore possibilities for collaboration between local and mainstream Red cattle breeds, with the main aim of increasing the utilization of local breeds to be able to better conserve genetic diversity. The simulated scenarios included different proportions of selected bulls that could originate from the mainstream breeding program. However, even with very restricted selection, the breed proportion of the local breed dropped significantly after ten years of genomic selection. To really conserve a local breed such as RDN or LIR, the proposed selection strategies need to be applied for a shorter time span, or a different selection strategy is needed. An example could be to select animals based on foreign breed proportions instead of breed born into or to apply optimum contribution selection that accounts for migrant contributions.

CRedit authorship contribution statement

Margot Slagboom: Conceptualization, Formal analysis, Investigation, Visualization, Writing – original draft. **Viktor Milkevych:** Conceptualization, Software, Writing – review & editing. **Huiming Liu:** Conceptualization, Software, Writing – review & editing. **Jørn Rind Thomassen:** Conceptualization, Writing – review & editing. **Morten Kargo:** Conceptualization, Project administration, Funding acquisition, Writing – review & editing. **Christin Schmidtmann:** Formal analysis, Investigation, Visualization, Writing – review & editing.

Declarations of Competing Interest

none

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.livsci.2022.104936](https://doi.org/10.1016/j.livsci.2022.104936).

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