

# Short- and long-term consequences of collaboration between Northern European Red dairy and dual-purpose cattle

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## Abstract

In Northern European countries, a great variety of Red cattle populations exists which can be broadly categorized in two groups: specialized dairy and dual-purpose breeds. Collaboration between these breeds (i.e. the exchange of sires across breeds) can be beneficial but is limited so far. The aim of this study was to demonstrate and evaluate consequences of collaboration between Red breeds using stochastic simulations. Two breeding lines (dairy type and dual purpose) were simulated. As a special aspect of this study, differences in genetic levels of breeding traits (milk production, beef production, mastitis resistance, fertility, feed efficiency) have been taken into account. Various scenarios were investigated where across-breed selection was either restricted or allowed and with different correlations between breeding goals in the two lines. The results of this study were influenced by the different genetic levels in breeding traits only in the first years of simulation. In the long run, the breed differences did not affect the degree of collaboration between lines. When the correlation between breeding goals was close to unity, the selection of external bulls was highly beneficial in terms of genetic gain and total monetary gain. Additionally, the lowest rate of inbreeding was found in that case. With decreasing correlations between environments, degree of cooperation between lines rapidly terminated and lines operated individually. In last years of simulation, cooperation was only found when the correlation between breeding goals was close to unity. From a long-term perspective, the exchange of breeding sires across lines also caused negative effects. In the dual-purpose line, deterioration of genetic gain in mastitis resistance and fertility was observed. Additionally, breeding lines genetically converged, which decreased genetic diversity. Collectively, short-term benefits and long-term negative effects have to be reconciled if collaboration between Red breeds in Northern Europe is to be pursued.

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## KEYWORDS

breeding strategy, collaboration, dairy cattle, dual-purpose cattle, stochastic simulation

## 1 | INTRODUCTION

There is a great variety of Red cattle populations across Northern Europe, with breeding programmes that are primarily organized at national level. Although Red cattle are typically lower yielding than Holstein Friesian, they often outperform Holstein Friesian in functional traits such as fertility, direct health and calving traits (Ahlman et al., 2011; Ferris et al., 2014; Sørensen et al., 2018; Sveberg et al., 2015). Furthermore, it was reported that some Red breeds are genetically more diverse and less inbred compared with Holstein Friesian (Thomasen et al., 2020; Zhang et al., 2015). Thus, Red breeds can strongly contribute to sustainable production of dairy and beef products. Two types of Red breeds with different orientations in their breeding goals are found in Northern European countries. On the one hand, more specialized dairy breeds are present that are primarily used for intensive farming practices. Although their breeding objectives include functional traits to a high degree, historically and presently milk production traits are mainly emphasized. On the other hand, dual-purpose breeds exist, which are usually selected for a broader range of traits in their breeding programmes, for example beef production traits are included in selection indices with adequate importance. Dual-purpose breeds are often characterized by good functional traits (Begley et al., 2009; Ferris et al., 2014) and can cope with suboptimal production circumstances such as lower quality roughage-based diets (Delaby et al., 2009).

Transnational cooperation across breeds and breeding organizations can help promote and preserve Red cattle in Northern European countries. The idea of “borderless” cooperation was already raised in different studies (Lohuis & Dekkers, 1998; VanRaden et al., 2009). The value of collaboration is influenced by the presence of genotype by environment interactions (Mulder & Bijma, 2006) or differences in breeding goals (Banos & Smith, 1991), which both lower the genetic correlation between environments. Generally, cooperation between breeding programmes takes place when additional genetic gain is expected due to the use of foreign genotypes, which fit well in the own environment.

Running breeding programmes is costly for breeding organizations and requires large investments. By collaboration, particular costs can be shared with other breeding companies (Dürr & Philipsson, 2012). In practical breeding, successful cooperation across borders is seen for Red breeds in Scandinavian countries. Denmark,

Sweden and Finland recognized the potentials of cooperative work and introduced common breeding strategies for the breeds Danish Red, Swedish Red and Finish Ayrshire consolidated as VikingRed. The conditions for this were favourable as production circumstances in these countries are very similar (Kargo et al., 2014). However, collaboration between other Northern European Red breeds is still limited.

The objective of this study was to investigate advantages and disadvantages of collaboration across breeds belonging to the group of Red cattle in Northern European countries. In the present study, collaboration was defined as the selection of bulls across populations. For that purpose, two breeding lines were simulated representing Red dairy and dual-purpose cattle. As a special aspect of this study, breed differences in genetic levels of breeding traits for the two breeding lines were taken into account. In the simulations, different breeding strategies were applied with across-line selection of sires restricted and allowed. Consequently, breeding strategies were assessed in terms of genetic gain, rate of inbreeding and total monetary gain. A specific aim was to investigate the number of selected external bulls in both lines depending on varying genetic correlations between their breeding goals. In doing so, short and long-term potentials but also limitations of cooperative breeding activities for Red cattle breeds in Northern Europe were investigated and discussed.

## 2 | MATERIALS AND METHODS

Two breeding lines were simulated, which emulated Red cattle breeds present in Northern Europe. One breeding line resembled the dairy type Red cattle breeds, whereas the other breeding line resembled dual-purpose Red cattle breeds. Within the simulations, these breeding lines were assumed to operate in different environments with their own breeding goals. The stochastic simulations in this study covered a time horizon for a total of 40 years. To adequately reflect the present situation of breeds, the first 10 years of simulation (from year –10 to 0) were used to create realistic differences in genetic levels of breeding traits across the lines. In subsequent 30 years of simulation (from year 1 to 30), six different scenarios were run with the aim of studying the effect of different breeding strategies on genetic gain and the long-term development of the lines. Breeding strategies differed in the restriction of selection of breeding bulls within environment or across

environment. In the scenarios where across-environment selection was allowed, the correlation between the breeding goals in both breeding lines was varied.

## 2.1 | Simulations

The simulations were performed using the stochastic software ADAM (Pedersen et al., 2009), which traces genetic changes in a population using selective breeding schemes. Each scenario was simulated with 25 replicates. Estimation of breeding values was performed using DMU (Madsen & Jensen, 2014). All simulations were run with a pseudo-genomic setup according to Dekkers (2007), which enables the inclusion of genetic information without explicitly simulating genetic markers and QTLs. In this pseudo-genomic setup, a genomic indicator trait was simulated for each breeding trait. The correlation between the genomic indicator trait and the breeding trait was equal to the accuracy of direct genomic values (DGV) for that simulated trait. A detailed description of this approach can be found in Buch et al. (2012).

## 2.2 | Differences in breeding lines (year –10 to 0)

The dairy type (DT)-breeding line reflected intensive conventional dairy production as it is the predominant kind of dairy farming for breeds such as Danish Red, Swedish Red or Finnish Ayrshire. The dual-purpose (DP) line reflected more beef-oriented breeds found in Northern European countries like Norwegian Red or the local breeds German Red and White Dual-Purpose and Dutch Meuse-Rhine-Yssel. Five different breeding traits were considered in the simulations: milk production (305d energy-corrected milk

(ECM)), beef production (average daily gain), mastitis resistance (incidence rate of mastitis), fertility (interval from 1st to last insemination) and feed efficiency (residual feed intake). Generally, the DT-line had a higher genetic potential for milk production, whereas the DP-line was superior in beef production and functional traits. The assumptions for average levels in breeding traits characterizing the two breeding lines are shown in Table 1. All assumptions were set in accordance to scientific literature, relevant official breed reports or information directly obtained from breeding organizations. DT was marked by a higher level in milk yield compared to DP with a difference of 900 kg in 305d-ECM yield over all lactations. By contrast, DP was assumed to be superior for average daily gain, mastitis resistance and fertility. Additionally, DP had a lower residual feed intake corresponding to better feed efficiency.

The initial 10 years of simulation (from year –10 to 0) were used to create the aforementioned different genetic levels in both breeding lines. To determine the breeding goal weights for creating the desired genetic differences between the breeding lines, an in-house developed R-script was used. This optimization programme calculated the expected genetic gain in each breeding trait depending on breeding goal weights, heritabilities, genetic correlations and the reliabilities of genomic breeding values for each trait. The index weights that approximately resembled the desired differences in traits as shown in Table 1 were used as breeding goal weights for the initial 10 years of simulation.

## 2.3 | Genetic parameters

All genetic parameters used in the present study originated from Interbull evaluations, scientific literature or relevant reports from breeding organizations. Genetic and residual

**TABLE 1** Assumptions on phenotypic levels for both breeding lines and resulting differences in breeding traits

Trait	Breeding line		Differences in phenotypic units
	Dairy type	Dual purpose	
305d ECM over all lactations (kg)	8850 <sup>a</sup>	7950 <sup>b</sup>	900
Average daily gain (kg/day)	0.56 <sup>a</sup>	0.60 <sup>c</sup>	0.04
Mastitis incidence rate (%)	24.2 <sup>a</sup>	19.9 <sup>c</sup>	4.3
Fertility, interval from 1st to last insemination (d)	45.0 <sup>a</sup>	42.0 <sup>c</sup>	3.0
Residual feed intake (kg/day)	0.0 <sup>d</sup>	–1.0 <sup>d</sup>	1.0

<sup>a</sup>NTM report (Sørensen et al., 2018).

<sup>b</sup>Average milk yield of Norwegian Red, German Red and White Dual Purpose and Dutch Maas-Rhine-Yssel weighted by the number of cows per population.

<sup>c</sup>Assumptions based on information from breeding organizations.

<sup>d</sup>Assumptions based on internal discussions.

correlations between traits were assumed to be the same in both breeding lines (Table 2). Phenotypic and genetic correlations were average estimates reported in several studies (Kadarmideen, 2004; Koeck et al., 2014; Li et al., 2020; Liinamo et al., 2015; Pritchard et al., 2013; Søndergaard et al., 2002; Tempelman et al., 2015; Vallimont et al., 2013; Veerkamp et al., 1995; Weller & Ezra, 2008). Residual correlations were calculated based on genetic and phenotypic correlations and variances. To obtain positive-definite genetic and residual correlation matrices, a bending procedure was applied (Hayes & Hill, 1981). The initial matrices were adjusted only slightly to ensure positive eigenvalues.

Heritabilities of traits used in the simulations were assumed to be the same for both breeding lines (Table 3). However, genetic standard deviations (*SD*) for traits differed between the lines. Genetic *SD* for milk production, mastitis resistance and fertility in DT were obtained from the Interbull evaluations for Nordic Red dairy cattle (Interbull, 2012, 2014, 2016). Genetic *SD* for these traits in DP were calculated based on coefficients of variation defined as the ratio of *SD* to the mean. For feed efficiency, estimates from literature were used (van Arendonk, 2011; Li et al., 2017; Tempelman et al., 2015; Williams et al., 2011) and genetic *SD* were assumed to be the same in both breeding lines. Accuracies of DGVs were calculated according to Goddard (2009) and are shown in Table 3. Parameters (heritabilities and size of reference population) for the computation of accuracies differed for the traits.

## 2.4 | Simulated scenarios (year 1 to 30)

From year 1 to 30, the breeding programmes in both breeding lines were run with different scenarios applied. In the first scenario (Strict), bulls were only selected and used within each breeding line. In the second scenario (Across), the selection of bulls across the breeding lines was allowed. Scenario Across was altered to create different correlations between the breeding goals in each environment. To achieve these differences, the breeding goal weight for milk production in the DP-breeding goal was lowered whilst the breeding goal weights of remaining traits kept constant. Correlation between the breeding goals in both environments was lowered to 0.9, 0.8, 0.7 and 0.6 in this way. Subsequently, the scenarios Across\_0.9, Across\_0.8, Across\_0.7 and Across\_0.6 were set up and simulated.

## 2.5 | Breeding goals (year 1 to 30)

To set up the breeding goals for each environment, economic values were derived using a stochastic bio-economic

model (Østergaard et al., 2005, 2016). The breeding goals represented balanced selection indices including production, functional and efficiency traits as they are currently used in practical breeding programmes in Scandinavian countries. The respective breeding goal weights for both breeding lines are shown in Table 3. In the DT-breeding goal, most emphasis was given to milk production, mastitis resistance and fertility, whilst no weight was given to beef production. In the DP-breeding goal, particular weight was given to beef traits as well as feed efficiency, however, functional traits were strongly emphasized in this breeding objective as well.

## 2.6 | Correlations between breeding goals and breeding goal traits

The correlations between each single trait and the overall breeding goal ( $r_{ij}$ ) was calculated according to Buch et al. (2009) using the following equation:

$$r_{ij} = \frac{b'_i G b_j}{\sqrt{b'_i G b_i b'_j G b_j}}$$

where  $b_i$  was a vector containing 1 for trait  $i$  and 0 for the other traits ( $i$  = milk production, beef production, mastitis resistance, fertility, feed efficiency),  $b_j$  represented a vector including the breeding goal weights for breeding goal  $j$  ( $j$  = DT-breeding goal, DP-breeding goal), and matrix  $G$  comprised the genetic correlations between all traits included in the breeding objectives. The same equation was used to compute the correlation between the overall breeding goals in the two breeding lines. In that case, however, the vectors  $b_i$  and  $b_j$  presented the index weights of the DT-breeding goal and DP-breeding goal, respectively (Table 3).

## 2.7 | Breeding schemes

The applied breeding schemes were based on those used in practical breeding for Nordic Red cattle in Scandinavian countries and are depicted in Figure 1. In both breeding lines, a breeding nucleus was simulated consisting of 10,000 cows with age classes of 1 to 5 years. In each time step, 3,000 heifers and 3,000 bull calves (1 year old) were selected for genotyping based on conventional parental average. Amongst the genotyped heifers, 500 animals were selected to be mated to two different bulls producing three offspring each from multiple ovulation and embryo transfer (MOET; Nicholas & Smith, 1983). All bull calves from MOET were tested genomically. From the genotyped bull calves, 100 AI

**TABLE 2** Genetic correlations<sup>a</sup> (above the diagonal) and residual<sup>b</sup> correlations (below the diagonal) between traits used in the simulations

Trait	305d-milk yield	Average daily gain	Mastitis incidence	Interval from 1st to last insemination	Residual feed intake
305d-milk yield	1.00	-0.44	0.37	0.33	0.01
Average daily gain	-0.46	1.00	-0.35	-0.40	0.01
Mastitis incidence	0.04	0.00	1.00	0.27	-0.08
Interval from 1st to last insemination	-0.10	-0.10	0.03	1.00	-0.15
Residual feed intake	0.00	-0.04	-0.09	-0.07	1.00

<sup>a</sup>Genetic correlations are average estimates reported in literature (Kadarmideen, 2004; Koeck et al., 2014; Li et al., 2020; Liinamo et al., 2015; Pritchard et al., 2013; Søndergaard et al., 2002; Tempelman et al., 2015; Vallimont et al., 2013; Veerkamp et al., 1995; Weller & Ezra, 2008).

<sup>b</sup>Residual correlations were calculated based on genetic and phenotypic correlations and variances.

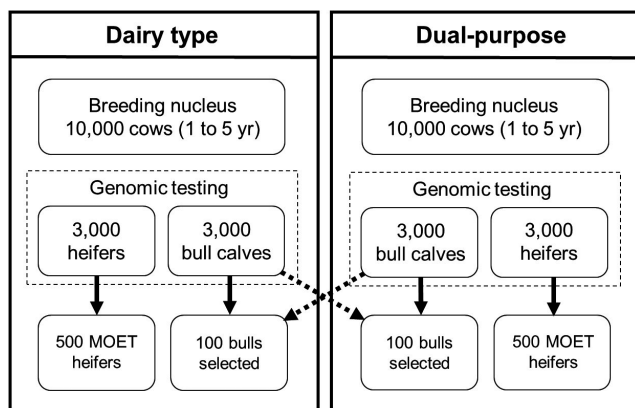
**TABLE 3** Input parameters for each trait used in the simulations of the breeding lines dairy type (DT) and dual purpose (DP)

Parameter	305d-milk yield		Average daily gain		Mastitis incidence		Interval from 1st to last insemination		Residual feed intake	
	DT	DP	DT	DP	DT	DP	DT	DP	DT	DP
Heritability	0.40	0.40	-	0.29	0.06	0.06	0.08	0.08	0.12	0.12
Genetic SD in trait unit <sup>a</sup>	807	667	-	0.05	4.7	3.9	9.2	8.5	0.50	0.50
BG weight <sup>b</sup>	153.30	121.00	-	24.00	75.23	64.87	62.89	55.62	15.00	22.00
DGV accuracy <sup>c</sup>	0.50	0.50	-	0.47	0.40	0.40	0.42	0.42	0.32	0.32

<sup>a</sup>Genetic SD are based on information from Interbull and the literature or have been calculated according to the coefficient of variation.

<sup>b</sup>Breeding goal weights are expressed in € per additive genetic standard deviation unit.

<sup>c</sup>Calculated according to Goddard (2009) using following parameters: length of genome = 30 morgans, historical effective population size = 800, number of informative markers = 38,000, size of reference population = 30,000 cows and 3,000 test bulls (milk production, mastitis resistance, fertility); 20,000 cows (beef production); 10,000 cows (feed efficiency).

**FIGURE 1** Schematic representation of the modelled breeding programmes/schemes in the environments dairy type and dual purpose. Dashed arrows indicate allowed exchange of bulls between the breeding schemes (scenarios Across)

bulls were selected for breeding either within each breeding line (Strict) or across the breeding lines (Across, Across\_0.90, Across\_0.80, Across\_0.70, Across\_0.60). In

this study, the AI bulls were used equally and, thus, produced similar numbers of offspring.

## 2.8 | Statistical analysis

Genetic gain per year (expressed in  $\sigma_A$ -units) was calculated for each trait in both breeding lines and all scenarios. To obtain stable estimates without short-term fluctuations, genetic gain was averaged from year 21 to 30. Furthermore, rate of inbreeding per generation was computed for all scenarios in each breeding line. In addition, total monetary gain per year was calculated for both breeding lines and the two scenarios Strict and Across by multiplying the genetic gain in each trait with the index weights of breeding goals in Table 3. In remaining scenarios, the DP-breeding goal was changed by lowering the index weight for milk production to obtain different correlations between the breeding goals in both environments. This hinders a fair comparison of monetary gain across scenarios; thus, total monetary gain was not calculated for the scenarios Across\_0.9, Across\_0.8, Across\_0.7 and Across\_0.6.



TABLE 4 Simulated differences in trait levels for the breeding lines in year 0 on both the genetic (in genetic standard deviation ( $\sigma_A$ -units) and phenotypic scale

Trait	Milk production	Beef production	Mastitis	Fertility	Feed efficiency
Phenotypic trait unit	kg 305d ECM	kg/day	%	d	kg/d
Dairy type					
Simulated genetic level in year 0 ( $\sigma_A$ -units)	0.064	2.881	1.123	1.835	-0.194
Simulated genetic level in year 0 (phenotypic trait units) <sup>a</sup>	89.27	0.086	5.349	17.941	-0.067
Dual purpose					
Simulated genetic level in year 0 ( $\sigma_A$ -units)	-1.561	3.089	2.621	2.361	0.486
Simulated genetic level in year 0 (phenotypic trait units) <sup>a</sup>	-991.64	0.123	9.859	20.981	0.260
Differences					
Achieved difference in year 0 (phenotypic trait units) <sup>b</sup>	-1103	+0.037	+4.46	+3.12	+0.34
Target difference in year 0 (phenotypic trait units)	-900	+0.040	+4.40	+3.00	+1.00

<sup>a</sup>Calculated as genetic level in  $\sigma_A$ -units times genetic SD from Table 3.

<sup>b</sup>Calculated as difference between genetic level in phenotypic trait unit in DT and genetic level in phenotypic trait unit in DP; average of all simulated scenarios.

Significant differences in genetic gain at trait level, rate of inbreeding and total monetary gain between all combinations of scenarios within a breeding line were tested by ANOVA followed by Fisher's least significant difference (LSD) test implemented in the *Agricolae* package (De Mendiburu, 2020) with a level of significance of  $p \leq .05$ . All statistical analyses were performed using the software R (R Development Core Team, 2020).

### 3 | RESULTS

#### 3.1 | Differences in genetic levels of traits in year 0

The simulated differences in breeding traits in year 0 for the two breeding lines are presented in Table 4. Differences in the desired direction were obtained for all traits; DP was simulated being inferior in milk production but being superior to DT in remaining traits. For milk production, a difference of 1,103 kg 305d ECM between the lines was obtained. For beef production, breeding lines differed by 0.037 kg/day. Regarding functional traits, a trait difference of 4.46% in mastitis incidence and 3.12 d for interval from 1st to last insemination was simulated. For residual feed intake, a trait difference of 0.34 kg/d between the lines was obtained.

#### 3.2 | Correlations between breeding goals in year 1 to 30

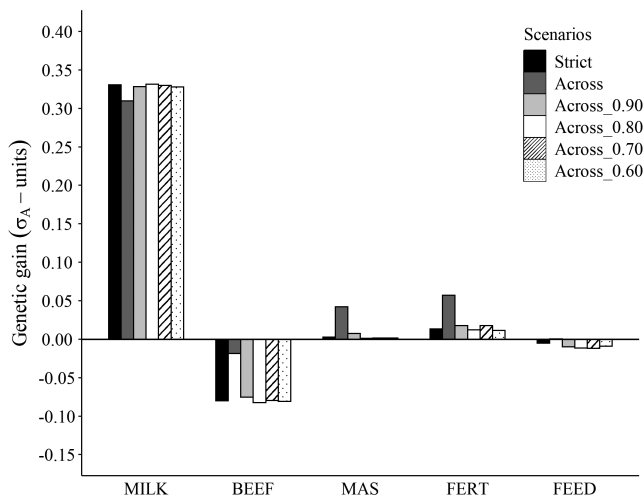
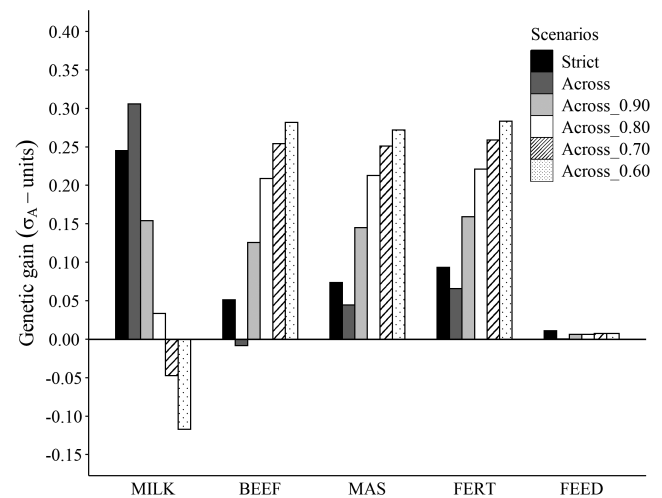
The genetic correlation ( $r_g$ ) between the overall breeding goals of the two breeding lines in the scenarios Strict and Across was 0.96. The genetic correlations between the individual traits and the breeding goals in each breeding line for all simulated scenarios are shown in Table 5. For DT, the correlations between single traits and the overall index remained the same across all scenarios, because the breeding goal was not changed. The DT-breeding goal showed highest correlation with milk production ( $r_g = 0.73$ ) and was moderately correlated with mastitis resistance ( $r_g = 0.24$ ) and fertility ( $r_g = 0.21$ ). The correlation between the overall index and feed efficiency was nearly zero ( $r_g = 0.01$ ) and negative for beef production ( $r_g = -0.11$ ).

In the DP-line, correlations between the overall index and single traits differed across the scenarios. In scenarios Strict and Across, genetic correlation between the breeding goal and individual traits was highest for milk production ( $r_g = 0.58$ ), mastitis resistance ( $r_g = 0.36$ ), and fertility ( $r_g = 0.34$ ). The genetic correlation with beef production and feed efficiency was  $r_g = 0.14$  and  $r_g = 0.09$ , respectively. With lower emphasis on milk production in the

**TABLE 5** Genetic correlations between traits and the overall breeding goals in the simulated environments depending on the correlation between the breeding goals

Trait	Environment					
	DT-breeding goal	DP-breeding goal				
		Scenarios				
All <sup>a</sup>	Strict/across	Across 0.90	Across 0.80	Across 0.70	Across 0.60	
Milk production	0.73	0.58	0.41	0.21	0.06	-0.08
Beef production	-0.11	0.14	0.26	0.38	0.45	0.52
Mastitis resistance	0.24	0.36	0.49	0.61	0.68	0.73
Fertility	0.21	0.34	0.46	0.57	0.63	0.67
Feed efficiency	0.01	0.09	0.09	0.10	0.10	0.10

<sup>a</sup>In the DT-line, breeding goal did not change across scenarios.

**FIGURE 2** Genetic gain in  $\sigma_A$ -units per trait and year averaged over years 21 to 30 for the dairy type line and all scenarios. BEEF, beef production; FEED, feed efficiency; FERT, fertility; MAS, mastitis resistance; MILK, milk production**FIGURE 3** Genetic gain in  $\sigma_A$ -units per trait and year averaged over years 21 to 30 for the dual-purpose line and all scenarios. BEEF, beef production; FEED, feed efficiency; FERT, fertility; MAS, mastitis resistance; MILK, milk production

remaining scenarios, correlation between milk production and the overall breeding goal decreased. In scenario Across\_0.60, the correlation between milk production and the overall index was negative ( $r_g = -0.08$ ). By contrast, genetic correlations of beef production, mastitis resistance and fertility with the overall DP-breeding goal increased. The correlation between feed efficiency and the DP-breeding goal was stable across scenarios and was between  $r_g = 0.09$  and  $0.10$ .

### 3.3 | Genetic gain in breeding lines

For the DT-line and DP-line, genetic gain per year ( $\sigma_A$ -units) in all traits and for all scenarios is depicted in

Figures 2 and 3, respectively. For the DT-line, genetic gain in milk production remained fairly constant across scenarios (Figure 2). In scenario Across, however, genetic gain was significantly lower ( $p < .05$ ) compared with all other scenarios. For beef production, negative genetic gain was observed in all scenarios with least negative genetic gain in scenario Across. Here, the LSD-test revealed a significant difference ( $p < .05$ ) compared with remaining scenarios. Similarly, genetic gain was significantly higher in scenario Across for mastitis resistance ( $p < .05$ ) and fertility ( $p < .05$ ). Genetic gain in feed efficiency was slightly negative. In scenario Across, however, genetic gain in feed efficiency was nearly zero and significantly differed ( $p < .05$ ) from genetic gain in scenarios Across\_0.9, Across\_0.8, Across\_0.7 and Across\_0.6.

Genetic gain in feed efficiency was not significantly different between scenarios Strict and Across.

For the DP-line, genetic gain differed greatly across the scenarios (Figure 3). For milk production, largest genetic gain was found in scenario Across with a significant difference ( $p < .05$ ) to all other scenarios. When the correlation between breeding goals in both environments decreased, genetic gain in milk production successively declined and genetic gain in the traits beef production, mastitis resistance and fertility successively increased. Genetic gain across all scenarios was significantly different ( $p < .05$ ) from each other for the traits milk production, beef production, mastitis resistance and fertility. For feed efficiency, the highest and lowest genetic gain was found in Strict and Across. Genetic gain in feed efficiency hardly changed in the remaining scenarios.

### 3.4 | Distribution of bulls from different environments

The distribution of bulls selected from both environments differed for the breeding lines and across scenarios (Figure 4). A considerable amount of bulls from the respective foreign environment was used with a high

genetic correlation between breeding goals in the breeding lines (Across). For DT, only bulls from the own environment were selected in the initial years of simulation, with an increasing use of bulls from the DP-line in subsequent years. The proportion of bulls selected from the foreign environment stayed fairly constant after year 10. Almost only bulls from the DT-line were selected in initial years of simulation in scenario Across in the DP-line. Afterwards, the proportion of foreign bulls selected decreased over time. As in the DT-line, the proportions of selected bulls stayed quite constant after year 10.

A lower proportion of foreign bulls was selected in both breeding lines with a decreasing genetic correlation between breeding goals. Very few bulls from DP were used in the DT-line in scenario Across 0.9, from year 5 to 15. Almost solely bulls from the own environment were selected from year 20. In the DT environments, bulls were exclusively selected from the own environment in the remaining scenarios. In the DP environment, the amount of selected foreign bulls decreased with genetic correlation between environments declining. Although in scenario Across\_0.90 a large amount of DT-bulls was selected in initial years, the number of selected foreign bulls decreased fast in later years of simulation. From around year

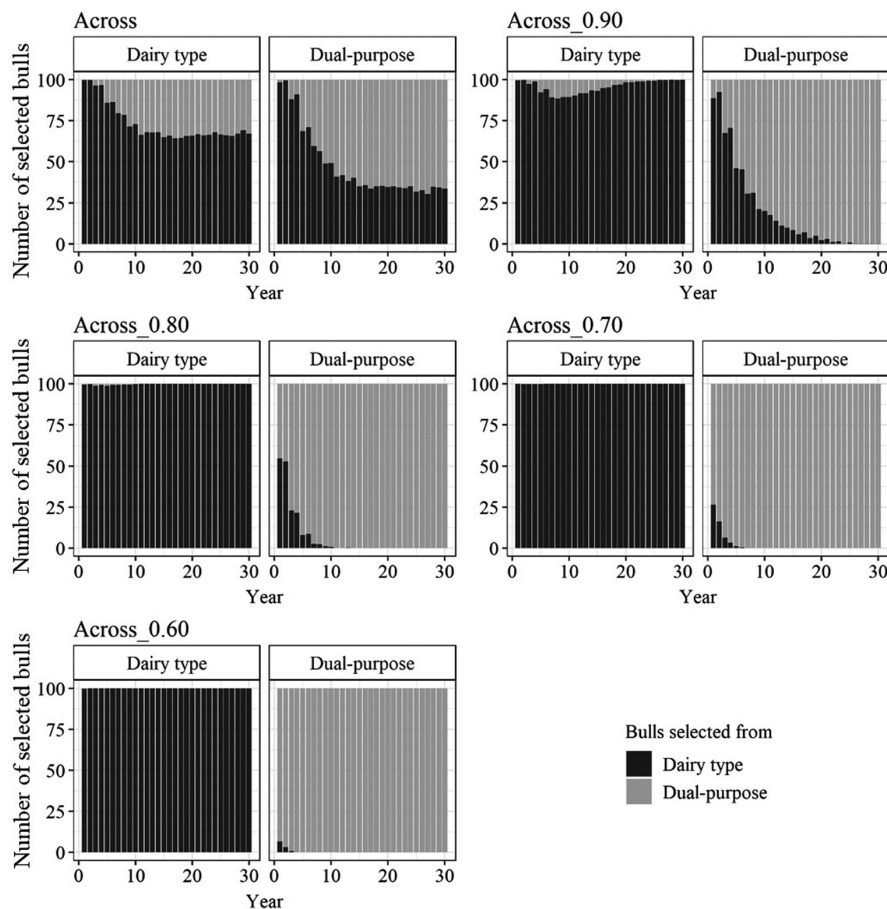


FIGURE 4 Distribution of bulls selected in the dairy type line and the dual-purpose line for simulated scenarios where selection across environments was allowed



25, the DP-line relied solely on own bulls. A low amount of bulls from the DT-line was selected in the first years of the simulation in the remaining scenarios. In subsequent years, bulls were completely selected within the DP environment.

### 3.5 | Inbreeding and total monetary gain per environment

Rates of inbreeding differed slightly between scenarios in both lines (Table 6). In the DT-line the average rate of inbreeding was between 0.15% and 0.20% per generation. The lowest rate of inbreeding was found in scenario Across (0.15%), where the rate of inbreeding was significantly different ( $p < .05$ ) from inbreeding in scenarios Across\_0.90, Across\_0.80 and Across\_0.70. Scenarios Across\_0.90 and Across\_0.70 had the highest inbreeding per generation at a rate of 0.20% per generation. In the DP-line, the average rate of inbreeding ranged from 0.14% to 0.20% per generation. Highest rates of inbreeding were found in scenarios Strict (0.19%) and Across\_0.90 (0.20%), differences were statistically significant ( $p < .05$ ) compared to all other scenarios. Lowest rates of inbreeding were obtained in Across\_0.60 (0.14%) and Across\_0.70 (0.16%).

In the DT-line, annual monetary gain was significantly higher in scenario Across (€54.23 ± 1.69) compared to scenario Strict (€51.62 ± 1.47,  $p < .05$ ) (Table 6). The same was observed for the DP-line, where annual monetary gain was significantly higher in scenario Across (€54.27 ± 1.62) compared to scenario Strict (€48.81 ± 1.40,  $p < .05$ ).

## 4 | DISCUSSION

The aim of this study was to investigate possibilities for cooperation (i.e. the exchange of sires) between two lines of Red cattle breeds in Northern Europe. Different breeding strategies with varying breeding goals between the two breeding lines were investigated. The present study revealed both advantages and disadvantages of collaboration between Red dairy and dual-purpose breeds, which are discussed considering short-term and long-term improvements of the populations.

### 4.1 | Collaboration across lines

In this study, both breeding lines have benefitted from collaboration at a high correlation between the environments (scenario Across). However, utility of

collaboration was different for the two breeding lines and for individual traits. For the DT-line, the use of DP-bulls enabled clear improvements in genetic gain for mastitis resistance and fertility. Although this improvement was accompanied by a reduction in genetic gain for milk production, the total monetary gain was significantly higher when across-environment selection was allowed. Functional traits mastitis and fertility had high economic weights in the DT-breeding goal. Thus, improvements in these traits resulted in a significant increase in total monetary gain when comparing scenarios Strict and Across. For the remaining scenarios in DT, genetic gain was similar to that in the Strict scenario because the same breeding goal was applied and there was no collaboration with the other environment in the last 10 years of simulation.

In the DP-line, genetic gain at trait level considerably differed across scenarios. Comparing the scenarios Strict and Across, significant improvement in genetic gain for milk yield was obtained by selecting bulls from the DT-line. This improvement, however, was accompanied by reduced genetic gain in beef production. Furthermore, genetic gain of the traits mastitis resistance and fertility deteriorated. Nevertheless, as in the DT-line, annual monetary gain substantially increased when cooperation between breeding lines was not restricted. This can be explained by the high economic importance of milk production in the DP-breeding goal. Accordingly, a large increase in genetic gain of milk production induced a high monetary gain. In remaining scenarios, genetic gain differed greatly, which was not surprising since breeding goals in the DP environment changed. This nicely demonstrated the effect of different breeding goal weights within the DP-line.

In general, collaboration between breeds results in additional genetic gain due to two different aspects. First, bulls can be selected from a larger number of selection candidates, thus, selection intensity increases. Second, sharing of genomic data on selection candidates is valuable as genomic information can be used across breeds. This positively affects genetic gain due to the enlargement of the reference population, which allows to predict GEBVs more accurately (VanRaden & Sullivan, 2010). For instance, Slagboom et al. (2019) showed that genetic gain in the total merit index increased by 13% only due to the exchange of genomic information between environments. This, however, depends on the genetic correlation between the environments and on the initial reliability of breeding values, that is the current size of the reference population. If the size of the reference population is already large, adding more genomic information does not increase accuracies of GEBVs to a great extent (Cao et al., 2020; Obšteter et al., 2019).

**TABLE 6** Rate of inbreeding and total monetary gain for the breeding lines dairy type and dual purpose and all scenarios. Total monetary gain in Euro per cow-year for the scenarios Strict and Across and both breeding lines. Different uppercase letters within columns indicate statistical significance ( $p < .05$ )

Scenarios	Dairy type		Dual purpose	
	Rate of inbreeding (%) <sup>a</sup>	Total monetary gain	Rate of inbreeding (%) <sup>b</sup>	Total monetary gain
Strict	0.18 <sup>ABC</sup>	51.62 <sup>A</sup> ( $\pm 1.47$ )	0.19 <sup>A</sup>	48.81 <sup>A</sup> ( $\pm 1.40$ )
Across	0.15 <sup>B</sup>	54.23 <sup>B</sup> ( $\pm 1.69$ )	0.16 <sup>B</sup>	54.27 <sup>B</sup> ( $\pm 1.62$ )
Across_0.90	0.20 <sup>A</sup>		0.20 <sup>A</sup>	
Across_0.80	0.19 <sup>AC</sup>		0.16 <sup>B</sup>	
Across_0.70	0.20 <sup>A</sup>		0.15 <sup>B</sup>	
Across_0.60	0.16 <sup>BC</sup>		0.14 <sup>B</sup>	

<sup>a</sup>Standard deviation of rate of inbreeding ranged from 0.04% to 0.08%.

<sup>b</sup>Standard deviations ranged from 0.03% to 0.06%.

The positive effect of additional genomic data is particularly evident when populations are genetically linked, for example through the exchange of genetic material (VanRaden & Sullivan, 2010). In this study, the focus was on Red breeds originating from Northern European countries. Previous studies described that Scandinavian Red breeds in particular show substantial degrees of genomic relatedness due to historical and current-day exchange of genetic material (Gautason et al., 2020; Olsen et al., 2011). For instance, Zhou et al. (2014) demonstrated an increase in accuracies of genomic estimated breeding values for production traits when using a joint genetic evaluation for Norwegian Red, Swedish Red, Danish Red and Finnish Ayrshire. Consequently, genetic progress is expected to accelerate by more accurately predicted GEBVs.

The genetic correlation between two environments is influenced by breeding goal differences and Genotype by Environment interaction ( $G \times E$ ).  $G \times E$  lowers the accuracies of GEBVs, since traits might be affected by different genes in different environments. Thus,  $G \times E$  is an obstacle for cooperative work between breeds. In this study, the genetic correlation between the breeding lines was only affected by differences in breeding goals. Nevertheless, it is reasonable to assume that moderate  $G \times E$  exists for Red breeds in Northern Europe. In genomic breeding schemes, however, collaboration amongst breeds or countries is advantageous, even in the presence of moderate  $G \times E$  (Cao et al., 2020).

The rates of inbreeding in the present study were low due to a large number of selected bulls with an equal number of offspring. This may deviate from the procedure in practical breeding, where usually a limited amount of bulls is heavily used and produces large cohorts of progeny. However, the results of the present study demonstrate that using bulls more evenly can effectively reduce the rates of inbreeding. Previously, it was recommended

to restrict genomic inbreeding to 0.5%–1% per generation (FAO, 2015). Generally, the use of external bulls lowers the rate of inbreeding in the breeding lines. This is associated with external bulls being less related to bulls in the own environment, thereby introducing new genetic variation. However, results of this study also showed, that selecting foreign bulls can actually increase inbreeding (scenario Across\_0.90). The extensive use of DT-bulls in the DP-line has resulted in progeny that were particularly suited for the DT-line. However, these offspring were direct descendants of DT-bulls and their use within the DT-line increased inbreeding. A good strategy here would be a restriction on using direct progeny even though they were born in the foreign environment. At this point, sophisticated selection methods such as optimum contribution selection (Grundy et al., 1998; Meuwissen, 1997) become relevant.

In summary, collaboration across the simulated breeding lines was beneficial in terms of genetic gain for individual traits, inbreeding and for the overall monetary gain when the correlation between the breeding goals in both environments was close to unity. With decreasing correlation between the environments, collaboration rapidly terminated and so does its utility.

## 4.2 | Effects of differences in genetic levels

In similar simulation studies, breeding programmes usually have the same initial genetic levels (Slagboom et al., 2019; Thomsen et al., 2020). With the application of different breeding goals, divergence of regarded breeds is observed. In most cases, however, this does not correspond to reality. In the present study, both breeding lines were calibrated to have different starting levels of breeding

traits. For most traits, the achieved breed differences were in line with the desired target differences. For feed efficiency, by contrast, the created difference between breeding lines was much smaller than the difference aimed for. This relates mainly to two aspects. Firstly, residual feed intake was assumed to be negatively correlated with both mastitis incidence and fertility. Secondly, the accuracy of DGVs for residual feed intake was low, thus, genetic progress was barely obtained in this trait.

Overall, the created different genetic levels in initial years of simulation influenced the utility and degree of collaboration between the two breeding lines. The DP-line was simulated to be clearly inferior in milk production compared to the DT-line. Because the breeding goal in the DP environment strongly emphasized milk (in scenarios Strict and Across), a situation was created, in which external DT-bulls were most suitable to use in the DP-line. As a consequence, when across-environment selection was allowed and the correlation between the breeding goals was high (scenario Across), in the DP-line almost only bulls from the foreign environment were selected in first years of simulation. With decreasing correlation between environments, the amount of selected external sires in the DP-line decreased.

The DT-line, on the other hand, was simulated to be inferior in mastitis resistance and fertility. To settle these differences, bulls from the DP environment were used as those were bred for a breeding goal with strong emphasis on functional traits. Interestingly, in scenario Across\_0.90, the DT-line suddenly started selecting external DP-bulls from around year 5 of simulation, although in previous years almost only own sires were selected. This relates to the selection of bulls in the DP environment, in which in the first two years a large number of bulls from the DT-line was used. In the DP environment, subsequently, animals with a high genetic level for milk production were born in the next generation. These animals were well suited to be used in the DT-line, thus, an increase of selected DP-bulls in the DT-line was observed. This also explains the slight increase in the rate of inbreeding observed in scenario Across\_0.90 compared to remaining scenarios. As the number of DT-bulls selected in the DP-line decreased, animals born in the DP environment became less suitable for the DT-line. Therefore, fewer foreign sires were selected in the DT-environment over time.

The created differences in genetic levels in breeding traits made collaboration in early years of the simulations very useful for breeding lines. In a way, the simulated breeding lines were complementary to each other in genetic levels of breeding traits, which makes external sires more suitable for the own environment. Furthermore, differences in the degree of collaboration between breeding lines have been observed. The more the correlation

between breeding goals decreased, the earlier the breeding lines separated and operated individually. The DT-line, however, operated even earlier by themselves than the DP-line. Previous studies have shown, that more animals are selected from the population which is genetically superior (Buch et al., 2009; Smith & Banos, 1991). As the DP-breeding goal strongly emphasized milk production, animals from the DT-line were still selected in the beginning of simulation, even in scenarios with a lower correlation between the breeding goals. Thus, the simulated differences affected the collaboration in the first years of simulation.

In the long run the created breed differences had little impact. An important concept regarding long-term cooperation of breeding programmes is the split-point genetic correlation, which describes the highest genetic correlation where breeding programmes still perform separately (Mulder & Bijma, 2006). With a genetic correlation above the split-point, cooperation across the breeding programmes starts as additional genetic gain is expected. In the present study, only in scenario Across, with a correlation between breeding goals close to unity, cooperation was still observed in last years of simulations. In this scenario, an equilibrium situation was established where approximately 70% own bulls and 30% foreign bulls were selected in both breeding lines. In remaining scenarios with lower correlated breeding goals, the sharing of bulls was terminated before year 30. Even though less generations were simulated compared to Mulder and Bijma (2006), it is reasonable to assume that in the present study the split-point correlation is high.

Mulder and Bijma (2006) demonstrated on a theoretical basis that above the split-point genetic correlation, a stable selection with half own bulls and the other half external bulls is expected, because animals are equally suited for both environments. However, this is only valid for single-trait selection. For instance, Slagboom et al. (2020) showed that although the correlation between breeding goals is high, the resulting genetic gain on trait level can differ substantially. In the present study, breeding goals were composed of five different traits. It can be concluded that, as long as breeding goal differences between environments exist, both environments will select a higher proportion of own bulls. In a way, this study transfers the theoretical results from Mulder and Bijma (2006) in a more practical setting.

The created trait differences in this study contributed to more realistic simulations. However, these differences affected the collaboration only in the beginning of the simulations. By contrast, these differences do not necessarily have to be taken into account in the long run when evaluating consequences of cooperative work between breeds.

### 4.3 | Benefits of separate breeding lines

Livestock breeding is characterized by constantly balancing short-term and long-term improvements of breeding populations. As stated in the previous sections, the study showed that future cooperation is beneficial for Red breeds in terms of genetic gain and inbreeding, provided the correlation between breeding goals is sufficiently high. This is, nevertheless, only a short-term consideration, which mainly relies on increased intensity and accuracy of selection (Hill, 2000). In the long term, there are relevant aspects to take into account that indeed argue against cooperation, that is the intensive exchange of breeding animals. In the present study, the exchange of breeding bulls resulted in a genetic convergence of the two breeding lines. This also means, that genetic diversity existing between breeds is lost. Additionally, the intensive use of higher-yielding DT-bulls in the DP-line will diminish the native genetic background within the DP-line. In the past, the introgression of genetic material from higher-yielding breeds has been frequently applied in many local breeds to improve their productivity (Schmidtmann et al., 2021; Wellmann & Bennewitz, 2019). This, however, poses a threat to the genetic variation provided by local breeds. Thus, considering the aspect of global genetic diversity, high degrees of exchange of genetic material between populations should be avoided.

Moreover, in the present study, cooperation negatively affected genetic gain in certain traits. For instance, in the DP-line, deterioration of functional traits was observed due to the use of external DT-bulls. Thus, as a consequence of cooperation, specific desirable properties were lost. Similarly, genetic gain of beef production in the DP-line was reduced when foreign bulls were used, thereby losing their dual-purpose breed character.

Animal breeding will be faced towards various challenges in the future including changes in climatic, environmental and production circumstances (Groeneveld et al., 2010). Breed diversification to serve different farming systems is prospectively of particular value. Dual-purpose breeds are known to handle external disturbances and suboptimal production conditions quite well, which is partly due to the manner they were selected in the past (Ferris et al., 2014). Another aspect that becomes increasingly important is the environmental compatibility of dairy farming. Increased production of meat as a by-product of dairy farming reduces the reliance on specialized pure-beef production, which has higher greenhouse gas emissions per calorie of food-stuff produced (de Vries et al., 2015; Puillet et al., 2014; Vellinga & de Vries, 2018). All these arguments oppose cooperative work (i.e. extensive exchange of breeding animals) between pure dairy and dual-purpose Red breeds.

Indeed, these aspects emphasize greater promotion of dual-purpose breeds and the need for more diversified cattle populations to serve different requirements of farmers. However, before a conclusive recommendation for or against cooperative work across Red cattle breeds in Northern Europe can be given, a cost-benefit analysis of the breeding schemes is essential; something that is beyond the scope of this study.

## 5 | CONCLUSIONS

This study compared different breeding strategies with and without collaboration between two types of Red cattle breeds in Northern Europe. From a short-term perspective, the exchange of breeding bulls across populations was desirable with respect to genetic gain, providing that the correlation between environments was close to unity. Similarly, total monetary gain was highest when across-selection of bulls was allowed. Thus, cooperative work of Red breeds seems to be appealing. In the long-term, however, extensive across-environment selection of bulls will result in the loss of specific desirable breed properties such as superiority in functional traits. Overall, the two breeding lines will become genetically more similar which will reduce genetic diversity. Ultimately, short- and long-term consequences of cooperative work between Red breeds in Northern European countries must be carefully reconciled.

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### CONFLICT OF INTEREST

The authors declare that they have no competing interests.

### DATA AVAILABILITY STATEMENT

This study was based on simulated data; no real data were used or generated.

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