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Simulation of long-term impact of dairy cattle mating programmes using genomic information at the herd level

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ABSTRACT

Genotyping provides breeders with new information at the single nucleotide polymorphism level that can be used in mating programmes. This study used stochastic simulation to explore the long-term effects of genomic mating allocations combining economic scores and linear programming at the level of commercial herds. The economic scores included genetic level, a favourable monogenic trait (polledness), a recessive genetic defect, and parent relationships. The results showed that compared with only maximising genetic level, including genomic or pedigree relationship in the economic score lowered the rate of pedigree and genomic inbreeding with minimal effect on genetic gain. Including the cost of a recessive genetic defect in the score almost eliminated the risk of expression. We set the start allele frequency of polledness to ~12%, and the value of polledness varied in the different scenarios (€0, €10, €50, and €100). Including an economic value for polledness of (≥ €50) in the economic score increased the frequency of polled animals by up to 0.037 per generation, without negatively impacting other comparison criteria. The use of genomic relationships was favourable for the rate of genomic inbreeding and performed as well as pedigree relationships concerning the rate of pedigree inbreeding. Limiting the number of females per bull and herd to a maximum of 5% instead of 10% also decreased the rate of inbreeding. The 5% females per bull and herd constraint lowered the variation in carrier frequency for genetic defects, which reduced the risk of mating two carriers of an unknown genetic defect in future generations after the widespread use of carriers in previous generations. However, the 10% females per bull constraint accelerated the increase in the polled allele. Therefore, planning matings with genomic information at the herd level involves important risk management decisions, such as balancing the trade-off between using fewer bulls to increase the polled allele frequency more quickly and using more bulls to reduce the rate of inbreeding and the variation in carrier frequency for genetic defects.

Implications

Mating programmes increasingly incorporate genomic information. We explored the long-term impact of genomic mating allocations, considering genetic level, a favourable monogenic trait (polledness), recessive genetic defects, and parent relationships. The results indicated that planning matings with genomic information at herd level involves important risk management decisions, such as balancing the trade-off between using fewer bulls to increase the polled allele frequency more quickly and using more bulls to reduce the rate of inbreeding and the variation in carrier frequency for genetic defects. Including information on relationships and monogenic traits had minimal effect on genetic gain in the breeding goal.

Introduction

Mating programmes at herd level are important support tools for farmers, helping them to identify the best parental matings for optimal profit in the next generation (Bengtsson et al., 2022a; Bérodier et al., 2021; Carthy et al., 2019). A common goal of

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herd-level mating programmes is maximising the genetic level of newborn calves while minimising expected inbreeding using pedigree information (Weigel and Lin, 2000). Genotyping provides breeders with new information at the single nucleotide polymorphism (**SNP**) level that can be used in mating programmes. For example, SNP markers offer the possibility to use genomic relationships between parents when making mating plans. They also provide information about certain known monogenic traits, including genetic defects and economically valuable traits such as polledness and monogenic milk quality traits (Borchersen, 2019).

Exploiting these new genetic possibilities requires new methods when setting up mating plans. Several studies have employed economic scoring systems to combine relevant information when ranking each potential mating (Bengtsson et al., 2022a; Bérodier et al., 2021; Carthy et al., 2019). The economic score typically includes genetic level, expected inbreeding, and the probability of conceiving an offspring homozygous for a genetic defect. In some cases, favourable monogenetic traits such as polledness and β-casein have also been included (Bengtsson et al., 2023). Linear programming is a fast and effective method for maximising the mean economic score of herds, subject to necessary constraints, and has been shown to outperform other mating methods, such as sequential mate allocation (Bérodier et al., 2021; Carthy et al., 2019; Sun et al., 2013).

Genomic information and linear programming have been applied previously to mating programmes in studies using real data (Bengtsson et al., 2022a; Bérodier et al., 2021; Carthy et al., 2019), but are inherently limited to the current breeding population and the immediate offspring, and not on the long-term consequences of mating strategies. Studies by Cole (2015) and Mueller et al. (2019) used simulations to examine the impact of mating programmes based on an economic score, over multiple generations, that incorporated net merit, genetic relationships, several recessive lethal alleles, and polledness. However, both studies used sequential solving instead of linear programming, and relied on pedigree relationships rather than genomic relationships. Therefore, the long-term impact of mating programmes using genomic information and linear programming remains to be explored.

Genetic defects and polledness are important monogenic traits to consider in mating programmes. Decreasing the probability of producing offspring that are homozygous for recessive genetic defects has economic value for farmers (Pryce et al., 2012) and is also important for animal health and welfare (European Forum of Farm Animal Breeders (EFFAB, 2020). Dehorning of cattle is a common practice to reduce the risk of injury to other cattle and improve safety for animal keepers. However, dehorning can be painful and stressful for the animals, as indicated by behavioural, neuroendocrine, and physiological changes (Stock et al., 2013). There is also a financial cost of dehorning that varies from e.g., €2.7–7.3 per animal in Denmark, Finland, and Sweden (Sørensen et al., 2018) to US$6–25 in the United States (Thompson et al., 2017). Since 2022, the procedure requires a special permit for organic farms within the European Union (EU Commission Regulation No 889/2008). This new EU regulation has increased demand for semen from bulls carrying the polled allele, and several breeding companies have started marketing polled bulls more heavily (Hanna Driscoll, product manager Holstein, VikingGenetics, personal communication, 24 September 2024).

With the increasing incorporation of genomic information into mating programmes at herd level, a comprehensive study on the long-term impact of this and its effects on genetic gain, genetic diversity, and monogenic traits is needed. The objective of this study was therefore to simulate the long-term impact of genomic mating programmes, when each herd in the population used a mating programme combining economic scores and linear programming. The mating allocations considered genetic level, a favourable monogenic trait (polledness), recessive genetic defects, and parent relationships.

Material and methods

We used stochastic simulation to investigate the long-term impact of genomic mating allocations combining economic scores and linear programming. The economic scores included genetic level, a favourable monogenic trait (polledness), a recessive genetic defect, and parent relationships. We examined various scenarios, with or without penalty for a known recessive genetic defect and parent relationships, and compared different economic values for polledness.

Simulation of the genome, founder population, and breeding goal

Our stochastic simulation approach for modelling breeding programmes utilised the AlphaSimR package version 1.3.4 (Gaynor et al., 2021) in R version 4.1.3 (R Core Team, 2020). We simulated a closed population under selection with discrete generations. The genomes of the founder population were created with the MaCS coalescent simulator (Chen et al., 2009), which was run within the AlphaSimR package (runMacs function), using the "CATTLE" population history (MacLeod et al., 2013). The founder population was generated once and was the same for all scenarios and replicates. We simulated 29 chromosomes of equal size and 6 000 segregating sites per chromosome. The breeding goal trait was constructed by adding an additive trait in AlphaSimR (addTraitA function), with a mean of 0 and a genetic SD of 10, which was assigned 4 000 quantitative trait loci per chromosome. The effects of the quantitative trait loci were sampled from a normal distribution. In addition, an SNP chip with 1 600 markers per chromosome was constructed in AlphaSimR (addSnpChip function) to approximate the marker density of the EuroGenomics mid-density chip (Borchersen, 2019).

Breeding scheme

The basic breeding scheme, which was the same across all scenarios (Fig. 1), was derived from earlier dairy cattle genetic simulation studies (Bengtsson et al., 2022b; Slagboom et al., 2019; Thomasen et al., 2014). Breeding animals were selected based on a total merit breeding goal trait. The accuracy of selection was approximately 0.7, which is similar to the accuracy of genomic prediction for total merit indices (**TMI**) used in dairy cattle breeding (Thomasen et al., 2016). The accuracy was calculated through the correlation between the true and the estimated TMI. In AlphaSimR, the phenotype represented the estimated TMI, and the accuracy of 0.7 was achieved by setting the heritability to 0.55. Hence, no actual genomic evaluation was performed. We simulated a nucleus population of 8 000 females across 40 herds. All animals in the nucleus were genotyped. In order to obtain a large number of progeny at a low age of the donor, the breeding scheme utilised advanced reproductive technologies (**RT**) such as ovum pick-up and *in vitro* fertilisation, and multiple ovulation and embryo transfer, hereafter referred to as RT. In every generation, we selected the best 200 females based on TMI for RT. Each donor produced 20 offspring (50:50 sex ratio). Of the 2 000 males produced via RT, the 100 best were selected as sires of the next generation. Following RT, the donors and the remaining females were inseminated with sexed semen, and all offspring were assumed to be female. Thus, approximately 10 000 females were available for the next generation (sometimes less if one of the lethal genetic defects was expressed), with the top 8 000 females selected for breeding.

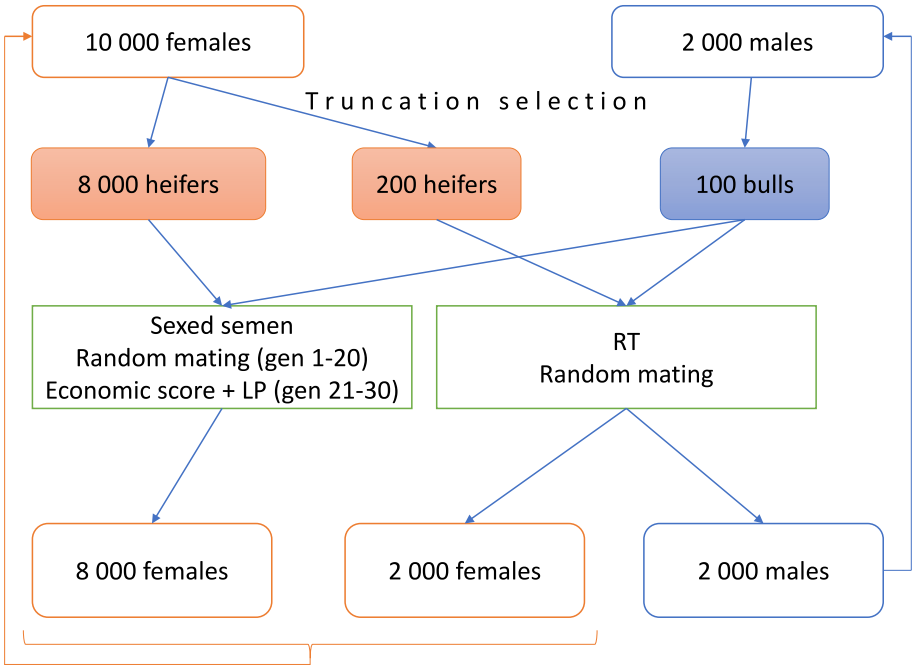

Fig. 1. Chematic overview of the simulated breeding scheme in dairy cattle. In the first 20 generations (gen) of each replicate, random matings were performed among all animals. In the last 10 generations, non-RT matings were planned with an economic score and linear programming (LP). RT = reproductive technologies, including ovum pick-up and *in vitro* fertilisation and multiple ovulation and embryo transfer.

The simulation spanned 30 generations, and each scenario was replicated 30 times. In the first 20 generations, random matings (with the randCross function in AlphaSimR) were performed among all selected animals. In the last 10 generations, matings with sexed semen were assigned based on an economic score that defined the scenario (Table 1), and matings of the donors were still assigned at random. The objective of this study was to study the consequence of different mating strategies at the level of commercial herds, and no attempt was made to optimise the overall breeding programme. The following sections provide more information about the economic scores used for mate allocation.

Monogenic traits

In generation 20, 3 SNP markers were selected to represent three monogenic traits. We considered one dominant trait, with an allele frequency of 0.12 (range 0.11–0.13), which represented polledness; one known lethal recessive genetic defect, with an allele frequency of approximately 0.05 (range 0.04–0.06); and one unknown lethal recessive genetic defect, with an allele frequency of approximately 0.09 (range 0.08–0.10), which served as a reference for risk management. We assumed that conceptuses/offspring homozygous for the recessive genetic defects were not available for breeding.

Relationship measures

We used two genetic relationship measures, one pedigree-based and one genomic-based. The pedigree relationship coefficient between potential parents was based on all available pedigree information ($\mathbf{a_{Ped}}$) and was calculated with the optiSel package in R (Wellmann, 2019). The genomic relationship coeffi-

Table 1
Description of the mating scenarios in dairy cattle evaluated in the simulation study.

Mating scenario[1]	Economic score includes:			
	TMI	Relation-Ship	Known Genetic defect value	Polled value (€)
MaxTMI	Yes	No	No	0
Ped	Yes	a_{Ped}	Yes	0
GSNP	Yes	g_{SNP}	Yes	0
PedPolled10	Yes	a_{Ped}	Yes	10
PedPolled50	Yes	a_{Ped}	Yes	50
PedPolled100	Yes	a_{Ped}	Yes	100
GSNPPolled10	Yes	g_{SNP}	Yes	10
GSNPPolled50	Yes	g_{SNP}	Yes	50
GSNPPolled100	Yes	g_{SNP}	Yes	100
Random	Matings were randomly assigned with an equal number of offspring (females 1 offspring and bulls 80 offspring)			

Ped: mates were selected based on maximising an economic score including TMI, a pedigree relationship (a_{Ped}) including all available ancestors, and a penalty for genetic defects.
GSNP: mates were selected based on maximising an economic score including TMI, a genomic relationship (g_{SNP}) calculated according to VanRaden (2008), and a penalty for genetic defects.
Polled €10, €50, €100: the economic value of a polled offspring, added to the economic score GSNP or Ped.
[1] MaxTMI: mates were selected based on maximising an economic score including Total Merit Index (TMI).

cient ($\mathbf{g_{SNP}}$) between potential parents was calculated according to VanRaden (2008) in R with the 1 600 SNP per chromosome, as:

$$g_{SNP_{ij}} = \frac{\sum_m (x_{im} - 2p_m) \times (x_{jm} - 2p_m)}{2\sum_m p_m(1 - p_m)}$$

where x_{im} and x_{jm} are the genotype scores of animal *i* and animal *j* at marker *m*, coded: 0 = homozygote, 1 = heterozygote, and 2 = alternative homozygote, and p_m is the frequency of the alternative allele of marker *m* in the founder population.

Economic score

For the females selected for insemination with sexed semen in generation 20 onward, we calculated an economic score between female *i* and male *j*, as:

$$Score_{ij} = \left(\frac{TMI_i + TMI_j}{2} + \lambda F_{ij}\right) \times \text{prob}(♀) -$$

$$p(aa)_r \times v_r + p(P) \times v_P$$

where TMI_i and TMI_j are the value of the Total Merit Index in Euros for female *i* and bull *j*, λ is the economic consequence of a 1% increase in inbreeding, F_{ij} is the pedigree- or genome-based coancestry (relationship/2), prob(♀) is the probability of producing a female conceptus, $p(aa)_r$ is the probability of expression of the known genetic defect *r* in the conceptus, given the genotype of the female *i* and bull *j* for this defect, v_r is the economic cost associated with the known recessive genetic defect *r*, p(*P*) is the probability of a polled offspring, given the genotype of the female *i* and bull *j* for polledness, and v_P is the value of a polled offspring compared with a horned offspring.

The value of one TMI index unit was set to €25.4, based on Nordic Total Merit (Fikse and Kargo, 2020). The economic consequence of an 1% increase in inbreeding was set to €25.4, as done in Bengtsson et al. (2022a, 2023). The probability of producing a female with sexed semen was set to 0.9 (Burnell, 2019). To keep the herd structure intact over generations (200 females per herd), we only considered the 0.9 factor in the economic score. We assumed that the known recessive genetic defect was early abortion and set the cost of this to €80, based on the resulting longer calving interval (€30–40/month) and the cost of extra insemination(s) (€30) (Sørensen et al., 2018; Oskarsson and Engelbrekts, 2015). The value of a polled offspring compared with a horned offspring varied in the different scenarios (€0, €10, €50, €100). For comparison, we investigated one scenario that involved only maximising genetic value and random mating (Table 1).

Mate allocation

Mate allocation with sexed semen in the last 10 generations of each scenario was done using the mixed integer linear programming solver in the 'Lp_solve' package (Berkelaar and others, 2020), as done in Bengtsson et al. (2022a, 2023). A mating linear programming problem has several integer properties (e.g., the number of offspring can only take integer values). However, linear programming can be used instead of integer programming; for details see Jansen and Wilton (1985). A mating R script provided by Bérodier et al. (2021) was used to set different constraints considered in linear programming optimisation. The mating R script maximises the different economic scores (Table 1), subject to constraints in one herd at a time. We used the constraints of one mating per female and a threshold percentage for the maximum number of females per bull and herd, for which we evaluated two different levels, 5 and 10%, similar to Bérodier et al. (2021) and Bengtsson et al. (2022a, 2023).

Statistical analysis

In the last 10 generations of the simulation, the different scenarios were compared by: (1) genetic gain in TMI per generation; (2) rate of pedigree inbreeding per generation calculated with the optiSel package in R (Wellmann, 2019); (3) rate of genomic inbreeding per generation from the diagonal of the VanRaden relationship matrix (excess homozygosity relative to the base population); (4) change in carrier frequency per generation of the known and unknown recessive alleles; (5) change in number/frequency of polled offspring per generation; (6) number of conceptuses affected by the known and unknown genetic defect in the last 10 generations; (7) number of bulls used per generation; and (8) number of bulls used per generation to the maximum number of doses allowed for the threshold (5 and 10%) of females per bull and herd.

We performed statistical analysis using R version 4.1.3 (R Core Team, 2020). Tables 2 and 3 report the mean and 5th and 95th percentiles for the MaxTMI scenario across replicates, with results outside this interval (treated as significant) marked with an asterisk (*). The mean across replicates is shown in Fig. 2, Supplementary Fig. S1 and S2, and the mean and 5th and 95th percentiles across replicates are shown in Figs. 3 and 4.

Results

The inclusion of a genomic relationship in the economic score significantly reduced the rate of increase for both pedigree and genomic inbreeding compared with only maximising genetic level (scenario MaxTMI) (Tables 2 and 3). Incorporating a pedigree relationship into the economic score reduced the rate of increase for both pedigree and genomic inbreeding compared with MaxTMI, although there were some exceptions regarding the level of significance. The scenario Random had lower rates of inbreeding and genetic gain than most other scenarios analysed. The rates of pedigree inbreeding were similar when either genomic or pedigree relationship was included in the economic score, but the inclusion of genomic relationship led to a lower rate of genomic inbreeding (Tables 2 and 3). In generation 21, which was the first generation born from matings based on economic score, a decrease in inbreeding level was observed in scenarios that included a genetic relationship in the economic score, indicating a reduction in both pedigree and genomic inbreeding relative to that in scenarios MaxTMI and Random (Supplementary Fig. S1 and S2).

The frequency of polled offspring increased on average over time when the value of polledness was €50 or higher, while it remained constant when the value was €10. The genetic gain and the rate of genomic and pedigree inbreeding in scenarios that increased polled frequency were similar to those in MaxTMI. The largest change in frequency of polled offspring per generation (0.037) occurred in one of the scenarios when the value of polled was €100 (GSNPPolled100) using 10% females per bull and herd (Tables 2 and 3, Fig. 2). The frequency of polled offspring increased faster over generations with the 10% females per bull and herd constraint compared with the 5% constraint. For example, in GSNPPolled100, the increase in frequency of polled offspring was 0.037 per generation when allowing up to 10% females per bull and herd, compared with 0.028 per generation when using the limitation of 5% females per bull and herd (Tables 2 and 3).

There was a large variation in the frequency of monitored monogenic traits across replicates and scenarios. In general, using fewer bulls resulted in higher variation across replicates regarding the monogenetic traits. We illustrate this variation with some selected results for the carriers of the unknown recessive genetic defect in Fig. 3 and the frequency of conceptuses affected by the unknown recessive genetic defect in Fig. 4. For example, the

Table 2
Results of 10 mating scenarios[1] in dairy cattle during the last 10 generations (gen) of the simulation. The maximum bull usage was 5% females per bull and herd.

Comparison criterion[2]	Random	MaxTMI[3]	Ped	Ped			GSNP	GSNP		
				Polled €10	Polled €50	Polled €100		Polled €10	Polled €50	Polled €100
Genetic gain (per gen) (σ_A[4] = 10)	7.59*	7.93 (7.61–8.27)	7.91	7.87	7.89	7.87	7.86	7.82	7.87	7.83
Pedigree inbreeding rate (per gen)	0.0025*	0.0041 (0.0032–0.0052)	0.0032*	0.0033	0.0031*	0.0033	0.0031*	0.0032*	0.0031*	0.0031*
Genomic inbreeding rate (per gen)	0.0073*	0.0092 (0.0081–0.010)	0.0085	0.0085	0.0084	0.0084	0.0080*	0.0080*	0.0080*	0.0080*
Carrier frequency change of the known defect (per gen)	−0.005	−0.002 (−0.0092 – 0.0093)	−0.004	−0.004	−0.004	−0.003	−0.003	−0.004	−0.004	−0.003
Carrier frequency change of the unknown defect (per gen)	−0.007	−0.009 (−0.021 – −0.001)	−0.008	−0.007	−0.008	−0.006	−0.006	−0.005	−0.003	−0.007
Polled offspring frequency change (per gen)	−0.005	−0.007 (−0.02 – 0.014)	−0.003	0.000	0.017*	0.032*	−0.004	0.00	0.015*	0.028*
Average frequency of conceptuses affected by the known defect	0.0013	0.002 (0.0001–0.006)	0.0*	0.0*	0.0*	0.0*	0.00015	0.00015	0.00010	0.00017
Average frequency of conceptuses affected by the unknown defect	0.0049	0.0040 (0.001–0.0088)	0.0033	0.0037	0.0047	0.0048	0.0032	0.0048	0.0040	0.0032
Average (per gen) number of bulls used	100	21	24	24	24	25	47	47	47	45
Average (per gen) number of bulls used to a maximum	NA[5]	20	17	17	17	17	13	13	13	13

MaxTMI: mates were selected based on maximising an economic score including a Total Merit Index (TMI).
Ped: mates were selected based on maximising an economic score including TMI, a pedigree relationship (a_{Ped}) including all available ancestors, and a penalty for genetic defects.
GSNP: mates were selected based on maximising an economic score including TMI, a genomic relationship (g_{SNP}) calculated according to VanRaden (2008), and a penalty for genetic defects.
Polled €10, €50, €100: the economic value of a polled offspring, added to the economic score GSNP or Ped.
[1] Random: Matings were randomly assigned with an equal number of offspring (females 1 offspring and bulls 80 offspring).
[2] Genetic gain in TMI per generation; rate of pedigree; rate of genomic inbreeding per generation from the diagonal of the VanRaden relationship matrix (VanRaden, 2008), change in carrier frequency per generation of the known and unknown recessive alleles; change in number/frequency of polled offspring per generation; number of conceptuses affected by the known and unknown genetic defect; number of bulls used per generation; and number of bulls used per generation to maximum number of doses allowed for the threshold 5% of females per bull and herd.
[3] Mean and 5th and 95th percentiles (in brackets) for the MaxTMI scenario across replicates, results in the rest of the table outside this interval were treated as significant and marked with an asterisk (*).
[4] genetic SD.
[5] NA = not applicable.

variation was higher for 10% females per bull and herd (Fig. 4), even though the mean frequency was similar in both sets (Tables 2 and 3). The scenario with a limit of 5% females per bull was more similar to Random in terms of variation than the scenario with a limit of 10% females per bull. There was no clear pattern in carrier frequency variation between the different scenarios using an economic score, including extra weight for polledness or one only considering genetic level, when the same constraint for females per bull and herd was used (Fig. 3).

The carrier frequency of both known and unknown recessive genetic defects decreased on average over generations in all scenarios. The number of conceptuses affected by the known recessive genetic defect decreased when the cost of this known genetic defect was included in the economic scores. Using pedigree relationship with a cost of the recessive genetic defect avoided almost all affected conceptuses in most scenarios and replicates. The risk of mating two carriers was slightly higher when a genomic relationship was used instead of a pedigree relationship together with the cost of the recessive genetic defect (Tables 2 and 3).

Discussion

In this study, we simulated the long-term consequences of genomic mating programmes at the level of commercial herds on genetic gain, genetic diversity, and monogenic traits. Compared with only maximising genetic level, including any genetic relationship in the economic score lowered the rate of increase in pedigree and genomic inbreeding, with minimal effect on genetic gain. Including the cost of a recessive genetic defect in the score helped to reduce the risk of expression. Including an economic value for polledness in the economic score increased the frequency of the polled allele in the population, again without negatively impacting other comparison criteria.

We also compared scenarios where genomic relationships or pedigree relationships were considered in the economic score. We found that genomic relationships resulted in a slightly higher risk of conceptuses affected by the known recessive defect compared with pedigree relationships. However, genomic relationships resulted in more bulls being used, which was favourable for lowering the rate of genomic inbreeding and performed equally well as pedigree relationships concerning the rate of pedigree inbreeding. Limiting the number of females per bull and herd to 5% instead of 10% also decreased the rate of inbreeding. The 5% females per bull and herd constraint lowered the variation in carrier frequency for genetic defects, which minimised the risk of mating two carriers of an unknown genetic defect in future generations after widespread use of carriers in previous generations. However, allowing 10% females per bull could accelerate the increase in the polled allele. Therefore, planning matings with genomic information at herd level involves important risk management decisions, such as balancing the trade-off between using fewer bulls to increase the polled allele frequency more quickly and using more bulls to reduce the rate of inbreeding and the variation in carrier frequency for genetic defects.

Genetic defects and inbreeding

A higher rate of inbreeding was generally associated with more variation in carrier frequencies, leading to a higher probability of mating two carriers, especially for the unknown genetic defect

Table 3
Results of 10 mating scenarios[1] in dairy cattle during the last 10 generations (gen) of the simulation. The maximum bull usage was 10% females per bull and herd.

Comparison criterion[2]	Random	MaxTMI[3]	Ped	Ped			GSNP	GSNP		
				Polled €10	Polled €50	Polled €100		Polled €10	Polled €50	Polled €100
Genetic gain (per gen) (σ_A[4] = 10)	7.59*	8.00 (7.67–8.37)	7.97	7.93	7.97	7.98	7.98	8.02	7.94	7.88
Pedigree inbreeding rate (per gen)	0.0025*	0.0053 (0.0041–0.0068)	0.0039*	0.0039*	0.0039*	0.0040*	0.0039*	0.0037*	0.0038*	0.0038*
Genomic inbreeding rate (per gen)	0.0073*	0.011 (0.0091–0.0122)	0.0093	0.0091*	0.0092	0.0093	0.0086*	0.0087*	0.0086*	0.0086*
Carrier frequency change of the known defect (per gen)	−0.005	−0.005 (−0.015 −0.009)	−0.007	−0.004	−0.005	−0.005	−0.0026	−0.0026	−0.0022	−0.0033
Carrier frequency change of the unknown defect (per gen)	−0.007	−0.008 (−0.021 – 0.011)	−0.0068	−0.0073	−0.0060	−0.007	−0.0073	−0.0043	−0.0050	−0.0071
Polled offspring frequency change (per gen)	−0.005	−0.0037 (−0.022 – 0.0025)	−0.0071	0.002	0.020	0.034*	−0.004	−0.0019	0.020	0.037*
Average frequency of conceptuses affected by the known defect	0.0013	0.0012 (0.00013 – 0.0041)	0	0.000001*	0.000001*	0.00001*	0.0002	0.0003	0.0002	0.0002
Average frequency of conceptuses affected by the unknown defect	0.0049	0.0044 (0.0004 – 0.0089)	0	0.004	0.005	0.005	0.004	0.004	0.004	0.005
Average (per gen) number of bulls used	100	10	14	14	14	15	30	30	30	30
Average (per gen) number of bulls used to a maximum	NA[5]	10	8	8	8	8	6	6	6	6

MaxTMI: mates were selected based on maximising an economic score including Total Merit Index (TMI).
Ped: mates were selected based on maximising an economic score including TMI, a pedigree relationship (a_{Ped}) including all available ancestors, and a penalty for genetic defects.
GSNP: mates were selected based on maximising an economic score including TMI, a genomic relationship (g_{SNP}) calculated according to VanRaden (2008), and a penalty for genetic defects.
Polled €10, €50, €100: the economic value of a polled offspring, added to the economic score GSNP or Ped.
[1] Random: Matings were randomly assigned with an equal number of offspring (females 1 offspring and bulls 80 offspring).
[2] Genetic gain in TMI per generation; rate of pedigree per generation; rate of genomic inbreeding per generation from the diagonal of the VanRaden relationship matrix (VanRaden, 2008), change in carrier frequency per generation of the known and unknown recessive alleles; change in number/frequency of polled offspring per generation; number of conceptuses affected by the known and unknown genetic defect; number of bulls used per generation; and number of bulls used per generation to the maximum number of doses allowed for the threshold 10% of females per bull and herd.
[3] Mean and 5th and 95th percentiles (in brackets) for the MaxTMI scenario across replicates, results in the rest of the table outside this interval were treated as significant and marked with an asterisk (*).
[4] genetic SD.
[5] NA = not applicable.

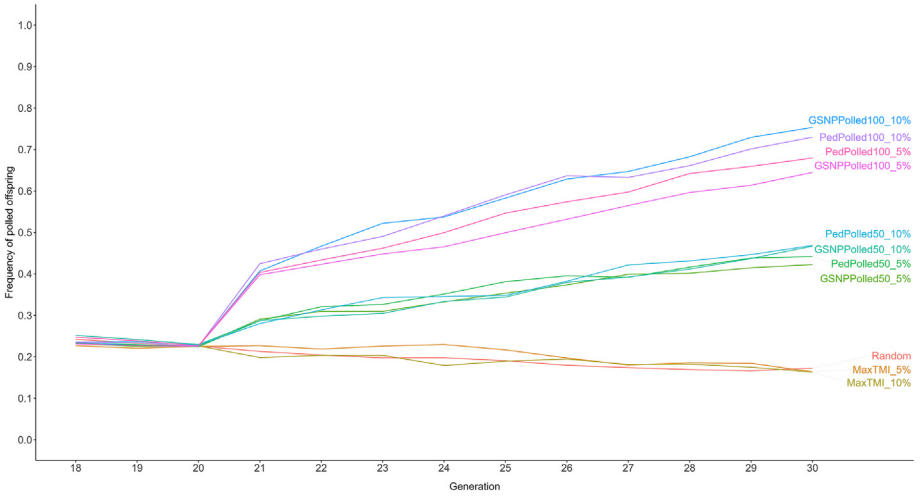

Fig. 2. Average frequency of polled animals across replicates in the last 12 generations of the simulation in dairy cattle. In the last 10 generations of the simulation, matings were assigned based on an economic score that defined the mating scenario (see Table 1 for details). MaxTMI: mates were selected based on maximising an economic score including Total Merit Index (TMI). PedPolled(50–100): mates were selected based on maximising an economic score including TMI, a pedigree relationship (aPed) including all available ancestors, a penalty for genetic defects, and an economic value for polledness of €50 or €100. GSNPPolled(50–100): PedPolled but with genomic relationship (gSNP) calculated according to VanRaden (2008) instead of a pedigree relationship. Maximum bull usage was 5 or 10% females per bull and herd (indicated with scenario name_5 or_10%).

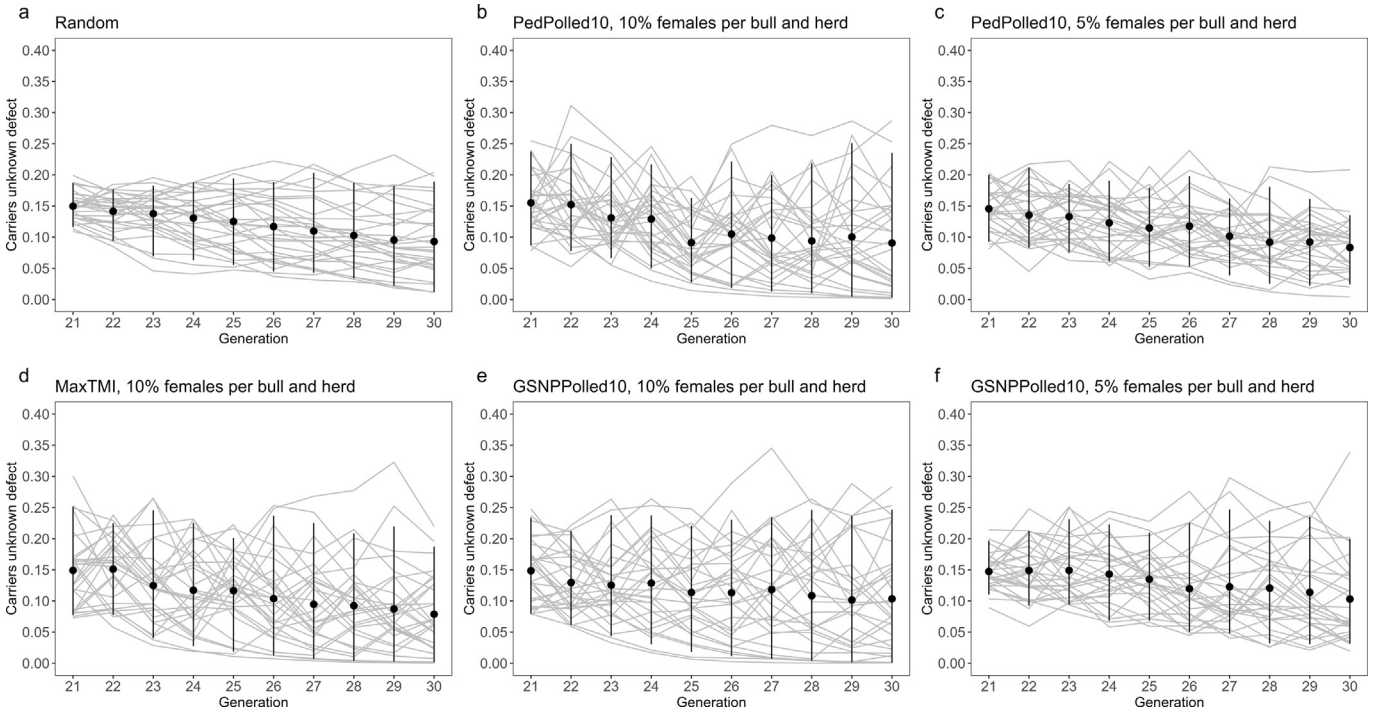

Fig. 3. Frequency of carriers of the (assumed) unknown recessive genetic defect in dairy cattle during the last 10 generations of the simulation, which defined the scenario studied (see Table 1 for details). Points show mean of replicates, error bars show 5th and 95th percentiles. MaxTMI: mates were selected based on maximising an economic score including Total Merit Index (TMI). PedPolled10 mates were selected based on maximising an economic score including TMI, a pedigree relationship (a_{Ped}) including all available ancestors, a penalty for genetic defects, and an economic value for polledness of €10. GSNPPolled10: PedPolled but with genomic relationship (g_{SNP}) calculated according to VanRaden (2008) instead of a pedigree relationship in PedPolled. Maximum bull usage was 5 or 10% females per bull and herd. Average SD: (a) 0.043, (b) 0.061, (c) 0.042, (d) 0.063, (e) 0.070, (f) 0.054.

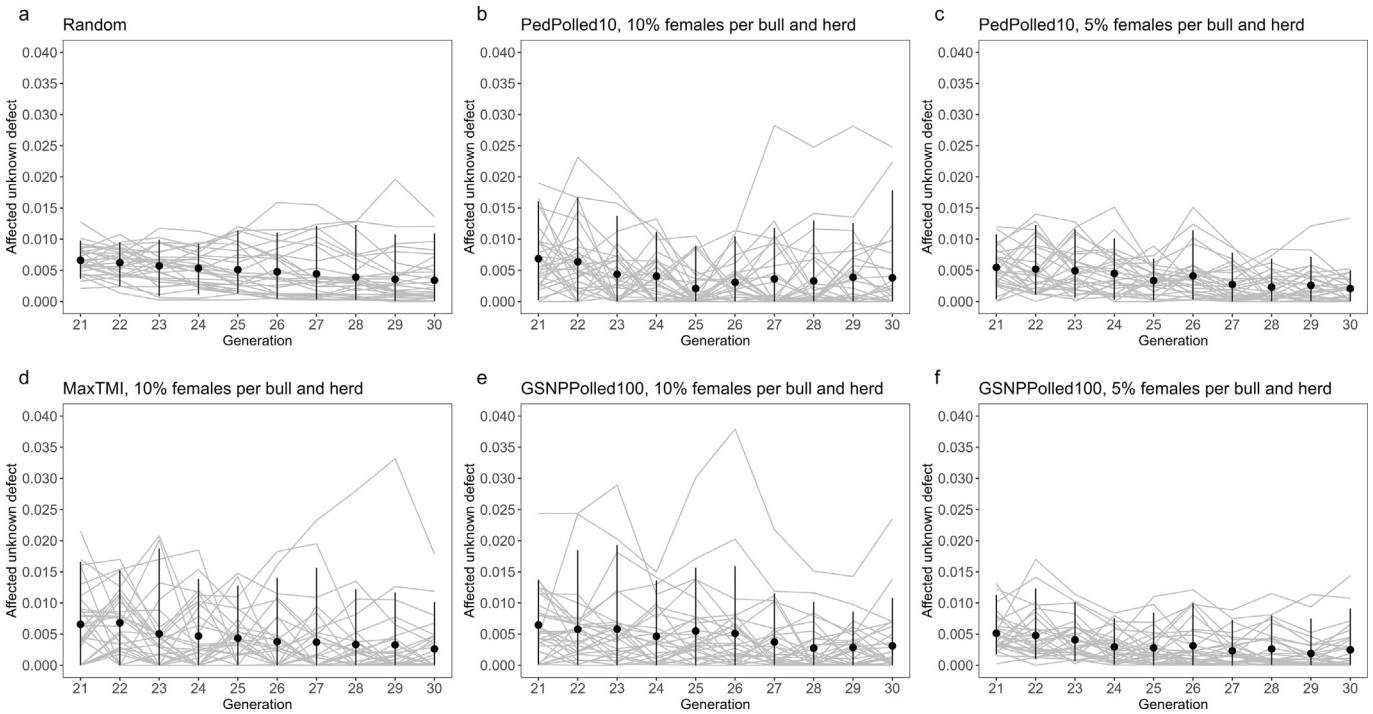

Fig. 4. Average frequency of conceptuses affected by the unknown defect in dairy cattle during the last 10 generations of the simulation, which defined the scenario studied (see Table 1 for details). Points show mean of replicates, error bars show 5th and 95th percentiles. MaxTMI: mates were selected based on maximising an economic score including Total Merit Index (TMI). PedPolled10: mates were selected based on maximising an economic score including TMI, a pedigree relationship (a_{Ped}) including all available ancestors, a penalty for genetic defects, and an economic value for polledness of €10. GSNPPolled100: PedPolled but with genomic relationship (g_{SNP}) calculated according to VanRaden (2008) instead of a pedigree relationship, and an economic value for polledness of €100. Maximum bull usage was 5 or 10% females per bull and herd. Average SD: (a) 0.0032, (b) 0.0045, (c) 0.0030, (d) 0.0048, (e) 0.0047, (f) 0.0037.

(Fig. 4). This is consistent with the population genetic expectation that an effectively small population has higher variance in allele frequency due to drift, and supports the idea that inbreeding is an important measure with regard to risks in a breeding programme (Meuwissen et al., 2020; Quinton and Smith, 1995). One way to control inbreeding is to limit the number of females per bull and herd, as done in the 5 and 10% scenarios in this study. Using few bulls when only maximising genetic level, with 10% females per bull and herd, could in some cases be favourable regarding the reduced risk of offspring affected by the unknown genetic defect, since it was unlikely for a carrier bull to be selected and allocated to females (Fig. 4). However, this outcome must be weighed against the higher rate of inbreeding seen in MaxTMI and the cost of that compared with no extra genetic gain (Tables 2 and 3). We expected that using more bulls in scenarios with a genomic relationship (Tables 2 and 3) would reduce the variation in carrier frequency (Fig. 3) with the same constraint for females per bull and herd. However, we did not observe this pattern clearly in our results.

Risk of mating two carriers for genetic defects

The risk of expression of the known recessive genetic defect increased slightly when the economic score included a genomic relationship instead of a pedigree relationship (Tables 2 and 3). This was mainly due to low genomic relationships that made it worthwhile to mate two carriers. In our previous studies based on real data (Bengtsson et al., 2022a, 2023), we did not observe this. A possible explanation is that we did not encounter enough different situations in our previous studies, as we only examined one or two different bull sets and looked only one generation ahead, with no replicates. In contrast, in this study, we explored a new bull set in every generation, scenario, and replicate. Another possible explanation for the difference between pedigree and genomic relationships in managing recessive genetic defects could be that the pedigree relationships reflect more identity by descent than VanRaden's relationships matrix, which depends more on identity by state (Alemu et al., 2021; VanRaden, 2008), and it could be argued that an identity by descent genetic relationship is favourable in avoiding mating of two carriers. Alternative genomic relationships, including segment-based relationships or relationships based on linkage analyses (Meuwissen et al., 2020), could possibly capture more identity by descent. However, in earlier studies, we found only small differences between SNP-by-SNP-based and segment-based relationships in allocated matings (Bengtsson et al., 2022a, 2023). Thus, in the practical implementation of genomic mating allocation, different relationship matrices for the particular population under study should be evaluated.

The hypothetical recessive genetic defect considered in this study caused early embryo loss, which has lower economic consequences than other defects resulting in late-term abortions or defective or dead calves. More severe defects should be assigned a higher economic cost in the economic score, e.g., the defect at BTA23 in Nordic Red Dairy Cattle has an estimated cost of €160 (Bengtsson et al., 2022a). This would likely decrease the probability of expressing the defect even further, as mating two carriers would be more costly. The cost of €80 assumed in this study reduced the frequency of mating between two carriers to almost zero, so a slightly higher cost would most likely eliminate such matings.

A study by Bérodier et al. (2021) considered known recessive genetic defects in a similar way as done in this study and found that linear programming was better than random and sequential mating in reducing the number of genetic defects expressed. However, they could not completely avoid the expression of recessive genetic defects using either pedigree or genomic relationship. Their study had more restrictions on bull usage compared with our study, e.g., only eight bulls could be mated to heifers because of restrictions for ease of calving (Bérodier et al., 2021). An earlier study by Cole (2015) using sequential solving, rather than linear programming, found that more conceptuses were affected by recessive genetic defects when using an economic score similar to that in our scenarios considering pedigree relationships compared with random mating, whereas we found that fewer conceptuses were affected. This discrepancy in findings may be due to the use of sequential solving, which can suffer from order dependence. Additionally, Cole (2015) applied the constraint of a maximum of 5 000 matings per bull (for a cow population of 35 000–100 000 individuals), rather than females per bull and herd as used in this study. This may have led to individual bulls being used for much more than the 10% females per bull and herd considered in this study. Moreover, unlike linear programming, sequential solving cannot account for the value of one mating being affected by other matings, which is the case with a limited amount of permitted matings per bull and herd. For example, linear programming accounts for the fact that a bull carrying a recessive genetic defect brings the most value (in most cases) when mated to a non-carrier female, if the bull has a limited number of inseminations.

Polledness

The number of polled offspring increased faster with a 10% females per bull and herd constraint than with a 5% constraint. However, this benefit should be balanced against the risk of inbreeding and recessive genetic defects discussed earlier. A rapid initial increase in the frequency of polled animals was observed in generation 21 (Fig. 2), which is consistent with findings in Bengtsson et al. (2023). However, this effect was not always maintained in generation 22 in the simulations, possibly because the polled animals were more related and that the other economic score parameters were more important when allocating matings. However, it probably mainly arose because there was no active selection for polledness when selecting females for RT or bulls for semen production in the simulations. Selecting for polledness in those steps could potentially speed up the increase in the polled allele, but could also have negative effects on the inbreeding rate and genetic gain. In addition, the number of polled bulls could be regulated through the number of progeny per donor in the RT programme. This trade-off and interaction between the RT programme and mating based on an economic score could be a worthwhile topic for future research.

The frequency of polled offspring increased on average over time when the value of polledness was €50 or higher, while it remained constant when the value was €10. The value of €50 is much higher than the estimated cost of dehorning in the Nordic countries (€3–25 per head) (Sørensen et al., 2018) or the United States ($6–25 per head) (Thompson et al., 2017). However, with strict regulations in place for organic herds in the EU, the incentive for farmers to breed polled animals is increasing, and this may change the economic value of the polledness trait. Nevertheless, even when the value for polledness was set at €100, it had minimal effect on genetic gain in the population (Tables 2 and 3). The main sources of genetic gain in a modern breeding programme are the selection of bulls for semen production and selection of females for RT. In this study, those selection steps were consistent across all scenarios and did not take polledness into account. A previous study examining the effects of using an economic score with polledness in mating over multiple generations found that a value of $40 (~€37) was insufficient to increase the frequency of the polled allele (Cole, 2015). This was primarily because carriers of the polled allele were unlikely to rank high based on net merit (frequency of the polled allele was approximately 1%). Similar findings were made in a simulation study by Mueller et al. (2019) where

frequency of the polled allele was slightly higher (approximately 2% for Holstein and 4% for Jersey). Consequently, Mueller et al. (2019) concluded that gene editing appears to be a better option than conventional breeding. However, gene editing is still strictly regulated in most parts of the world (Bruetschy, 2019). In the present study and in Bengtsson et al. (2023), we demonstrated that mating plans can increase the frequency of polled offspring with a value set at ≥ €50. In Bengtsson et al. (2023), the polled allele frequency in Nordic Holstein sires born 2017–2019 was ~7%, so in this study, we assumed that selection for polledness since that period would have increased the frequency of polled animals and thus, we set the allele frequency to ~12%.

The increase in frequency of the polled allele was reduced by the presence of female offspring from RT matings in the next generation, which were the result of random mating and not mated based on the economic score with an extra value for polledness (Fig. 1). A higher increase in frequency of the polled allele would have been observed if all females available for matings were the result of mating with an economic score that included an extra economic value for polledness. However, this scenario is unrealistic in practice, as not all herds will include an extra economic value for polledness in the economic score.

Limitations

The breeding scheme simulated in this study reflects a future breeding programme set up with a genetically superior nucleus utilising effective reproductive technologies. The simulated breeding scheme could have been more advanced with a more complex interaction of recruitment of breeding animals from commercial herds. However, we argue that it was appropriately designed to study mating strategies at the level of commercial herds. For example, optimal contribution selection (**OCS**) in the nucleus could enhance selection in the RT programme by maximising genetic gain while limiting inbreeding (Meuwissen et al., 2020; Bouquet et al., 2015). However, even without using OCS, all scenarios incorporating a genetic relationship in the economic score had a pedigree inbreeding rate lower than 0.5% per generation, which is well below the FAO guideline of a maximum 1% increase in inbreeding per generation (FAO, 2013). We emphasise that the mating allocation suggested in this study should not be considered a substitute for nucleus optimal contribution selection for breeding organisations. It is important to note that OCS, while theoretically advantageous, is not as commonly implemented in practice (Cole, 2024). For instance, the presence of multiple competing artificial insemination organisations makes the application of an OCS scheme across the entire Holstein population highly impractical. Furthermore, a larger population could help to increase selection intensity (e.g., females selected for RT), which would have a positive effect on genetic gain, but it would be similar regardless of mating strategy at the herd level. Hence, we considered the extra computation time not worthwhile for the purposes of this study. We also considered some additional scenarios with increased sample size and obtained similar results, so our conclusions remain the same.

Another limitation of this simulation study is that the genetic parameters analysed cannot represent all real populations. For example, the frequency of the polled allele and of the recessive genetic defects vary across populations. We chose frequency values based on our previous studies of Nordic dairy cattle populations (Bengtsson et al., 2022a, 2023), where the polled allele frequency is slightly higher than that in the Holstein population (Bengtsson et al., 2023). There has been an increase in the frequency of the polled allele since the time of that study (Hanna Driscoll, product manager Holstein, VikingGenetics, personal communication, 24 September 2024). Moreover, the known recessive genetic defect frequency was set to an intermediate value to that observed in our recent studies (Bengtsson et al., 2022a, 2023). In this study, we assumed that all animals were genotyped. An option for ungenotyped animals could be to impute their genotype, e.g., by using the H matrix in single-step genomic evaluation, as suggested by Sun et al. (2013). Until then, farmers who do not genotype their females should avoid using bulls carrying known recessive genetic defects, in order to avoid mating two carriers of the same genetic defect and the negative consequences of this.

Implementation opportunities

This study demonstrated the importance of controlling parental relationships when planning matings at the herd level. Scenarios that incorporated a pedigree or genomic relationship resulted in a significantly lower rate of inbreeding, without compromising genetic gain. Therefore, we suggest that using a genetic relationship should be the first priority when setting up mating plans at herd level. In addition, avoiding mating of relatives (e.g., by a penalty on the genetic relationships) is also a general approach to reduce the risk of expression of unknown recessive genetic defects. Genomic relationships outperformed pedigree relationships in the economic score, with a lower rate of genomic inbreeding and a comparable level of pedigree inbreeding. Therefore, using genomic relationships would not increase the rate of pedigree inbreeding relative to using pedigree relationships, and we recommend the use of genomic relationships when available. However, it is important to note that genomic relationships slightly increased the risk of conceptuses affected by the known recessive defect slightly more than pedigree relationships. Such matings are not advisable in practice and may even break animal welfare laws in some countries, such as Sweden (SJVFS 2019:31). As discussed earlier, it could be argued that an identity by descent genetic relationship is favourable in avoiding mating of two carriers compared with VanRaden's relationship matrix as used in this study. Another recommendation is to set a similar constraint on bull usage within commercial herds, as applied in this study. To minimise the risk of unknown recessive genetic defects at herd level, we suggest that 5% females per herd and bull is the best option. We do not recommend going higher than 10% females per bull and herd, to avoid greater variation in carrier frequencies. However, if farmers want to achieve rapid change in the frequency of polled offspring, there could be some benefits of using 10% females per bull and herd.

In this study, we likely overestimated the effectiveness of pedigree relationships for some populations, since we had a perfect pedigree in terms of completeness and correctness. The correlation between pedigree and genomic relationships was very high (~0.87, results not shown), while other studies have found a wide range of strength of correlation (0.57–0.88) between genomic and pedigree relationships (Bengtsson et al., 2022a, 2023; Pryce et al., 2012; VanRaden et al., 2011). With lower pedigree correctness, the relative benefits from using genomic relationships would likely be greater. However, we acknowledge that some genotyping errors might exist in a real population, which could also influence the results.

Conclusions

In this simulation study, we investigated the long-term effects of using genomic mating allocations that combined economic scores and linear programming at the level of commercial herds. Compared with only maximising genetic level, including genomic or pedigree relationship in the economic score lowered the rate of pedigree and genomic inbreeding, with minimal effect on genetic gain. Including the cost of a recessive genetic defect in the score almost eliminated the risk of expression. Including an

economic value for polledness of ≥ €50 in the economic score increased the frequency of polled animals by up to 0.037 per generation, without negatively affecting other comparison criteria. Using genomic relationships resulted in more bulls being used than when using pedigree relationships. The use of genomic relationships was favourable for the rate of genomic inbreeding and performed as well as pedigree relationships concerning the rate of pedigree inbreeding. Limiting the number of females per bull and herd to a maximum of 5%, instead of 10%, also decreased the rate of inbreeding. Additionally, the 5% females per bull and herd constraint lowered the variation in carrier frequency for genetic defects, which reduced the risk of mating two carriers of an unknown genetic defect in future generations after the widespread use of carriers in previous generations. However, a 10% females per bull constraint could increase the frequency of the polled allele. Therefore, planning matings with genomic information at the herd level involves important risk management decisions, such as balancing the trade-off between using fewer bulls to increase the polled allele frequency more quickly and using more bulls to reduce the rate of inbreeding and the variation in carrier frequency for genetic defects.

Supplementary material

Supplementary Material for this article (https://doi.org/10.1016/j.animal.2025.101498) can be found at the foot of the online page, in the Appendix section.

Ethics approval

Not applicable.

Data and model availability statement

None of the data were deposited in an official repository. AlphaSimR was used to generate all data, and the script can be obtained upon request. However, the rights and access to the mating R script provided by Bérodier et al. (2021) belong to them.

Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work the author(s) did not use any AI and AI-assisted technologies.

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Declaration of interest

None.

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