


Genomic selection strategies to improve maternal traits in Norwegian White Sheep

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Abstract

This study tested and compared different implementation strategies for genomic selection for Norwegian White Sheep, aiming to increase genetic gain for maternal traits. These strategies were evaluated for their genetic gain in growth, carcass and maternal traits, total genetic gain, a weighted sum of the gain in each trait and rates of inbreeding through a full-scale stochastic simulation. Results showed genomic selection schemes to increase genetic gain for maternal traits but reduced genetic gain for other traits. This could also be obtained by selecting rams for artificial selection at a higher age. Implementation of genomic selection in the current breeding structure increased genetic gain for maternal traits up to 57%, outcompeted by reducing the generation interval for artificial insemination rams from current 3 to 2 years. Then, total genetic gain for maternal traits increased by 65%–77% and total genetic gain by 18%–20%, but at increased rates of inbreeding.

KEYWORDS

genomic selection, optimization, sheep, stochastic simulation

1 | INTRODUCTION

Maternal traits are important for sheep produced in pasture-based production systems where overall production efficiency depend heavily on the maternal abilities of ewes (Conington, Bishop, Waterhouse, & Simm, 2004). The Norwegian White Sheep (NWS) breeding programme has experienced a large genetic gain in litter size (Eikje, Ådnøy, & Klemetsdal, 2008), and this increases the demand for a ewe that can feed and raise multiple lambs. In addition to milk yield, maternal traits such as udder conformation, lambing difficulties and mastitis have large effects on production costs and animal welfare and need to be considered in the breeding goal. The conventional breeding programme is a progeny testing scheme, which is optimized to improve growth related

traits and slaughter traits. With increasing importance of maternal traits, a revision of the breeding programme is needed.

Implementation of genomic selection is expected to improve genetic gain for maternal traits already included in the breeding goal and facilitate effective selection for new maternal traits to be included in the future. Several studies on the implementation of genomic selection have suggested a large potential for improving traits not measured directly on selection candidates both in sheep (Brito et al., 2017; Pickering, Dodds, Auvray, & McEwan, 2013) and other species (Goddard, 2009; Ibañez-Escriche & Gonzalez-Recio, 2011; Lillehammer, Meuwissen, & Sonesson, 2013). Typical challenges when genomic selection is to be implemented in sheep are the large number of breeds. These tend to be numerically small, causing small reference populations and

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have low linkage disequilibrium and sometimes lack of phenotypic recording (Rupp, Mucha, Larroque, Mcewan, & Conington, 2016). Across breed genomic evaluation has shown to give low selection accuracy (Daetwyler, Kemper, Werf, & Hayes, 2012). However, genomic selection has been implemented for meat sheep in Australia and New Zealand, but with low cost-benefit margins at the current genotyping cost (Rupp et al., 2016). When it comes to number of animals available to build and update a reference population, this is also a challenge in Norway. NWS is numerically a large population (100,000 breeding ewes per year), but limited use of artificial insemination (AI) gives few animals with accurate progeny proofs available to update the reference population.

The aim of this study was to test different implementation strategies for genomic selection, designed to increase genetic gain for maternal traits. The strategies were compared with a conventional pedigree-based breeding scheme and with a pedigree-based breeding scheme with prolonged generation intervals from including a progeny test for maternal traits. The comparisons were made through stochastic simulations. The tested scenarios were limited to those relevant and economically feasible for NWS.

2 | MATERIALS AND METHODS

2.1 | The conventional breeding programme in NWS

The breeding goal of NWS in Norway consists of several traits, which can be divided into three categories, depending on their source of information. The categories are (a) growth related traits measured on all animals at 6 months of age, (b) carcass traits measured on slaughtered lambs, and (c) maternal traits measured on ewes when they have offspring. The NWS breeding population counts approximately 100,000 ewes, in a number of ram circles (breeding units) with on average 1,000 ewes each. Usually, a ram circle includes more

than one flock. Flocks exchange males within circles, but not between circles due to health restrictions (Eikje et al., 2008). Selection of rams takes place in several stages. Test rams are selected within ram circles among half-year-old ram lambs. The selection is based on a combination of estimated breeding value, exterior traits and wool quality traits. The breeding organization “The Norwegian Association of Sheep and Goat Breeders” (NSG) decides the minimum score needed to be eligible for selection. The selection decision is then made by the farmers in the ram circle, among the eligible rams. In total, 1,800 test rams are progeny tested every year. Elite rams (300 in total) are selected within ram circles among the previous year's test rams, and 20 rams for artificial insemination (AI) are selected each year across ram circles among the previous year's elite rams. In all stages, rams are selected based on their total merit index and to some extent on the pedigree relationship. Rams for AI are selected by NSG, based on EBV. The AI rams are usually used for one year only, giving a generation interval for the AI rams of 3 years. Approximately 10% of the lambs born every year are from AI sires. This scheme has been optimized, assuming the use of pedigree based BLUP breeding value estimation and simultaneous use of local elite rams and central AI rams (Eikje, Schaeffer, Adnoy, & Klemetsdal, 2011). With access to BLUP-EBV on an animal level based on analyses of the whole national breeding population, dams are selected within herd, and selection decisions as well as mating decisions are made by the farmers.

The average amount of phenotypic information available for the different categories of male candidates, on the candidates themselves and on their progeny groups, is shown in Table 1. The first row of Table 1 corresponds to the information available when selecting lambs to become test rams, which is only own phenotype for growth related traits (in addition to information from sibs and older relatives). The next two rows of Table 1 represent the available information when selecting elite rams and AI rams, respectively. Selection of elite rams among the test rams takes place in the autumn at

TABLE 1 Accumulated, average amount of phenotypic information for rams and traits (own performance and/or number of progeny with records)

Age	GROW ^a		CARC ^a		MAT ^a	
	Phenotype	Progeny	Phenotype	Progeny	Phenotype	Progeny
0.5 years ^b	1	–	–	–	–	–
1.5 years ^b	1	60	–	25	–	–
2 years ^b	1	60	–	50	–	–
3 years ^b	1	120	–	80	–	20

^aThe traits were defined as follows: GROW—trait measured on male and female candidates before the first round of selection; CARC—trait measured on slaughtered lambs; MAT—trait measured on females when having the first litter.

^bAge class when information becomes available; 0.5 years corresponds to the stage when selecting young males for progeny testing, 1.5 years is when selecting elite males to be used for a second year locally, 2 years is when selecting AI males, and 3 years is when selecting AI males one year delayed (scheme PED-4) or to be used for a reference population in the genomic selection schemes.

1.5 years of age. By this time, the first offspring group will have live weight information and some of them have already become slaughtered. Successive selection of AI rams among the elite rams takes place in the summer at 2 years of age, with access to all the slaughter information for the first offspring group, but yet with no information about the second offspring group (Table 1). The final row of Table 1 shows the cumulative information obtained on the elite rams after having two rounds of offspring that will contribute to increased selection accuracy for relatives of the male candidates in the conventional breeding scheme.

All selection steps in the conventional breeding programme are based on BLUP-EBV. This progeny test scheme is well designed to produce genetic gain in growth and slaughter traits, because the test rams get progeny records for these traits before being selected for AI. For maternal traits, however most information about the daughters, like for instance litter size, health and maternal ability are not available in time before the rams are selected to become elite rams or AI rams. Improvement in maternal traits is therefore dependent on information about sisters, aunts and more distant relatives to the male candidates. To increase the genetic gain for maternal traits, two options exist; either to increase the generation interval to allow for a progeny test for maternal traits (i.e. to wait for the information in the last row of Table 1) or to use genomic selection to get more accurate breeding values for maternal traits without relying on progeny testing.

2.2 | Description of the simulations

A historical population was simulated by random mating for 2000 generations according to the Fisher-Wright population model (Fisher, 1930; Wright, 1931) assuming an effective population size of 200. To create polymorphisms in the genome and linkage disequilibrium between genes and between the genes and the molecular markers, mutation and recombination events were sampled at random positions throughout the period as in Sonesson and Meuwissen (2009). The last generation of the historical population was used as a base for the breeding population. Among the polymorphisms that were present at this stage, 100 randomly selected polymorphisms with minor allele frequency above 0.05 per chromosome were used as QTL, and the 500 polymorphisms with highest minor allele frequency per chromosome were used as neutral markers. Each animal was simulated to have 10 pairs of chromosomes although sheep is known to have 27 pairs of chromosomes. Each chromosome was 100cM long. Downsizing of the total genome size from 34 M down to 10 M was necessary to reduce the computational requirements. A smaller genome size increases the accuracy of genomic selection (Daetwyler, Villanueva, Bijma, & Woolliams, 2007); thus, the resulting accuracies and genetic gains will require

in practice larger training population sizes than were used in the simulation.

Starting with the base population, the breeding population was set up to mimic the conventional breeding population of NWS (100,000 ewes) and run for 12 years. Only the selection candidates were individually simulated, being the offspring of AI or elite sires. It was assumed that 74% of the ewes were mated with a test ram. Consequently, the number of ewes to give birth to selection candidates (i.e. mated to the 300 elite or 20 AI sire, see below) was 26,000 (26% of 100,000). A total of 12,800 lambs were simulated with an AI sire and a dam randomly selected among the top 25% of the ewes and 28,800 lambs were simulated with an elite sire and a dam randomly selected among the top 40% of the ewes. Consequently, each elite sire and AI sire got 96 and 640 lambs, respectively, and the numbers of selection candidates from each mating category reflected the numbers in the real population. Each ewe had on average 1.6 lambs, which corresponds to the average number of available selection candidates from each litter in the NWS population, accounting for that some lambs born dies, get sick, get fostered by a different ewe etc., which will exclude the lamb from being a selection candidate. Simulated females were those needed to mate with the three categories of males, and all females were candidates from age 1 until age 4, but ewes were randomly culled (33% every year) from the age of 2 to reflect the NWS ewe population and ewe selection, which is decided by the farmers, and not necessarily based on EBV, although EBVs are available. No random culling of males occurred, but non-selected males were culled after each stage of selection.

The simulated breeding programme consisted of three traits, where each simulated trait reflects an index of the traits with information from the same group of animals. The simulated traits were denoted GROW (growth related traits measured on selection candidates), CARC (carcass traits measured on slaughtered lambs) and MAT (maternal traits measured on ewes when they have their first litter). Selection was based on a weighted index of the single trait breeding values (GEBV or BLUP-EBV), assuming 50% weight on MAT, 30% weight on GROW and 20% weight on CARC. The genetic parameters

TABLE 2 Genetic parameters assumed for the simulated traits

	GROW ^a	CARC ^a	MAT ^a
GROW ^a	0.1		
CARC ^a	-0.2	0.25	
MAT ^a	0/-0.2 ^b	0	0.05

Note: The table shows heritabilities on the diagonal and correlations (phenotypic, genetic and residual) on the lower triangular. Genetic variances were standardized to 1.

^aThe traits were defined as follows: GROW—trait measured on male and female candidates before the first round of selection; CARC—trait measured on slaughtered lambs; MAT—trait measured on females when having the first litter.

^bTwo different levels of this correlation were tested.

assumed for the simulated traits are as shown in Table 2. Since each simulated trait reflects a typical set (index) of real traits, heritabilities and correlations do not reflect actual traits, but are typical parameters found for each category of traits in NWS and other breeds (Brito et al., 2017; Eikje et al., 2011). For the correlation between MAT and GROW, we tested two different levels, 0 and -0.2 , as indicated in Table 2, since the MAT index may consist of a wide variety of already included, but also future maternal traits, and the correlations between these traits and GROW are unknown. In the simulations, it was further assumed that the residual and phenotypic correlations between traits equalled the genetic correlations.

Male selection was conducted in three steps, as in the conventional breeding programme. The number of test rams in the simulation was set to 1,500, somewhat reduced from the 1,800 used in the conventional breeding programme, to account for that some test rams fail to produce enough progeny records. All selection was truncated selection without inbreeding restrictions. The first selection step occurred when the lambs were approximately 6 months of age, where 1,500 test rams were selected among the 20 800 male lambs born from elite or AI sires, assuming a sex ratio of 0.5. The 1,500 test rams got offspring when they were 1 year of age, and the best 300 were selected to get offspring again when they were 2 years of age and then denoted elite rams. Finally, among the elite rams, 20 AI rams were selected to obtain a third offspring group when they were 3 years of age. At each stage of selection, male selection candidates were assumed to have the average size of the progeny group as described in Table 1. Females were assumed to obtain own phenotype for GROW at the age of 0.5 years and for MAT at the age of 1.5 years. In addition, they were assumed to accumulate 1–5 progeny with records, depending on trait, over their lifetime.

2.3 | Simulated records and breeding value estimation

For all animals, QTL-effects were sampled from a multivariate normal distribution (MVN), assuming that the QTL-effects were normally distributed, with mean 0 and variance $V = 1/1,000 \times \mathbf{g}$, where \mathbf{g} is the genetic covariance matrix of the three traits, scaled to give genetic variance of 1 for each trait and genetic covariance to fit with the assumed correlations in Table 2. The total number of QTL was 1,000. True breeding values (TBV) were calculated as the sum of the QTL effects for each trait per individual.

The records ($\mathbf{y}_i = [\mathbf{y}_{i\text{GROW}} \mathbf{y}_{i\text{CARC}} \mathbf{y}_{i\text{MAT}}]'$) of individual i were simulated as: $\mathbf{y}_i = \text{TBV}_i + \mathbf{r}_i$, where \mathbf{r}_i is a random deviate vector $\sim \text{MVN}(0, \mathbf{R})$, and \mathbf{R} is the residual covariance matrix, scaled to give heritabilities and residual correlations between the traits as given in Table 2. When an animal (male or female) had progeny with records, the progeny record

(PROG) for animal i , trait j , was produced as: $\text{PROG}_{ij} = 1/2\text{TBV}_{ij} + r_{ij}$, where TBV is as defined above and r_{ij} is a standard normal random deviate, $N \sim \left(0, \left(0.75\sigma_{gj}^2 + \sigma_{rj}^2\right)/n_{ij}\right)$, where n is the number of progeny assumed for animal i , trait j . Since progeny records were produced directly for the sires, progeny group size was assumed to be equal for all sires within a category, and the progeny record also includes records from animals not individually simulated, like daughters of test rams. Progeny records for sires were simulated also after the sire was culled, to add to the accuracy of GEBV when the sire exists in the reference population.

Selection of females was always based on conventional pedigree-based BLUP breeding values (BLUP-EBV), predicted with a univariate animal model: $y_{ij} = \mu_j + u_{ij} + e_{ij}$, in which y_{ij} was the phenotype or progeny record for animal i , trait j , μ_j was the overall mean for trait j , u_{ij} was breeding value for animal i , trait j , assumed to have a variance of $\mathbf{A} \times \sigma_{uj}^2$, where \mathbf{A} was the relationship matrix estimated from the pedigree and σ_{uj}^2 was the genetic variation of trait j , and e_{ij} was the random residual for individual i , trait j , assumed to have a variance of σ_{ej}^2 .

Males were in some schemes and stages selected based on genomic breeding values, estimated with the SNP-BLUP method (GEBV) (Meuwissen, Hayes, & Goddard, 2001). In SNP-BLUP, the following single trait statistical model was

used: $y_{ij} = \mu_j + \sum_{k=1}^{5000} X_{ik} a_{kj} + e_{ij}$, where X_{ik} was the marker gen-

otype; a_{kj} was the random effect of the k^{th} marker on trait j , with variance equal to the total additive genetic variance for trait j , σ_{uj}^2 divided by number of SNP-markers (5,000) and

other traits were as defined in the pedigree based BLUP model. Additive breeding values (u_{ij}) for candidates were estimated as a sum of the SNP effects of all their SNP markers for each trait. All genotyped animals were selected based on GEBV, while selection among non-genotyped individuals was based on BLUP-EBV.

Level of inbreeding, estimated from the pedigree, was monitored every generation and reported as an output of the simulation programme.

2.4 | Simulated selection schemes

The simulated schemes were denoted “method-x_y,” where methods were either PED or GS, depending on whether breeding value estimation for the males was based on pedigree BLUP-EBV or on GEBV, x denotes the generation interval for AI males and y is the number of genotyped animals

per year (for GS schemes only). The scheme PED-3 aimed to estimate the genetic gain of the conventional breeding programme. The other schemes tested were designed to increase genetic gain for MAT, without compromising genetic gain in other traits.

One strategy to obtain increased genetic gain for maternal traits would be to increase the generation interval and select AI rams at a higher age. This was tested in the scheme PED-4, where elite sires were used for two years in the herds, and the AI sires were selected one year later than at current, giving a generation interval of 4 years for the AI rams. In scheme PED-4, selection was based on BLUP-EBV.

Alternatively, genomic selection could be used to obtain increased accuracy of selection for maternal traits at a younger age through the use of GEBV (Meuwissen et al., 2001). This was tested by the use of four different genomic selection (GS) schemes. In the GS-schemes, it was assumed that prior to the start of the selection scheme, 320 proven rams and 30,000 females with records were genotyped. The reference population consisted of the accumulated data from these genotyped animals and animals genotyped after the GS scheme was started. Two of the tested genomic selection schemes introduced genomic selection without altering the generation interval. These were denoted GS-3_300 and GS-3_1500. In GS-3_300, the elite rams ($n = 300$) were genotyped every year, and genomic selection was used to select the AI rams among the elite rams, keeping the generation interval for the AI rams at 3 years. In GS-3_1500, all test rams were genotyped after they had produced offspring groups. Selection of elite rams were based on BLUP-EBV, while selection of AI rams among the elite rams was based on GEBV. The generation intervals for all categories remained the same, but all test rams were genotyped, increasing the number of males with progeny information available to update the reference population every year, thereby increasing the accuracy of male selection.

Other studies have shown that replacing progeny test by genomic selection can increase the effect of implementing genomic selection through reduced generation interval (Schaeffer, 2006; Shumbusho et al., 2015). This was tested by reducing the generation interval for AI rams to 2 years (GS-2_1500) or 1 year (GS-1_1540). In GS-2_1500, all test rams were genotyped, and genomic breeding values were assumed to be available before selecting elite rams. Among the tested rams, the 20 best (ranked on GEBV) were selected as AI rams, and the next 300 from the same age class were selected to become elite rams. Hence, genomic selection was used to select AI rams one year earlier than in PED-3 and was also used to select the elite rams among the test rams. In GS-1_1540, the 1,540 lambs born with the highest BLUP-EBV were genotyped shortly after birth. Based on GEBV, 40 lambs were selected for use in AI directly, while the remaining 1,500 became test rams. The GEBV were updated after

the test rams had slaughtered offspring and used to select 300 rams as elite rams, to be used for a second year. The reason for doubling the number of AI rams in scheme GS-1_1540 was biological limitations on how much semen the rams can produce at such young age.

2.5 | Output from the simulations

All schemes were run for 12 years with 50 replicates. Average genetic gain per year and trait were calculated over years 6–12. For the scheme PED-3, genetic gain was given in genetic standard deviations, while for the other schemes, a percentage relative to that of PED-3 was used. Generation intervals for males (m) were calculated from relative contributions of AI males and elite males to the next generation, measured as fraction of selected test rams with an AI sire or an elite sire. This was calculated by: $L_i = C_{i,AI} (L_{i,AI,m} + L_{i,AI,f}/2) + (1 - C_{i,AI}) (L_{i,E,m} + L_{i,E,f}/2)$, where L_i is the generation interval for scheme i ; $C_{i,AI}$ is the relative contribution of AI males to the next generation in scheme i ; and $L_{i,j,k}$ is the generation interval for mating category j , where j is either AI (AI) or elite (E), in scheme i . For females (f), generation intervals for each mating category were reported from the simulation software and weighted, as for the males. Average rate of inbreeding per year for the different schemes from year 6 to 12 of the simulation was estimated as $1/6 \sum_{t=7}^{12} F_t - F_{t-1} / (1 - F_{t-1})$, where F_t is the average level of inbreeding in year t . Rates of inbreeding per generation were estimated by multiplying rate of inbreeding per year by the generation interval for each scheme.

3 | RESULTS

The genetic gain achieved per trait under the different scenarios is shown in Table 3. The genetic gain achieved with PED-3 was very similar to what is estimated genetic gain for NWS under the current breeding programme (https://www.sauea.vl.nsg.no/ringanalyse_utvikling_list.cfm). Relative to PED-3, all genomic selection schemes facilitated a large increase in genetic gain for maternal traits, but this was accompanied by a reduction in gains for the other two trait categories. When the correlation between MAT and GROW was set to 0, the effect of implementing genomic selection on total genetic gain was small and a reduction in generation interval was needed to increase the total genetic gain. When the correlation between MAT and GROW was negative, genomic selection gave an improvement of total genetic gain, also without shortening the generation interval. In this scenario, shortening the generation interval (moving from GS-3 to GS-2 or GS-1) had minor effects on total genetic gain. Reducing the generation interval did, however, increase the effect of genomic selection on MAT,

TABLE 3 Genetic gain per trait and year and in total under the different scenarios. Gain of alternative schemes are shown relative to PED-3

Trait	PED-3 ^a (σ_g)	PED-4 ^a (%)	GS-3_300 ^a (%)	GS-3_1500 ^a (%)	GS-2_1500 ^a (%)	GS-1_1540 ^a (%)
Correlations between GROW and MAT were assumed to be 0						
GROW ^b	0.35	95	74	74	85	111
CARC ^b	0.23	94	61	77	63	72
MAT ^b	0.25	105	116	129	165	169
Total ^c	0.28	100	91	100	118	131
Correlations between GROW and MAT were assumed to be -0.2						
GROW ^b	0.27	85	92	117	90	117
CARC ^b	0.26	81	74	78	64	65
MAT ^b	0.19	121	143	157	177	157
Total ^c	0.23	99	109	120	120	122

^aThe schemes were named by their breeding value estimation method for AI rams-generation interval for AI rams _ number of genotyped rams per year (in schemes involving genotyping). The breeding value estimation method for males was either pedigree based BLUP (PED) or SNP_BLUP (GS).

^bThe traits were defined as follows: GROW—trait measured on male and female candidates before the first round of selection; CARC—trait measured on slaughtered lambs; MAT—trait measured on females when having the first litter.

^cAn index with weights being 0.3 for GROW, 0.2 for CARC and 0.5 for MAT was assumed.

TABLE 4 Rate of inbreeding and generation interval achieved with each tested scheme

Scheme	Rate of inbreeding per year (%)	Rate of inbreeding per generation (%)	Generation interval (years)
Correlations between GROW and MAT were assumed to be 0			
PED-3 ^a	0.31	0.57	1.81
PED-4 ^a	0.18	0.36	1.98
GS-3_300 ^a	0.46	0.90	1.94
GS-3_1500 ^a	0.41	0.79	1.95
GS-2_1500 ^a	0.55	0.87	1.58
GS-1_1540 ^a	1.12	1.31	1.17
Correlations between GROW and MAT were assumed to be -0.2			
PED-3 ^a	0.38	0.69	1.83
PED-4 ^a	0.23	0.46	2.01
GS-3_300 ^a	0.51	0.96	1.89
GS-3_1500 ^a	0.59	1.10	1.88
GS-2_1500 ^a	0.61	0.96	1.59
GS-1_1540 ^a	1.03	1.21	1.17

^aThe schemes were named by their breeding value estimation method for AI rams-generation interval for AI rams _ number of genotyped rams per year (in schemes involving genotyping). The breeding value estimation method for males was either pedigree based BLUP (PED) or SNP_BLUP (GS).

irrespective of the correlation between MAT and GROW. To continue with conventional breeding value estimation and increasing the generation interval for AI rams to 4 years (PED-4) caused no change in total genetic gain but transferred genetic gain from other traits to maternal traits. This transfer of gains was highest when the correlation between MAT and GROW was negative.

Table 4 shows that all tested schemes except GS-1_1540 still gave rates of inbreeding below 1% per generation when the correlation between MAT and GROW was 0; that is,

the schemes may be regarded as sustainable (Meuwissen & Woolliams, 1994). When the correlation between MAT and GROW was negative, rates of inbreeding increased for all schemes, and GS-3_1500, as well as GS-1_1540, caused rates of inbreeding per generation > 1%. The other GS schemes were also close to this limit. Even though the simulations tested generation intervals between 1 and 4 years for the AI rams, the generation interval for the entire populations, including elite rams and females, had a lower span; from 1.17 to 2.01 years. Therefore, the main conclusions were unaffected

TABLE 5 Fraction of the selected rams with an AI sire

Scheme	Corr 0	Corr -0.2
PED-3 ^a	0.42	0.44
PED-4 ^a	0.39	0.40
GS-3_300 ^a	0.64	0.64
GS-3_1500 ^a	0.69	0.63
GS-2_1500 ^a	0.70	0.68
GS-1_1540 ^a	0.81	0.84

^aThe schemes were named by their breeding value estimation method for AI rams-generation interval for AI rams_number of genotyped rams per year (in schemes involving genotyping). The breeding value estimation method for males was either pedigree based BLUP (PED) or SNP_BLUP (GS).

by whether the schemes were compared based on rate of inbreeding per year or per generation. GS schemes gave higher rate of inbreeding than PED schemes, and rate of inbreeding increased with decreasing generation intervals.

One cause for differences in rate of inbreeding between the schemes is the relative contribution of the AI males to the next generation, as shown in Table 5. Since test rams were selected across ram lambs from AI sires and from elite sires, the relative contribution of AI rams was an output from the simulation. For both levels of correlation between MAT and GROW, AI rams were shown to contribute more when genomic selection was applied (Table 5) and especially with schemes with a reduced generation interval (Table 4), probably because more accurate selection increased the difference in performance between the more intensively selected AI rams and the less intensively selected elite rams. Increased contributions of AI sires to the next generation increased rate of inbreeding since the number of simulated AI males was considerably smaller than the number of elite males, which explains some of the differences between the schemes found in Table 4.

4 | DISCUSSION

4.1 | Genetic gain

In the breeding programme for Norwegian White Sheep, the final selection of males is being conducted when the males have received progeny test records for growth and slaughter traits only. This system gives relatively low genetic gain for maternal traits, for which information becomes available too late to be taken into account in the male selection, compared to the other traits under selection. There is a need for restructuring the breeding programme to reduce the gap between the importance of maternal traits and the achieved improvement for these traits. Two solutions to resolve this discrepancy were tested in this study: select the AI males later (PED-4), when offspring with records on maternal traits

are available, or to introduce genomic selection (GS-3_300, GS-3_1500, GS-2_1500 or GS-1_1540). The results showed that implementation of genomic selection could significantly increase the genetic gain for maternal traits, while later selection of AI males had lower potential. When genomic selection was applied, the increased genetic gain for maternal traits came partly at the expense of gain in other traits, as also shown in similar simulations for several species (Granleese, Clark, Swan, & Werf, 2017; Granleese, Clark, & Werf, 2019; Lillehammer et al., 2013; Van der Werf et al., 2014). To achieve an increased total genetic gain, genomic selection had to be combined with a reduced generation interval (GS-2_1500 or GS-1_1540). This is in concordance with findings when optimizing genomic selection schemes for meat sheep in France (Shumbusho et al., 2015) and Australia (Van der Werf et al., 2014), which also showed a low increase in overall genetic gain, but potentials to shift selection pressure from early measured traits to later measured traits and to reduce the generation interval. The benefit of combining genomic selection with reduced generation interval in sheep has also been reported in New Zealand, for carcass traits (Brito et al., 2017), sex-limited traits and traits measured late in life (Pickering et al., 2013) and in Australia for multi-trait selection in various breeds (Swan et al., 2014). All GS schemes tested in this study included preselection of ram lambs before genotyping, on a conventional breeding value based on pedigree and, to some extent, own performance. This made the tested schemes economically realistic. Granleese et al. (2019) found that genotyping around 20% of the ram lambs born (selected breeding value) gave the lowest cost per rate of genetic improvement. This could indicate that genotyping more lambs than tested in our study would be economically beneficial, as our 1,500 lambs genotyped corresponds to 7% of the male lambs born. However, the results are probably not fully comparable because of differences in population structure and information available at the time of preselection. In addition, our population size was much larger than the one simulated in Granleese et al. (2019). Population size could affect the optimal fraction of lambs to genotype, since selection accuracy is driven by the number of genotyped rams rather than the percentage.

The combination of genomic selection and reduction of generation interval has also been shown to be advantageous over a conventional progeny testing programme in dairy cattle (Lillehammer, Meuwissen, & Sonesson, 2011; Schaeffer, 2006), which is comparable with sheep in the sense that conventional programmes rely on a progeny test. However, in dairy cattle, most traits under selection are recorded on females only, and the progeny test is designed to include records on maternal traits. In the conventional breeding scheme of NWS, the generation interval is kept short by not including maternal traits in the progeny test, that is by not waiting for maternal records. This reduces the scope for additional

shortening of the generation interval but enlarges the scope for improvement of genetic gain for maternal traits through increased accuracy of selection. The PED-4 approach mimics a typical dairy cattle progeny testing scheme, but with inclusion of natural matings with younger rams in the flocks. This gave no increase in total genetic gain and only a minor shift from other traits to maternal traits, compared to the conventional scheme (PED-3). However, the reduced rates of inbreeding make PED-4 advantageous over PED-3, assuming that maternal traits constitute 50% of the breeding goal.

4.2 | Rate of inbreeding

When the correlations between MAT and GROW was assumed to be 0, all schemes, apart from GS1_1540, gave rates of inbreeding within an acceptable range, that is less than 1% per generation (Table 4) (Meuwissen & Woolliams, 1994). With a negative correlation between MAT and GROW, all implementations of genomic selection were close to or exceeding 1% rate of inbreeding per generation. Differences in rates of inbreeding between schemes were high and need to be taken into account when evaluating genetic gain. Simultaneous increases in total genetic gain and rate of inbreeding, as seen from implementing genomic selection in this study, could in theory have been accomplished by increasing the selection intensity. Thus, the major finding of this study is the large improvement in genetic gain for maternal traits, obtained in the genomic selection schemes, that is the potential of genomic selection to shift selection pressure from other traits to maternal traits.

Other studies have shown that the rate of inbreeding per generation is reduced when genomic selection is implemented, because genomic selection increases in particular the accuracy of estimates of the individual Mendelian sampling component of breeding values (Daetwyler et al., 2007; Granleese et al., 2019; Raoul, Swan, & Elsen, 2017). However, a reduced generation interval in genomic selection schemes can increase rate of inbreeding per year despite a reduction in rate of inbreeding per generation (Schaeffer, 2006), due to faster turnover of generations. In addition, a shorter generation interval may increase inbreeding per year and per generation due to fewer selected parents per generation. In this study, implementation of genomic selection was shown to shift selection pressure from growth to maternal traits. More emphasis on traits not measured on selection candidates could increase rate of inbreeding due to higher importance of family selection and less on the individual Mendelian sampling component. Another factor to affect rate of inbreeding is the relative contribution of the different categories of males in each of the scenarios (Table 5). Since the group of AI rams is much smaller than the group of elite males, the higher contribution of the AI rams to the next generation will reduce the effective

population size and hence increase rates of inbreeding. This is probably the most important reason why genomic selection increased rate of inbreeding in this study, as the increase was shown to affect rate of inbreeding both per year and per generation. This result could therefore be seen as a result of the population structure and the use of multiple male categories with different information content, progeny group size and contribution to the next generation. In a similar simulation study for sheep with a simpler population structure, genomic selection was shown to reduce rate of inbreeding (Granleese et al., 2019). Genomic selection must have resulted in more accurately estimated breeding values for AI rams relative to elite rams, explaining the increased contribution of AI rams to the next generation (Table 5), seemingly unaffected by the assumed genetic correlation between MAT and GROW. If schemes were compared at a fixed relative contribution of AI rams to test rams, rates of inbreeding are expected to be more similar across schemes. Within the current NWS breeding programme, the relative contribution of AI rams to the next generation is, however, already around 80%, probably because farmers tend to prioritize offspring from AI matings when selecting test rams. Implementation of genomic selection in this population is hence expected to have smaller effects on rate of inbreeding than indicated in this study, since the potential to increase the contribution of AI males in reality is small. The female generation intervals obtained in the simulations were somewhat lower than what is obtained in the real breeding programme of NWS, which means that rate of inbreeding per generation will probably be lower in real life, for all schemes, due to a longer generation interval. A recommendation for implementing GS into this or similar breeding programmes is to put some penalty on inbreeding through optimal contribution selection or other similar methods to avoid increase in rate of inbreeding because of higher contributions from a small number of AI rams.

4.3 | Implementation costs

Optimization of breeding programmes is about weighing costs against benefits. Compared to the conventional NWS scheme, all the alternatives proposed will increase the cost of the breeding programme because phenotypic recording was not reduced while genotyping costs were introduced in all GS schemes, keeping more males alive for a longer period increases costs (PED-4), and increasing the size of the AI station enlarges costs (GS-1_1540). For PED-4 without more intense selection, the improvement in genetic gain is too small to defend any increased costs. GS-1_1540 is the most expensive scheme among all compared schemes, including both genotyping and an increased number of AI rams. For the other three GS schemes, GS-2_1500, GS-3_1500 and GS-3_300, the additional cost will be due to genotyping, causing

the 1,500 schemes to have similar costs and be approximately five times marginally more expensive than the 300 schemes. Even though the low-cost programme GS-3_300 could potentially increase genetic gain for maternal traits, the total genetic gain was reduced under this scheme, relative to PED-3, when the correlation between MAT and GROW was 0. Implementation of GS-3_300 would hence increase costs and reduce genetic gain and is not recommendable. The two tested schemes that could be recommended are thus GS-3_1500 and GS-2_1500, which have similar costs, and where GS-2_1500 seems the logical choice, as it gives higher gain for maternal traits or the same or higher total genetic gain than GS-3_1500 (Table 3). GS-2_1500 gave 10% higher rate of inbreeding per generation than GS-3_1500 when the correlation between MAT and GROW was 0 (Table 4), but when the correlation between MAT and GROW was negative, GS-3_1500 gave 10% higher rate of inbreeding than GS-2_1500. Within GS-2_1500, genomic selection is utilized to select AI rams as well as locally selected elite rams, and the generation interval for AI rams is reduced from 3 to 2 years. It is hence also intuitively appealing, when all test rams are going to be genotyped anyway, to make sure that the GEBV are available in time to utilize them also to select local elite rams. Whether implementation of GS is economically profitable will depend on the genotyping costs. Other studies of implementation strategies of GS in sheep have shown that low-cost genotyping is more profitable, than medium to high density, because of significantly reduced costs and smaller reductions in genetic gain (Raoul et al., 2017; Santos, Werf, Gibson, Byrne, & Amer, 2017). The large number of animals assumed to be genotyped before GS was implemented would represent a large investment cost which comes on top of the running costs of these schemes. In real life, a smaller number would probably be genotyped initially, which could cause selection response to be reduced the first years until a sufficient reference population has been built.

4.4 | Updating the reference population

The accuracy of genomic breeding values depends on the size and updates of the reference population (Goddard, 2009; Hayes & Goddard, 2008). The accuracy is also dependent on the relationship between the candidates and the animals in the reference population (Pickering, Auvray, Dodds, & Mcewan, 2015; Pszczola, Strabel, Mulder, & Calus, 2012), which is why it is necessary to update the reference population every generation (Sonesson & Meuwissen, 2009). In this study, we assumed a large number of animals (30 320) to be genotyped before GS was implemented, to study the need for additional updates of the reference population after a reference population has been established. The updating was accomplished by genotyping 300 or 1,500 rams every year; that is all rams

that have or will get progeny groups with records for all relevant traits. Accuracy is also directly dependent on the generation interval, as a shorter generation interval reduces the relationship between the most recent updates of the reference population and the candidates (Lillehammer et al., 2011). To compare the number of genotyped animals between studies is therefore difficult, when the studies assume different population structures and phenotypic information. The results from this study showed a considerable increase in genetic gain when genotyping 1,500 males every year, compared to 300. Hence, given the population structure and information available for progeny tested rams, it seems that 300 genotyped rams every year are not sufficient to obtain and maintain accuracy of genomic breeding values over time. To increase the number of genotyped rams each year to 1,500 increased accuracy of genomic selection and hence genetic gain. Since only two levels of number of genotyped rams were tested, it is not clear how levels in between 300 and 1,500 rams or numbers beyond 1,500 will affect accuracy of selection. Within the recommended scheme GS-2_1500, a change in number of genotyped males will affect both accuracy of selection and the number of candidates to select among, since the genotyped young males act first as selection candidates and later as reference animals. Genotyping more than 1,500 males every year was not regarded an option, because this reflects the total number of rams from this breed being progeny tested every year. However, if the value of adding more animals to the reference population is high and/or genotyping costs are low, possibilities to progeny test more males or genotype females with records should also be investigated. Other studies have suggested low-density genotyping to make genotyping of a larger number of animals economically feasible (Van der Werf et al., 2014), which could be an alternative strategy to save costs, rather than reduce on the number of animals to genotype.

4.5 | Differences between the stochastic simulations and practical schemes

Some simplifications were made in the simulations for computational reasons, including the reduction of genome size, exclusion of offspring of test rams as selection candidates, reduction from many single traits to three index traits and ignoring the ram circle structure. The latter was tested in a pilot study with a reduced population size and found to have only marginal effects on genetic gain and rate of inbreeding (results not shown). The genome size was reduced, compared to the actual genome of sheep, with 10 independent chromosomes to mimic a genome. With a larger genome size, a larger reference population will be needed to reach the same level of accuracy (Daetwyler et al., 2007). The simulated marker density gave a linkage disequilibrium between

adjacent markers of $r^2 = 0.452$. This is a quite high marker density with markers closer than 10kb apart, depending on the breed (Kijas et al., 2014), and hence corresponds to a high density SNP chip.

The reduction in trait dimensionality from many single traits to three index traits was necessary to reduce the computational load in this study. This reduction makes it impossible to take into account all the trait information, as some of the traits behind an index trait may have more information than assumed for the index traits. For example, all maternal trait information was assumed to be available in the autumn when the litter was 6 months old. Ignoring information that is available earlier, for example litter size and birth weight, will affect all schemes, but take the largest effects in schemes where phenotypic information has the highest value, that is in the PED schemes. Thus, ignoring some sources of maternal trait information may contribute to overestimate the impact of genomic selection on genetic gain for maternal traits. In addition, the assumed genetic parameters for the index traits will not reflect all traits behind the index. Traits with heritabilities and/or correlations to other traits that is most different from what was assumed for the index will produce the largest deviance in gain relative to that expected (Table 3). On the other hand, a benefit of working with sub-indexes rather than single traits is that we do not make assumptions about parameters and information content on single traits. Many possible maternal traits are not yet included in the breeding programme, and their genetic parameters are unknown. We tested two levels of the correlation between maternal traits and growth traits, which varies in literature, and found low sensitivity for this assumption, as the same scheme was found optimal, whether this correlation was assumed 0 or negative. However, results on a more detailed level, like genetic gain for each sub-index, were affected by this assumption.

Another discrepancy between simulations and real life is that progeny group sizes vary in practice but was assumed constant for males from the same ram category in the simulations. In this perspective, the simulations overestimate the information content from the progeny groups under the progeny testing scheme. With varying progeny group size in the progeny testing scheme, selection of males will be less effective and genomic selection, which is less sensitive for individual progeny group sizes will be more beneficial. In addition, the reference population for genomic selection will be updated also after older genotyped rams are culled, when new information on their offspring occurs. In this study, we limited the included information to what is presented in Table 1, even though AI males will have more offspring information later.

Schemes were tested only when found economically realistic for the NWS breeding programme. Hence, scenarios requiring more extensive genotyping, like genotyping

females to increase the reference population or genotyping a larger number of male lambs to select test rams based on GEBV, were not included. A similar study, but with a slightly different perspective, found that applying GS for males was much more economically feasible than to use GS on females, even when including novel reproduction technology (Granleese et al., 2019). The effect of genotyping females to update the reference population was not investigated here and could be an option to further increase accuracy of selection.

5 | CONCLUSION

The optimal implementation design for genomic selection to increase genetic gain for maternal traits, among those tested, would be to genotype all 1,500 test rams at one year of age and use this information to select both elite males and AI rams at two years of age (GS-2_1500). Generation interval for AI rams is hence reduced from 3 years in today's system to 2 years, and accuracy of selection increases for both elite rams and AI rams. This implementation strategy has the potential to increase genetic gain per year for maternal traits by 65%–77% and total genetic gain by 18%–20%. Rate of inbreeding is also expected to increase, from 0.57%–0.69% per generation in the conventional system to 0.87%–0.96% with GS2_1500 when the same number of parents is selected as before.

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CONFLICT OF INTEREST

There are no conflict of interests.

DATA AVAILABILITY STATEMENT

This research was based on simulations. Hence, no data files are available.

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