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The predicted benefits of genomic selection on pig breeding objectives

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Abstract

The premise was tested that the additional genetic gain was achieved in the overall breeding objective in a pig breeding program using genomic selection (GS) compared to a conventional breeding program, however, some traits achieved larger gain than other traits. GS scenarios based on different reference population sizes were evaluated. The scenarios were compared using a deterministic simulation model to predict genetic gain in scenarios with and without using genomic information as an additional information source. All scenarios were compared based on selection accuracy and predicted genetic gain per round of selection for objective traits in both sire and dam lines. The results showed that GS scenarios increased overall response in the breeding objectives by 9% to 56% and 3.5% to 27% in the dam and sire lines, respectively. The difference in response resulted from differences in the size of the reference population. Although all traits achieved higher selection accuracy in GS, traits with limited phenotypic information at the time of selection or with low heritability, such as sow longevity, number of piglets born alive, pre- and post-weaning survival, as well as meat and carcass quality traits achieved the largest additional response. This additional response came at the expense of smaller responses for traits that are easy to measure, such as back fat and average daily gain in GS compared to the conventional breeding program. Sow longevity and drip loss percentage did not change in a favourable direction in GS with a reference population of 500 pigs. With a reference population of 1000 pigs or onwards, sow longevity and drip loss percentage began to change in a favourable direction. Despite the smaller responses for average daily gain and back fat thickness in GS, the overall breeding objective achieved additional gain in GS.

KEYWORDS
breeding objective, deterministic simulation, genetic gain, genomic selection, pig breeding

1 | INTRODUCTION

Genomic selection (GS) is a method of predicting the genetic merit of selection candidates utilising dense marker genotyping covering a whole genome. It uses a reference population that has both genotypes and phenotypes (Meuwissen et al., 2001). This method has resulted in increased prediction accuracy and reduced generation intervals substantially in a wide range of species and has impacted the structure of breeding programs. This has led to significant increases in genetic gain achieved, especially in dairy cattle because the generation interval in sires has fallen from 7 years to approximately 2.5 years (Meuwissen et al., 2016). It is possible to select these younger animals based on genomic breeding values with a very high accuracy (Garcia-Ruiz et al., 2016). The impact of GS largely depends on how well or to what extent traits in the breeding objective can be recorded before selection. In dairy cattle, most of the breeding objective traits are only measurable on females later in life, while genetic gain mainly depends on the selection of dairy bulls and progeny testing of female progeny from those sires.

In pigs, the gain from GS is the result of increased selection accuracy because the reduction in generation interval is significantly less compared to dairy cattle (Jonas & de Koning, 2015; Meuwissen et al., 2016). This genetic gain is also required to be balanced with the emphasis on each breeding objective trait and this depends on the accuracy of the estimated breeding value (EBV) for a trait within the breeding objective. Not all the traits achieve a similar level of improvement in prediction accuracy using genomic information compared to pedigree-based selection (Christensen et al., 2012; Mehrban et al., 2019). Traits that can be easily measured on many selection candidates before selection might achieve less additional improvement in prediction accuracy in GS compared to pedigree-based selection than traits that are difficult to measure or sex-limited traits. Optimisation of genetic gain usually pursues the traits where the most gain can be made i.e. traits with higher accuracy EBV and relatively higher economic weight. Lowly accurate EBV of traits having relatively lower economic weight will have less variation and therefore, lowly accurate EBV will contribute less to the overall ranking of individuals based on the breeding objective. If GS can improve the accuracy of traits with limited information at the point of selection, genetic gain of these traits is expected to improve more relative to commonly recorded traits.

Several simulation studies have been conducted to predict response to GS in pig breeding programs (e.g. Lillehammer et al., 2011, 2013; Tribout et al., 2012). These studies assumed one or two breeding objective traits only. In reality, pig breeding objectives consist of more than two traits. There might be both favourable and unfavourable correlations while it is generally expected to improve all traits simultaneously (Dekkers & Gibson, 1998; Ogawa et al., 2023). Predicting the direction and magnitude of response to GS with more traits in the breeding objective depends on the correlation structure between the traits. Therefore, more work is required to understand the response to GS in the dam and sire line of pig breeding objectives that include all traits usually used in a breeding program.

The size of the reference population is an important factor that has an impact on the accuracy of genomic prediction (Daetwyler et al., 2008; Dekkers, 2007). Reference populations are defined as the group of animals with both phenotypes and genotypes on their own and relatives' information. In general, the accuracy of genomic prediction is higher as the size of the reference population increases (Dekkers et al., 2021; Wei et al., 2022). Consequently, it is important to understand the benefits of GS in pigs with reference populations of different sizes. The objective of this study was to investigate the impact of GS in both sire and dam lines based on the genetic gain in each of the breeding objective traits, the overall economic merit of the breeding objective and the accuracy of different traits with or without reference population. This study hypothesises that GS increases the genetic gain of the overall breeding objective compared to the conventional breeding program in a multi-trait breeding objective and that the additional gain will be larger in some traits than others. This hypothesis was tested using deterministic simulation because this deterministic simulation study focused on the ballpark figure of the potential benefit of GS on pig breeding objectives with multiple correlated traits.

2 | MATERIALS AND METHODS

2.1 | Breeding scenarios

To simulate the scenarios, different sizes of reference populations were used to reflect different levels of genomic prediction accuracy. GS scenarios were simulated to predict response to selection in two different breeding objectives representing a sire and dam line. The dam line objective had both reproductive and production traits, as shown in Table 1. In comparison, the sire line breeding objective included both production traits and meat and carcass quality traits. Production traits are backfat thickness, average daily gain, feed conversion ratio and post-weaning survivability; carcase quality traits are belly fat % and middle portion %; and meat quality trait is drip loss percentage. Genomic breeding values of all breeding objective traits were included as selection criteria. The sources

TABLE 1 Heritability (h^2) and genomic prediction accuracies of traits used for simulation for both dam and sire line of pigs assuming different sizes of reference populations.

Traits	Trait units	h^2	Reference population									
			500	1000	1500	2000	2500	3000	3500	4000	4500	5000
No. born alive (NBA)	piglets/litter	0.08	0.20	0.28	0.33	0.38	0.42	0.45	0.48	0.50	0.52	0.54
Sow mature weight (SMW)	kg	0.17	0.29	0.39	0.46	0.51	0.56	0.59	0.62	0.65	0.67	0.69
Sow longevity (SL)	N parity	0.10	0.22	0.31	0.37	0.42	0.46	0.49	0.52	0.54	0.57	0.59
Survival proportion at birth (SPB)	%	0.01	0.07	0.10	0.12	0.14	0.16	0.17	0.19	0.20	0.21	0.22
Pre-weaning survival proportion (PSP)	%	0.02	0.10	0.14	0.17	0.20	0.22	0.24	0.26	0.28	0.29	0.31
Average age at puberty (AAP)	days	0.41	0.42	0.55	0.63	0.68	0.72	0.75	0.78	0.80	0.81	0.83
Maternal average daily gain (M ADG)	g/day	0.06	0.17	0.24	0.29	0.33	0.37	0.40	0.43	0.45	0.47	0.49
Back fat thickness (BFT)	mm	0.33	0.38	0.51	0.58	0.64	0.68	0.71	0.74	0.76	0.78	0.80
Average daily gain (ADG)	g/day	0.31	0.37	0.50	0.57	0.63	0.67	0.70	0.73	0.75	0.77	0.79
Feed conversion ratio (FCR)	kg/kg	0.12	0.24	0.33	0.40	0.45	0.49	0.52	0.55	0.58	0.60	0.62
Post-weaning survival (PWS)	0/1	0.05	0.16	0.22	0.27	0.31	0.34	0.37	0.39	0.42	0.44	0.46
Belly fat (BF)	%	0.34	0.39	0.51	0.59	0.65	0.69	0.72	0.75	0.77	0.79	0.80
Drip loss % (DLP)	%	0.14	0.26	0.36	0.43	0.48	0.52	0.55	0.58	0.61	0.63	0.65
Middle portion (MD)	%	0.23	0.33	0.44	0.52	0.57	0.61	0.65	0.68	0.70	0.72	0.74
Juvenile insulin like growth factor 1 (IGF-1)	Ng/mL	0.22	0.32	0.43	0.51	0.56	0.61	0.64	0.67	0.69	0.71	0.73
Muscle depth (MD)	mm	0.19	0.30	0.41	0.48	0.53	0.58	0.61	0.64	0.67	0.69	0.71

of information for different breeding objective traits are shown in Table 2. All the production traits, except meat and carcase quality and post-weaning survival traits, were available on selection candidates before selection. Production traits such as back fat thickness and average daily gain were measured on selection candidates along with records on 5 full sibs, 30 half-sibs, the sire and the dam. Since the feed conversion ratio is expensive to measure, it was recorded on two full sibs and 5 half sibs along with recordings on the sire and the dam. Post-weaning survival (assuming 97% survival rate) trait was recorded on 30 half sibs along with a record for the sire. Meat and carcase quality traits were recorded on 2 full sibs and 10 half sibs. Reproductive traits such as number born alive and sow mature weight were recorded on the dam and 3 half sibs. It was assumed that the dam had 2 parties and the records for the number born alive, survival proportion at birth and pre-weaning survival proportion in the two parties were assumed repeated records. One record from the dam for sow longevity was available on selection candidates (Table 2). It was assumed that genomic breeding values of all traits were available for all selection candidates. Economic weights derived by Hermesch et al. (2014) and Amer et al. (2014) for breeding objective traits are shown in Table 3. Production traits were assumed either uncorrelated with reproductive traits in Table 4 or correlated with reproductive traits in Table 5 because of inconsistency in correlations between production and reproductive traits found in the literature. All the heritabilities

and genetic correlations were collected from the literature (Hermesch, 2008, 2013; Hermesch & Jones, 2012; Hermesch & O'Shea, 2005; Kerssen et al., 2019; Lewis & Bunter, 2011; Lewis & Hermesch, 2013).

2.2 | Simulation procedure

The selection index (Hazel, 1943) method was used for incorporating multiple breeding objective traits to predict selection response and selection accuracy for overall merit as well as for individual objective traits. The method uses relative economic weight for each breeding objective trait and phenotypic and genetic parameters for breeding objective and selection criteria traits. Dekkers (2007) showed how genomic information can be added as just another information source in the selection index framework assuming genomic breeding value as an additional trait with a heritability of 0.99 and economic weight of zero (Dekkers, 2007).

The (co)variance structure between the true breeding value of the trait and the corresponding genomic breeding value in the two-trait setting is:

$$
\begin{bmatrix}
\sigma^2_{BV1} & r_g\sigma_{a1}\sigma_{a2} & r_1^2\sigma_a^2 & r_g\sigma_{a1}r_1^2\sigma_{a2} \\
 & \sigma^2_{BV2} & r_g\sigma_{a1}r_2^2\sigma_{a2} & r_2^2\sigma_a^2 \\
 & & \sigma^2_{GEBV1} & r_g\sigma_{a1}r_1\sigma_{a2}r_2 \\
sym & & & \sigma^2_{GEBV2}
\end{bmatrix}
$$

	Information source				
Traits	**Own**	**Sire**	**Dam**	**Full sibs**	**Half sibs**
No. born alive	0	0	2	0	3
Sow mature weight	0	0	1	0	3
Sow longevity	0	0	1	0	0
Survival proportion at birth	0	0	2	0	0
Pre-weaning survival proportion	0	0	2	0	0
Average age at puberty	0	0	1	0	5
Dam average age at puberty	1	1	1	5	30
Back fat thickness	1	1	1	5	30
Average daily gain	1	1	1	5	30
Feed conversion ratio	1	1	1	1	5
Post-weaning survival	0	1	0	0	30
Belly fat	0	0	0	2	10
Drip loss percentage	0	0	0	2	10
Middle portion	0	0	0	2	10
Juvenile insulin-like growth factor	1	1	1	2	12
Muscle depth	1	1	1	5	30

TABLE 2 Sources of information for different traits in dam and sire line breeding objectives.

TABLE 3 Genetic standard deviation (GSD) and economic weight (EW) of breeding objective traits used in the breeding program simulation.

Traits	% contribution to dam line breeding objective	% contribution to sire line breeding objective	GSD	EW/ gilt in dam line (A$)	EW/pig in sire line (A$)
NBA	12.90	–	0.80	91.93	–
SMW	6.80	–	9.50	–4.17	–
SL	11.10	–	0.70	86.90	–
SPB	0.60	–	0.03	107.17	–
PSP	7.70	–	0.04	1092.88	–
AAP	6.40	–	15.36	–2.41	–
M ADG	8.30	–	15.84	3.06	–
BFT	5.40	9	1.09	–28.61	1.70
ADG	10.10	17	39.53	1.49	0.09
FCR	10.20	17	0.13	–462.62	27.44
PWS	20.50	35	0.04	3130.52	182.88
BF	–	2	2.54	–	–0.20
DLP	–	6	0.58	–	–2.25
MidP	–	13	0.79	–	3.40
IGF-1	0.0	0.0	11.63	0	0
MD	0.0	0.0	2.02	0	0

Note: Economic weights have been collected from Amer et al. (2014) and Hermesch et al. (2014).

Abbreviations: AAP, average age at puberty (days); M ADG, dam average daily gain (g/d); NBA, number born alive (piglets/ litter); PSP, Pre-weaning survival proportion (%); SL, sow longevity (*n* parities); SMW, sow mature weight (kg); SPB, survival proportion at birth (%). Production traits: ADG, average daily gain (g/d); BFT, back fat thickness (mm); DLP, drip loss %; EW, economic weight; FCR, feed conversion ratio (kg/kg); IGF-1, Juvenile insulin-like growth factor 1 (ng/mL); MD, muscle depth (mm); MidP, middle portion %; PWS, post-weaning survival (0/1).

TABLE 4 Genetic (below diagonal) and phenotypic (above diagonal) correlations among breeding objective traits and selection criteria are used for simulation in the scenario where production and reproduction traits are assumed to be uncorrelated.

Traits	NBA	SMW	SL	SPB	PSP	AAP	M ADG	BFT	ADG	FCR	PWS	BF	DLP	MidP	IGF-1	MD
NBA	–	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SMW	−0.21	–	0	0	0	0	0	0	0	−0.01	0	0	0	0	0	0
SL	0	0.10	–	0	0	0	0	0.10	−0.05	−0.03	0	0	0	0	0	0.05
SPB	0	0	0	–	0	0	0	0	0	0	0	0	0	0	0	0
PSP	0	0	0	0	–	0	0	0	0	0	0	0	0	0	0	0
AAP	0	0	0	0	0	–	0	0	0	0	0	0	0	0	0	0
M ADG	0	0	0	0	0	0	–	0	0	0	0	0	0	0	0	0
BFT	0	0	0	0	0	0	0	–	0.11	0.11	0	0.50	0	0.24	0.21	−0.03
ADG	0	0	0	0	0	0	0	0.02	–	−0.20	0	−0.06	0.04	0.01	0.09	−0.01
FCR	0	0	0	0	0	0	0	0.10	−0.37	–	0	0.07	−0.05	0	0.15	0
PWS	0	0	0	0	0	0	0	0	0	0	–	0	0	0	0	0
BF	0	0	0	0	0	0	0	0.60	0.16	0.09	0	–	0	0.48	0.11	−0.07
DLP	0	0	0	0	0	0	0	0.14	0.09	−0.14	0	0	–	0	0	0
MidP	0	0	0	0	0	0	0	0.28	0.28	0	0	0.50	0	–	0	0.04
IGF-1	0	0	0	0	0	0	0	0.57	0.06	0.40	0	0.20	0	0	–	0
MD	0	0	0	0	0	0	0	−0.05	0.28	−0.16	0	−0.16	0.06	0.05	0.37	–

Abbreviations: AAP, average age at puberty (days); M ADG, dam average daily gain (g/d); NBA, number born alive (piglets/litter); PSP, Pre-weaning survival proportion (%); SL, sow longevity (n parities); SMW, sow mature weight (kg); SPB, survival proportion at birth (%). Production traits: ADG, average daily gain (g/d); BF, belly fat%; BFT, back fat thickness (mm); DLP, drip loss %; FCR, feed conversion ratio (kg/kg); IGF-1, Juvenile insulin-like growth factor 1 (ng/mL); MD, muscle depth (mm); MidP, middle portion %; PWS, post-weaning survival (0/1).

TABLE 5 Genetic (below diagonal) and phenotypic (above diagonal) correlations among breeding objective traits and selection criteria used for simulation in the scenario where production and reproduction traits were assumed to be correlated.

Traits	NBA	SMW	SL	SPB	PSP	AAP	M ADG	BFT	ADG	FCR	PWS	BF	DLP	MidP	IGF-1	MD
NBA	–	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SMW	−0.21	–	0	0	0	0	0	0	0	−0.01	0	0	0	0	0	0
SL	0	0.1	–	0	0	0	0	0.1	−0.05	−0.03	0	0	0	0	0	0.05
SPB	0	0	0	–	0	0	0	0	0	0	0	0	0	0	0	0
PSP	0	0	0	0	–	0	0	0	0	0	0	0	0	0	0	0
AAP	0	0	0	0	0	–	0	−.03	0	0.2	0	0	0	0	0	0
M ADG	0	0	0	0	0	0	–	0	0	0	0	0	0	0	0	0
BFT	−0.01	−0.12	0.37	0	0	−0.03	0	–	0.11	0.11	0	0.50	0	0.24	0.21	−0.03
ADG	−0.21	0	−0.28	0	0	0	0	0.02	–	−0.20	0	−0.06	0.04	0.01	0.09	−0.01
FCR	−0.07	−0.15	−0.02	0	0	0.2	0	0.10	−0.37	–	0	0.07	−0.05	0	0.15	0
PWS	0	0	0	0	0	0	0	0	0	0	–	0	0	0	0	0
BF	0	0	0	0	0	0	0	0.60	0.16	0.09	0	–	0	0.48	0.11	−0.07
DLP	0	0	0	0	0	0	0	0.14	0.09	−0.14	0	0	–	0	0	0
MidP	0	0	0	0	0	0	0	0.28	0.28	0	0	0.50	0	–	0	0.04
IGF-1	0	0	0	0	0	0	0	0.57	0.06	0.40	0	0.20	0	0	–	0
MD	0.11	0.12	0.01	0	0	0	0	−0.05	0.28	−0.16	0	−0.16	0.06	0.05	0.37	–

Abbreviations: AAP, average age at puberty (days); M ADG, dam average daily gain (g/d); NBA, number born alive (piglets/litter); PSP, Pre-weaning survival proportion (%); SL, sow longevity (*n* parities); SMW, sow mature weight (kg); SPB, survival proportion at birth (%). Production traits: ADG, average daily gain (g/d); BF, belly fat%; BFT, back fat thickness (mm); DLP, drip loss %; FCR, feed conversion ratio (kg/kg); IGF-1, Juvenile insulin-like growth factor 1 (ng/mL); MD, muscle depth (mm); MidP, middle portion %; PWS, post-weaning survival (0/1).

TABLE 6 Response per round of selection for the dam line breeding objective traits and the overall merit of the breeding objective (in $ value) in different sizes of reference population starting from 500 to 5000 in increments of 500).

Size of reference population	Responses in GSD											$index
	NBA	SMW	SL	SPB	PSP	AAP	M ADG	BFT	ADG	FCR	PWS	
0	0.043	−0.048	0.020	0.000	0.005	−0.126	0.096	−0.239	0.458	−0.362	0.106	84
500	0.070	−0.072	0.050	0.000	0.010	−0.167	0.097	−0.223	0.438	−0.344	0.124	90
1000	0.092	−0.088	0.072	0.001	0.013	−0.192	0.099	−0.210	0.424	−0.332	0.144	95
1500	0.108	−0.103	0.093	0.001	0.017	−0.207	0.101	−0.201	0.414	−0.334	0.160	101
2000	0.122	−0.112	0.109	0.001	0.021	−0.218	0.103	−0.196	0.408	−0.334	0.173	105
2500	0.134	−0.120	0.121	0.001	0.024	−0.225	0.106	−0.192	0.404	−0.335	0.185	108
3000	0.144	−0.126	0.132	0.001	0.026	−0.230	0.108	−0.189	0.401	−0.336	0.196	111
3500	0.153	−0.131	0.141	0.001	0.029	−0.234	0.110	−0.187	0.399	−0.338	0.205	114
4000	0.161	−0.135	0.148	0.001	0.031	−0.237	0.113	−0.185	0.398	−0.341	0.214	117
4500	0.168	−0.138	0.155	0.001	0.033	−0.239	0.115	−0.184	0.397	−0.344	0.222	119
5000	0.174	−0.141	0.161	0.001	0.036	−0.240	0.118	−0.182	0.397	−0.347	0.230	122

Note: The size of reference population zero indicates conventional breeding programs. Production traits and dam traits were assumed uncorrelated.

Abbreviations: AAP, average age at puberty (days); ADG, average daily gain (g/d); BFT, back fat thickness (mm); FCR, feed conversion ratio (kg/kg); M ADG, dam average daily gain (g/d); NBA, number born alive (*n* piglets/litter); PSP, Pre-weaning survival proportion (%); PWS, post-weaning survival proportion (%); SL, sow longevity (*n* parities); SMW, sow mature weight (kg); SPB, survival proportion at birth (%).

Where, σ^2_{BV1} and σ^2_{BV2} are the variances of true breeding values of traits 1 and 2, respectively. σ^2_{GEBV1} and σ^2_{GEBV2} are the variances of genomic breeding values of traits 1 and 2, respectively. r is the genomic prediction accuracy for different trait combinations (r1, r2), σ^2_a is the additive genetic variance, r_g is the genetic correlation between the two traits. The (co)variance structure can be extended for more than two traits. Different genomic section scenarios based on the sizes of the reference population were compared with a conventional pig breeding program.

Effective population size (N_e) was assumed to be 100 and genomic prediction accuracy was calculated using the formulas (Daetwyler et al., 2008; Goddard et al., 2011):

$$r = \sqrt{\frac{Nh^2}{Nh^2 + M_e}}$$

$$M_e = \frac{2N_e L K}{\log(N_e L)}$$

Where r is the genomic prediction accuracy, N is the reference population size, h^2 is the heritability of each trait, M_e is the effective number of chromosome segments, L is the pig average chromosome length in Morgans. The average chromosome length was assumed to be 1.2 Morgans (Haberland et al., 2013) and K, the number of chromosomes was assumed to be 19. The effective number of chromosome segments could also be estimated empirically from the genomic relationship matrix among the reference and target individuals (Lee et al., 2017). Real genotype data of pigs was not available for this study. Therefore, in this deterministic simulation study, M_e was calculated using the above equation proposed by Goddard et al. (2011).

A deterministic simulation was used to predict the genetic merit per selection round using the following formula: R = i $r_{iA}\sigma_I$, where R is the predicted genetic gain, i is the selection intensity assuming 1 and r_{iA} is the selection accuracy (correlation between true and EBV) and σ_I is the standard deviation of the breeding objective. The simulation was conducted using MTindex (https://jvanderw.une.edu.au/software.htm). The percentage contribution of a trait in the breeding objective was calculated as follows:

$$\left((GSD \times EW) \text{ of a trait} / \left(\sum_{i=1}^{n} abs(GSD \times EW) \right) \right) \times 100,$$

where GSD is the genetic standard deviation of a trait, EW is the economic weight of a trait, and n is the total number of traits in the breeding objective. The contribution of each trait to the breeding objective is shown in Table 3.

Different scenarios of GS were created by varying the accuracy of genomic prediction reflected by the different sizes of the reference population. Genomic prediction accuracies of different traits depend on the heritability of each trait and the sizes of the reference population, these are both shown in Table 1. Ten different GS scenarios were defined based on the size of the reference population ranging from 500 to 5000 pigs with an interval of 500 pigs. Preliminary results in this study showed that genomic prediction accuracy for different traits marginally increased when the size of the reference population increased from 5000 onwards. This marginal improvement in genomic prediction accuracy with the sizes of the reference population of more than 5000 individuals and an effective population size of 100 was also reported in the literature (Lee et al., 2017). Therefore, the reference population size was only up to 5000 individuals in this study. Furthermore, the sizes of the reference population were assumed to be the same for all traits in this simulation study for computational simplicity. In reality, the sizes of the reference population vary for traits such as growth traits versus reproductive traits (Song et al., 2017; Wang et al., 2022). However, it was assumed that the reference population was available for all traits from previous generations.

3 | RESULTS

3.1 | Predicted genetic gain

The dam line breeding objective consisted of both reproductive and production traits. Reproduction and production traits accounted for 53.80% and 46.20% of the total dam breeding objective relative to the genetic standard deviation of traits, respectively (Table 3). In the dam line breeding objective when production and dam traits were assumed uncorrelated, overall merit benefited from GS scenarios but not all the individual breeding objective traits benefited (Table 6). All reproductive traits and post-weaning survival achieved additional genetic gain compared to the conventional breeding program, but back fat thickness, average daily gain and feed conversion ratio achieved a smaller rate of genetic gain with GS compared to a conventional breeding program. For example, the number born alive, sow mature weight, sow longevity and the average age at puberty achieved 62% to 304%, 50% to 193%, 150% to 705% and 32% to 90% more genetic gain, respectively, in GS scenarios compared to the conventional program. In comparison, back fat thickness, average daily gain and feed conversion ratio achieved 6% to 23%, 4% to 13% and 4% to 5% less gain, respectively, in genomic scenarios. All the scenarios of GS predicted additional genetic gain for the overall breeding objective per round of selection, ranging from 7.20% to 44.50% when compared to the gain in a conventional breeding program.

TABLE 7 Response per round of selection for the dam line breeding objective traits and the overall merit of the breeding objective (in $ value) in different sizes of reference population starting from 500 to 5000 in increments of 500).

Size of reference population	Responses in GSD										Index ($)
	NBA	SMW	SL	PSP	AAP	M ADG	BFT	ADG	FCR	PWS	
0	0.041	−0.026	−0.041	0.006	−0.161	0.113	−0.078	0.318	−0.375	0.126	71
500	0.071	−0.058	−0.017	0.011	−0.203	0.112	−0.073	0.303	−0.349	0.147	78
1000	0.096	−0.077	0.005	0.015	−0.228	0.112	−0.070	0.295	−0.340	0.164	84
1500	0.112	−0.091	0.020	0.019	−0.244	0.113	−0.067	0.289	−0.339	0.181	89
2000	0.130	−0.100	0.033	0.023	−0.251	0.115	−0.067	0.286	−0.339	0.195	93
2500	0.144	−0.110	0.043	0.026	−0.257	0.118	−0.066	0.283	−0.340	0.206	97
3000	0.155	−0.115	0.050	0.028	−0.261	0.120	−0.066	0.281	−0.341	0.218	100
3500	0.166	−0.120	0.057	0.032	−0.266	0.123	−0.066	0.280	−0.344	0.225	103
4000	0.172	−0.126	0.061	0.035	−0.267	0.124	−0.066	0.279	−0.349	0.238	106
4500	0.178	−0.128	0.069	0.036	−0.266	0.127	−0.066	0.279	−0.352	0.246	109
5000	0.185	−0.131	0.073	0.039	−0.268	0.129	−0.067	0.280	−0.354	0.254	111

Note: Size of reference population zero indicates conventional breeding programs. Production traits and dam traits were assumed correlated.

Abbreviations: AAP, average age at puberty (days); ADG, average daily gain (g/d); BFT, back fat thickness (mm); FCR, feed conversion ratio (kg/kg); M ADG, dam average daily gain (g/d); NBA, number born alive (*n* piglets/litter); PSP, Pre-weaning survival proportion (%); PWS, post-weaning survival (0/1); SL, sow longevity (*n* parities); SMW, sow mature weight (kg).

TABLE 8 Response per round of selection for the terminal line breeding objective traits and the overall merit of the breeding objective (in $ value) in different sizes of reference population starting from 500 to 5000 in increments of 500).

| Size of reference population | Response in GSD | | | | | | | $index |
	BFT	ADG	FCR	PWS	BF	DLP	MidP	
0	−0.230	0.550	−0.380	0.100	−0.040	0.010	0.170	4
500	−0.220	0.540	−0.340	0.120	−0.030	0.000	0.190	5
1000	−0.220	0.530	−0.340	0.150	−0.030	−0.010	0.210	5
1500	−0.210	0.530	−0.340	0.170	−0.020	−0.020	0.220	5
2000	−0.210	0.530	−0.340	0.180	−0.020	−0.030	0.230	5
2500	−0.210	0.530	−0.350	0.200	−0.020	−0.030	0.230	5
3000	−0.200	0.530	−0.350	0.210	−0.010	−0.040	0.240	5
3500	−0.200	0.530	−0.350	0.220	−0.010	−0.040	0.250	5
4000	−0.200	0.530	−0.360	0.230	−0.010	−0.040	0.250	5
4500	−0.200	0.530	−0.360	0.240	−0.010	−0.040	0.250	6
5000	−0.200	0.530	−0.360	0.250	−0.010	−0.050	0.260	6

Note: Size of reference population zero indicates conventional breeding programs.

Abbreviations: ADG, average daily gain (g/d); BF, belly fat %; BFT, back fat thickness (mm); DLP, drip loss %; FCR, feed conversion ratio (kg/kg); MidP, middle portion %; PWS, post-weaning survival (0/1).

When production and reproductive traits were assumed to correlate with some unfavourable correlations, GS scenarios provided 9.60% to 56.12% additional genetic gain in the dam line breeding objective compared to the conventional breeding program (Table 7). With unfavourable correlations between sow longevity, back fat thickness, and average daily gain, genetic gain in sow longevity was in the unfavourable direction in conventional breeding programs and GS with a reference population of 500 pigs. As the size of the reference population increased, genetic gain started to change in a favourable direction. Pre-weaning survival proportion achieved the highest additional genetic gain of (83% to 550%) followed by sow mature weight (123% to 403%); number born alive (73% to 351%) and sow longevity (58% to 278%) in GS scenarios, compared to the genetic gain in a conventional breeding program (Table 7). With unfavourable genetic correlations between production and reproduction traits, production traits such as back fat thickness, average daily gain and feed conversion ratio had 6% to 14%, 4% to 11% and 7% to 9% smaller rates of improvement in GS scenarios, respectively, compared to a conventional breeding program. When the feed conversion ratio was assumed uncorrelated with reproductive traits, it achieved more genetic gain than assuming correlations with reproductive traits. However, the overall dam line breeding objective benefited more from GS by 2.40% to 11.60% when production and reproductive traits were assumed to be correlated in comparison to assuming zero correlation between production and reproduction traits.

In the sire line breeding objective, production traits accounted for 79% of the total breeding objective based on a genetic standard deviation of traits. Meat and carcase quality traits accounted for 21% of the total breeding objective. Not all objective traits benefited equally from GS scenarios in the sire line. Some traits achieved less gain in GS scenarios, for example, back fat thickness, average daily gain and feed conversion ratio achieved 4.4% to 13%, 1.8% to 3.64% and 25% to 75% less genetic gain compared to conventional breeding program, respectively. By contrast, the genetic gain for post-weaning survival, middle portion and drip loss percentage increased by 20% to 150%, 11% to 53% and 200% to 600% using genomic information, respectively. The overall responses on the sire line breeding objective increased by 3.50 to 27% in GS scenarios, compared to conventional breeding programs (Table 8).

3.2 | Selection accuracy

The overall increase in accuracy varied from 5% to 40% but with ever-diminishing increases as the reference population increased in the dam line breeding objective. Selection accuracy for all the traits in the dam line breeding objective increased in GS compared to conventional breeding programs. Reproductive traits achieved more accuracy than production traits in GS. The accuracy of multi-trait EBVs in the most accurate GS scenario with a reference population of 5000 pigs for individual dam line breeding objective traits such as number born alive, sow mature weight, sow longevity, survival proportion at birth, pre-weaning survival proportion, average age at puberty and maternal average daily gain increased by 140%, 106%, 248%, 225%, 214%, 79% and 33%, respectively.
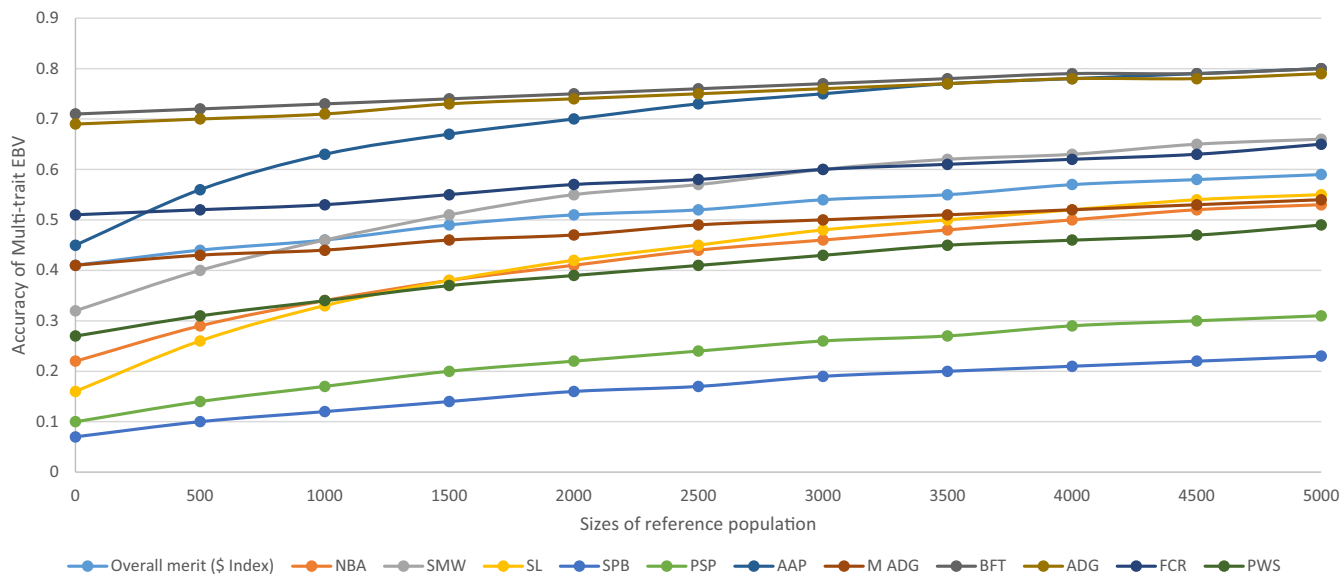
FIGURE 1 Accuracy of multi-trait EBV for breeding objective traits and the overall dam line index in scenarios with conventional breeding program (reference population size zero) and genomic selection with different size of reference population starting from 500 to 5000 in increments of 500). Production traits and reproduction traits were assumed uncorrelated. For trait definitions, see Table 1. [Colour figure can be viewed at wileyonlinelibrary.com]

Selection accuracy for production traits in dam line breeding objectives such as average daily gain, backfat and feed conversion ratio increased by 15.40%, 12.50%, 25.29%, respectively, in GS with a reference population of 5000 pigs (Figure 1). When reproduction and production traits were uncorrelated in the dam line breeding objective, selection accuracy for the overall breeding objective increased by 43% in GS with a reference population of 5000 pigs (Figure 1). When reproduction and production traits were correlated in the dam line breeding objective, selection accuracy for the overall breeding objective increased by 55% in GS with a reference population of 5000 pigs compared to the conventional breeding program (Figure 2). In comparison, the selection accuracy of multi-trait EBV for belly fat percentage, drip loss percentage, and middle portion percentage in the terminal sire line increased by 9% to 41%, 16% to 77% and 13% to 58%, respectively, in the GS scenarios compared to the conventional breeding program. Production traits such as backfat thickness, average daily gain and feed conversion ratio increased by 1.40% to 12.60%, 1.40% to 14% and 1.90% to 25.40%, respectively (Figure 3).

4 | DISCUSSION

4.1 | Genetic gain (dam line breeding objective)

This study compared the potential for additional genetic gain when genomic information is used for pig breeding in dam and sire lines. This study compared genetic gain in

two breeding objectives and at different levels of accuracy of GS. Not all the breeding objective traits achieved higher genetic gain in GS scenarios than in the conventional breeding program. However, the overall breeding objective benefitted from GS. Knol et al. (2016) gave an example of a commercial pig breeding where the overall benefit in breeding objective increased by 50% using GS for eight different breeding objective traits in a pig line. The genetic improvements for individual breeding objective traits were not outlined. van der Werf (2009) and Lillehammer et al. (2020) studied the magnitude of genetic improvement for individual breeding objective traits using GS in sheep. van der Werf (2009) investigated both meat and fine wool merino sheep breeding objectives, showing that GS shifted the emphasis on traits. Lillehammer et al. (2020) also found similar trends in Norwegian white sheep. The Norwegian white sheep breeding program was simulated with a breeding objective consisting of growth, carcass and maternal traits. Authors found that growth and maternal traits achieved larger genetic gain in GS compared to the pedigree-based selection, whereas the carcase trait was accompanied by a reduction in genetic gain. These examples show the impact of GS on a multiple-trait breeding objective, with a more positive impact on traits with those with the greatest accuracy increase. In pig breeding programs, the traits that benefit most are reproductive and post-weaning survival traits, as these are typically measured later in life or are lowly heritable. Traits that were disadvantaged were production traits such as average daily gain and back fat thickness, these are typically measured on selection candidates and have moderate to high heritability or had antagonistic correlations with the traits
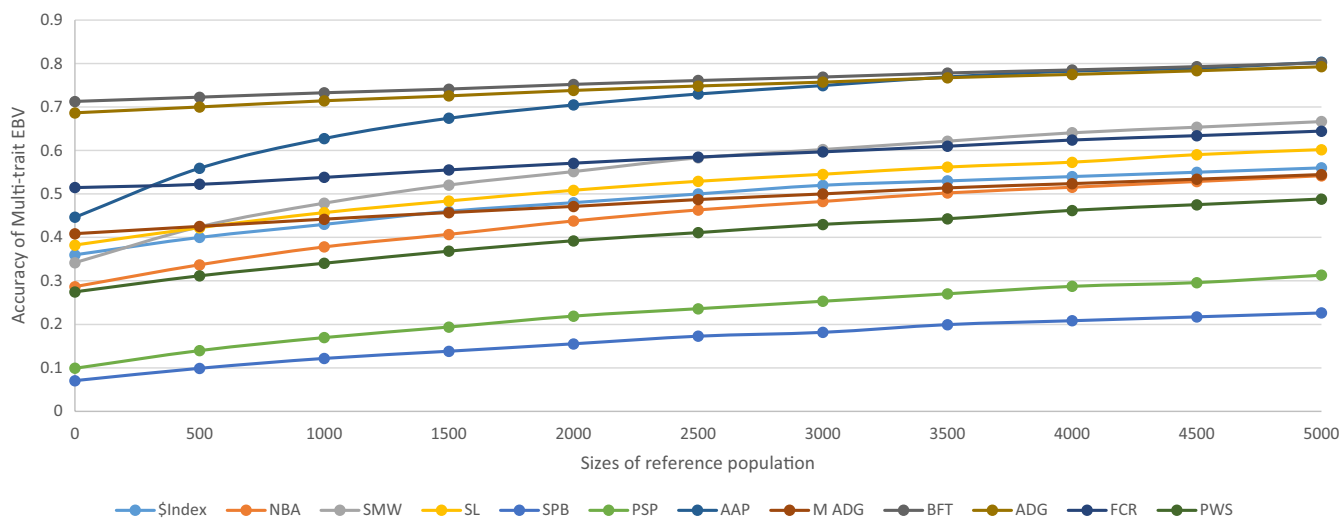
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FIGURE 2 Accuracy of multi-trait EBV for breeding objective traits and the overall dam line index in scenarios with conventional breeding program (reference population size zero) and genomic selection with different sizes of reference population starting from 500 to 5000 in increments of 500). Production traits and dam traits were assumed correlated. For trait definitions, see Table 1. [Colour figure can be viewed at wileyonlinelibrary.com]

that benefited in GS. For example, average daily gain and back fat thickness were assumed uncorrelated or unfavourably correlated with sow mature weight. However, in either case of uncorrelation and unfavourable correlation between sow mature weight, average daily gain and back fat thickness, average daily gain and back fat thickness achieved a smaller rate of genetic gain in GS than pedigree selection while sow mature weight benefited more in GS. This increase resulted the overall merit of breeding objective in GS. This demonstrates that smaller rates of genetic gain for some traits in GS compared to traditional selection are not of concern if the overall breeding objective benefits from the GS. These findings are relevant for any species with a multiple-trait breeding objective.

Individual breeding objective traits had different rates of genetic improvement in the GS scenarios. The relative improvement of different dam line breeding objective traits can be explained by the relative economic weight, correlation structure between production and reproduction traits and selection accuracy. Accuracy is determined by the sources of information available before selection. Phenotypic information for reproduction traits was not available on the selection candidates until after the first farrowing. In contrast, production traits in the dam breeding objective had phenotypic records on the selection candidates except for post-weaning survival. As a result, the accuracy of multi-trait EBV for reproduction traits was lower than production traits, for example, the accuracy of sow longevity and feed conversion ratio was 0.40 and 0.52; respectively. With a 5000 reference population, sow longevity achieved 243% more accuracy, whereas feed conversion ratio achieved 35.40% more accuracy. Furthermore, reproduction traits contributed 53.80% to

the total breeding objective. As a result, reproduction traits achieved larger genetic gain than production traits. However, smaller responses in some traits came at the same time as much larger responses response in other traits that increased the overall response by 9% (in $ value) in the least accurate GS scenario with 500 reference populations. This indicates that in a multi-trait context, GS is particularly beneficial for improving the traits that have fewer records or because of unfavourable correlation with other breeding objective traits.

In a simulation study by Wolc et al. (2015), the authors included 16 egg production and egg quality traits in breeding objectives for laying hens. The authors found that GS outperformed pedigree selection for all traits. However, phenotypic records of all the traits were not available on selection candidates at the time of selection. This is in agreement with our results because all reproduction traits in our study also benefitted from GS. However, the dam line breeding objective in the current study also included production traits, which were recorded on selection candidates and consequently, production traits had less additional genetic gain using GS. The magnitude of genetic improvement for different traits indicates a shift of genetic improvement towards the traits that have a limited number of records, a feature of GS that has not been well reported in pig breeding programs but has been reported in sheep breeding studies (Lillehammer et al., 2020; van der Werf, 2009). Therefore, our study can be used as a reference to explain if some traits in pig breeding programs are found to have a smaller rate of genetic gain in GS compared to pedigree selection.

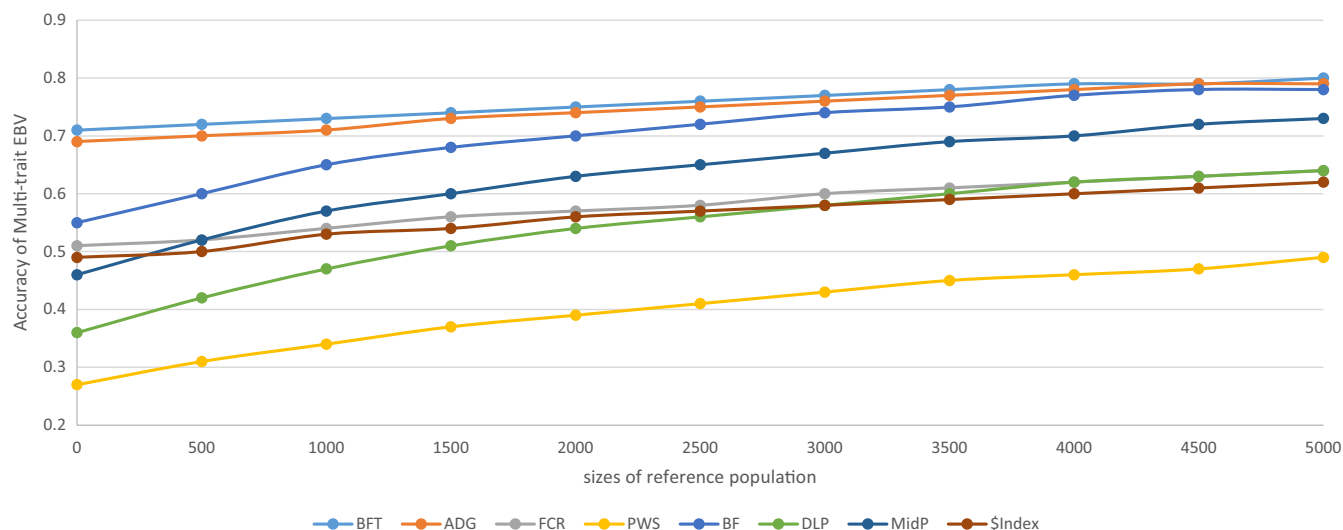Overall response in the breeding objective benefited from the GS scenarios, for example, the least accurate

FIGURE 3 Accuracy of multi-trait EBV for breeding objective traits and the overall sire line index in scenarios with conventional breeding program (reference population size zero) and genomic selection with different sizes of reference population starting from 500 to 5000 in increments of 500). For trait definitions, see Table 1. [Colour figure can be viewed at wileyonlinelibrary.com]

GS scenario with 500 reference populations achieved 9% more overall response ($value) in the dam line breeding objective compared to the conventional breeding program. Lillehammer et al. (2013) found 9% more overall genetic gain (in GSD) in the GS scenario compared to conventional breeding programs for a dam breeding objective that consisted of one dam trait and one production trait where the traits were unfavourably correlated. Additional genetic gain in the GS scenario resulted from the increased accuracy of the GS index. In this current study, the accuracy of the GS index was about 9% higher than the accuracy of the pedigree selection index. In our study, individual breeding objective traits also had increased accuracy with genomic information. However, increased accuracy for individual traits did not necessarily translate into higher genetic gain in the multi-trait breeding objective context, as was found in the current study. This implies that selection accuracy alone cannot be used to compare different breeding programs in a simulation study. Both genetic gain and selection accuracy should be used to assess breeding programs.

When the size of the reference population increased, the overall response to the breeding objective also increased in all scenarios. However, the overall response did not increase linearly with the increased size of the reference population. This non-linear increase in overall response is also in line with the findings reported by Shumbusho et al. (2013). Response to GS with the increase in the sizes of reference population can be explained by the changes in the accuracy of EBVs. The accuracy of the breeding objective did not increase linearly with the increase in the size of the reference population. The marginal effectiveness of extra records for increasing the size of the reference population is important for optimising

the investment into genotyping animals. As the accuracy did not increase linearly, there should be an optimal size of the reference population that would be economically efficient. Furthermore, members of the reference population might not be phenotyped for all the traits that require more investment. Therefore, it would be worthwhile to investigate the economic efficiency of the optimum size of the reference population for new traits that require investment.

Genomic prediction accuracy depends on the relationship between the selection candidates and the animals in the reference population. Updating the reference population is important for maintaining genomic prediction accuracy (Wolc et al., 2011). Genotyping more animals in successive generations will also contribute to updating SNP effects (Lillehammer et al., 2013). The number of animals genotyped in different studies is difficult to compare because of differences in population structure and phenotypic information (Lillehammer et al., 2020). Keeping the number of genotyped animals constant, the composition of the reference population can vary to increase the accuracy of GS and the rate of genetic gain. 1) Crossbred pigs might be included in the reference population because the inclusion of crossbred pigs in the reference population can increase the selection accuracy of purebred pigs. The inclusion of crossbred pigs in the reference population is more important for traits that are not usually recorded or not expressed in the nucleus population. For example, the length of productive life of a sow is only available in crossbred pigs because purebred sows are not kept for a long time in the nucleus population to limit the generation interval. However, the benefits of genotyping

crossbred pigs depend on the correlation between pure-bred and crossbred performance (van Grevenhof & van der Werf, 2015). 2) Genotyping more males versus more females also impacts genetic gain. Lillehammer et al. (2013) showed that genotyping more females increased the relative contribution of maternal traits trait to the total breeding objective in Norwegian Landrace pigs. This could be a useful strategy to shift the genetic gain towards the desired direction without compromising the total genetic gain.

4.2 | Genetic gain (sire line breeding objective)

In this study, the sire line breeding objective included both meat and carcass quality traits as well as production traits. The importance of including meat and carcass quality traits in the breeding objective is increasing because of consumers' desire for better pork quality (von Rohr et al., 1999; Willson et al., 2020). However, the recording of meat and carcase quality traits is difficult and expensive. The development of large reference populations for pork quality traits and the selection of young animals based on genomic breeding value would be a good strategy to improve pork quality traits (Miar et al., 2014). If the breeding objective trait is expensive to measure, pedigree-based selection might use indicator traits for multi-trait evaluation that are easy to measure. In this case, investment in building up a reference population for the trait of interest can be more effective than investing in phenotyping indicator trait (Calus & Veerkamp, 2011). Therefore, it is worthwhile to record pork quality traits to build up a large reference population for the improvement of pork quality traits.

This study found that the overall response in the sire line breeding objective increased in GS scenarios from 3.50% to 27%. The aim of breeding objective was to decrease the drip loss percentage, however drip loss percentage increased in GS with a reference population of 500 pigs and a conventional breeding program since the drip loss percentage was unfavourably correlated with average daily gain. GS scenarios with a reference population of 1000 or more pigs began to decrease drip loss percentage (favourable direction) while losing some gain for other traits such as back fat thickness, average daily gain and belly fat percentage. This demonstrates that hard-to-measure traits even with unfavourable correlations can be improved in a breeding program but it requires enough genomic prediction accuracy.

Shifting of genetic improvement for some breeding objective traits was also found in the sire line breeding objective as was found in the dam line breeding

objective. Tribout et al. (2012) also found 4% more predicted response (in GSD) on a breeding objective for a sire line in a GS scenario using one training population and 30% more response when two training populations were used for two breeding objectives traits (one trait represented easy-to-measure trait and another one represented expensive or hard-to-measure trait). The breeding goal for the Norwegian breeding program has a relative economic value of 19% to 41% for meat quality traits. As a result, Norsvin Duroc has a good combination of lean meat growth and high-meat quality (Gjerlaug-Enger et al., 2014).

The genomic selection comes with the extra cost associated with genotyping animals, sample collection, DNA isolation and storage, computing infrastructure, etc. (Abell et al., 2014). Extra genetic gain in the GS scenarios should compensate for the extra cost of implementing GS. It is also important to explore the possible economic value of each breeding objective trait based on the marketing system to make sure that farmers are paid for all the breeding objective traits.

In the current study, GS showed the opportunities for improving genetic gain both in the dam and sire line of pigs in different scenarios of GS on a breeding objective consisting of multiple correlated traits. However, GS caused a shift in emphasis among breeding objective traits resulting in more improvement in some traits at the expense of other traits. This study also found non-linear relations between genetic gain and the size of the reference population, an optimum size of the reference population should be further explored in terms of economic efficiency. The breed was undefined in this deterministic simulation. The ballpark figure of this study could be validated with stochastic simulation where genotypes of a particular breed and realistic population size could be simulated.

5 | CONCLUSIONS

GS made more genetic improvement for reproductive and pork quality traits than traits that are easily recorded such as average daily gain and back fat thickness. However, improvement in the overall responses for sire and dam line breeding objectives was found in all the GS scenarios. Improvement in genetic gain diminished as the size of the reference population increased. Improvement of genetic gain for pork quality traits showed the potential for incorporating meat quality traits in the sire line breeding objective. Because of the marginal improvement of overall response with the increase in the reference population, economic analysis should be conducted to investigate the optimum

size of the reference population for the specific trait. It is important to investigate which traits need more investment, particularly meat quality traits. So, for extra trait recording, it is good to know how many animals we need to measure and how many generations of data can be used.

CONFLICT OF INTEREST STATEMENT

There are no conflict of interests.

DATA AVAILABILITY STATEMENT

Data sharing does not apply to this article as no new data were created or analysed in this study.

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