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► To cite this version:

Jérôme Raoul, Jean-Michel Elsen. The levels of artificial insemination and missing sire information make genomic selection not always beneficial in meat sheep. *Animal*, 2021, 15 (2), pp.100040. 10.1016/j.animal.2020.100040 . hal-03156712

HAL Id: hal-03156712

<https://hal.inrae.fr/hal-03156712v1>

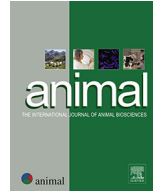
Submitted on 24 Jul 2023

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The levels of artificial insemination and missing sire information make genomic selection not always beneficial in meat sheep



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ARTICLE INFO

Article history:

Received 22 October 2019

Received in revised form 18 June 2020

Accepted 19 June 2020

Available online 11 January 2021

Keywords:

Breeding program

Genetic gain

Genomic selection

Small ruminants

Stochastic simulations

ABSTRACT

Numerous meat sheep breeding programs in developed and developing countries are characterized by incomplete sire information and a predominant use of natural matings. These two parameters potentially affect the benefit of genomic selection (GS), especially for the selection of a late-in-life trait. Using stochastic simulations, the genetic gains obtained using genomic and conventional strategies for a maternal trait were evaluated in meat sheep population. Natural mating and artificial insemination (AI)-based designs, inspired by the current diversity of designs used for French meat sheep breeds, were modeled and three genomic strategies were tested and compared with a conventional selection strategy: parentage assignment, GS based on a male or a female and reference population. Genomic selection based on a male reference population did not always outperform conventional selection. Its benefit depended on the design, the level of missing information on dam sires, and the level of AI. Genomic selection based on a male and female reference population always outperformed the conventional selection strategy, even if only 25 % of the females in the nucleus were genotyped.

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Implications

This simulation study assesses selection strategies for meat sheep populations characterized by incomplete pedigree information and a predominant or exclusive use of natural matings. The results make it possible to evaluate the benefit of moving to genomic selection and to optimize its deployment in these populations.

Introduction

Genomic selection (GS) seems promising for the selection of lowly heritable and/or late-in-life traits (Schaeffer, 2006; Meuwissen et al., 2013) and has been widely adopted in dairy cattle (Pryce and Daetwyler, 2012) and other species. If the accuracy of the genomic estimated breeding values (GEBV) is sufficient, GS allows early selection on traits measured later in life and is therefore an alternative to progeny testing (PT). Genotyping animals could also be used to assign parentage to animals born from multi-sire matings. Thus, GS can be particularly beneficial to select maternal traits for meat sheep breeding programs. Yet, only a few countries have implemented GS for meat sheep on a wide scale (Pickering et al., 2013; Swan et al., 2014). The review of Rupp et al. (2016) identified several factors that limit several factors limit the benefit of GS for these populations: the populations are

generally small, their effective sizes tend to be large, with a negative effect on GEBV precision, and the quality of phenotypes (accuracy of sire genetic values depending on progeny records per sire) is limited due to the low artificial insemination (AI) rate. Another difficulty is high cost of genotyping as compared to the animals' market values.

Previous studies have assessed selection strategies based on GS for meat sheep in Australia (Granleese et al., 2015), New Zealand (Santos et al., 2017) and France (Shumbusho et al., 2013; Raoul et al., 2017). These studies demonstrated the benefits of GS, but the sensitivity of the results to various levels of AI and pedigree knowledge needs to be assessed in order to support breeding societies in their decision to implement GS. The aim of this study was to assess the benefit of using genomic information (parentage assignment and GS) for the selection of a repeated maternal trait across a range of AI rates and pedigree knowledge levels. Using stochastic simulations, we modeled conventional strategies for meat sheep breeding programs and some genomic alternatives, such as parentage assignment, male reference populations, and male and female reference populations.

Material and methods

Simulation overview

To consider various scenarios, three conventional designs inspired by the French meat sheep breeding programs (Supplementary Material S1, Supplementary Table S1) were modeled: a natural mating-based

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breeding program (NM) and two AI-based breeding programs with or without PT of AI sires (NM + AI+PT, NM + AI). A maternal trait was the sole selection criterion in this study. We first established founder populations and ran breeding programs for 10 years with a conventional strategy (CS) to obtain populations similar to the existing ones. We then applied for the following 15 years either the same strategy (CS) or an alternative one: a parentage assignment (PAR_AS) or a GS strategy based on a reference population built either with only genotyped males (GS_M) or with genotyped males and females (GS_MF). For AI-based breeding programs, GS strategies were identical regardless of the previous CS (NM + AI or NM + AI+PT).

We derived input parameters for CS simulations from Supplementary Table S1 and analysis of the French official genetic database. The level of AI (% of dams inseminated each year) was derived from the % of lambs born from inseminated ewes and the fertility after AI per breed. The percentage of dams with sire information was linked to the proportion of lambs with sire information. To limit computation time, only scenarii that were relevant for the French industry were simulated. In total, we simulated 73 scenarii. For the NM design, 18 scenarii were defined: 5 CS, 4 PAR_AS, 5 GS_M, and 4 GS_MF depending on the % of dams with sire information and the % of genotyped dams (Table 1). For the current NM + AI design, 30 scenarii were defined: 6 CS, 6 PAR_AS, 6 GS_M, and 12 GS_MF depending on the AI level, the % of dams with sire information, and the % of genotyped dams (Tables 2 and 3). For the current NM + AI +PT design, 25 scenarii were defined: 5 CS, 3 PAR_AS, 5 GS_M, and 12 GS_MF depending on the AI level, the % of dams with sire information, and the % of genotyped dams (Tables 4 and 5).

We used a stochastic model coded in Fortran (founder population setup, gamete production, phenotype simulations, selection steps) and Blupf90 software (Miszta, 1999) to run the genetic evaluation based on BLUP or a single step GBLUP. This model is fully described in Supplementary Material S2 and Raoul et al. (2017). Study population genomes were derived from real 50 k genotypes. One thousand markers were randomly selected and assigned as QTLs. The QTL effects were drawn from a Gamma distribution and the sign randomly allocated. Individual true breeding values were computed according to genotypes at QTLs, assuming additivity. Individual phenotypes were simulated by adding random effects (year by flock, permanent environmental, and residual effects) to true breeding values. Selection and matings were defined using EBVs computed year by year. Following practical rules actually implementing in France, to prevent inbreeding, a male (AI or natural

mating) could not be mated to a female belonging to its dam's flock, regardless the strategies.

Population structure

To allow all designs assessed to be compared, a single population size of around 7000 females (dams) mated annually was considered. The demographic parameters were defined so that the population size remained constant across years: the probabilities of survival depended on the age and sex for all individuals and the reproduction type for males (natural mating or AI). All reproductive parameters such as AI fertility, litter size distribution, or within-litter size viability were constant across all designs. The female replacement rate was also constant across strategies: 60% of newborn females born from AI were candidates to replace culled dams. If AI was not used or could not meet dam replacement needs, newborn females born from natural mating sires were randomly kept until needs were met.

Conventional selection strategy

Natural mating-based breeding program

In "NM programs", AI is not used at all. To mimic selection differential losses due to the breed standard or the selection of functional traits, only half of newborn males (around 4 000) were included as candidates for selection. Based on their parents' EBVs, the top 500 were selected during their first year of life, with only a third still being candidates 1 year later after losses due to mortality and selection on secondary traits. The best (selection on parents' EBVs) were randomly allocated to flocks according to their flock requirement. In agreement with observed practices, a male could not be allocated to the flock in which he was born (self-replacement). Natural mating sires were used for 4 years at the most. Random culling was applied according to current demographic parameters. No exchanges of old males between flocks were simulated. For the CS, five NM breeding programs were simulated according to the proportion of dams whose sire information was known (0, 25, 50, 75, or 100%).

Animal insemination-based breeding programs without progeny testing

In NM + AI, 1-year-old male candidates were first selected as in NM. At 1 year of age, the best ranked males were selected for AI prior to males for natural mating. AI sires were used for 2 years at the most and mated to the best dams based on EBVs. AI matings were performed

Table 1 Annual genetic gain and inbreeding rates according to the genomic strategy for meat sheep. Natural mating-based breeding programs (NM), incomplete and complete pedigree.

Strategy ¹	% of genotyped ♀	% of NM ² ♀ with sire information	Annual genetic gain (σ_g/y)			Inbreeding rate ($\Delta F/y$)
			Mean (n = 30)	SD (n = 30)	%	Mean (n = 30)
CS	0	0	0.081	0.006	100	
CS	0	25	0.083	0.006	102	
CS	0	50	0.086	0.007	106	
CS	0	75	0.099	0.008	121	
CS	0	100	0.116	0.010	142	0.001
PAR_AS	25	25	0.092	0.010	113	
PAR_AS	50	50	0.099	0.009	122	
PAR_AS	75	75	0.107	0.006	131	
PAR_AS	100	100	0.115	0.007	141	0.001
GS_M	0	0	0.089	0.006	110	
GS_M	0	25	0.106	0.008	130	
GS_M	0	50	0.115	0.007	142	
GS_M	0	75	0.121	0.009	149	
GS_M	0	100	0.133	0.009	163	0.001
GS_MF	25	25	0.157	0.010	193	
GS_MF	50	50	0.158	0.008	194	
GS_MF	75	75	0.153	0.009	187	
GS_MF	100	100	0.161	0.008	198	0.001

¹ CS = conventional strategy; PAR_AS = parentage assignment, the sires of a proportion of females born from multi-sire matings are assigned. GS_M: genomic selection based on a male reference population (all sires); GS_MF: genomic selection based on a male and female reference population (all sires and a proportion of dams).

² NM ♀ = dams born from natural mating.

Table 2

Annual genetic gain and inbreeding rates according to the genomic strategy for meat sheep. Natural mating and AI-based breeding programs (NM + AI), dams with incomplete sire information.

Strategy ¹	% AI ²	Nb of AI ² ♂ selected per year	% of genotyped ♀	% of NM ♀ ³ with sire information	Annual genetic gain (σ_g/y)				Inbreeding rate ($\Delta F/y$)
					Mean (n = 30)	SD (n = 30)	%	%	Mean (n = 30)
CS	10	8	0	0	0.118	0.012	100		
CS	10	8	0	25	0.115	0.011	98		
PAR_AS	10	8	25	25	0.124	0.012	105		
PAR_AS	10	8	50	50	0.130	0.012	110		
PAR_AS	10	8	100	100	0.142	0.014	121		0.002
GS_M	10	8	0	0	0.111	0.014	94		
GS_M	10	8	0	25	0.131	0.009	111		
GS_MF	10	8	25	25	0.183	0.012	156		
GS_MF	10	8	50	50	0.180	0.011	153		
GS_MF	10	8	100	100	0.181	0.010	154		0.001
CS	20	8	0	0	0.138	0.017	117	100	
CS	20	8	0	25	0.144	0.017	123	105	
PAR_AS	20	8	25	25	0.144	0.017	123	105	
PAR_AS	20	8	50	50	0.144	0.013	122	104	
PAR_AS	20	8	100	100	0.152	0.016	129	110	0.003
GS_M	20	8	0	0	0.129	0.014	110	93	
GS_M	20	8	0	25	0.159	0.018	135	115	
GS_MF	20	8	25	25	0.217	0.019	185	157	
GS_MF	20	8	50	50	0.215	0.017	183	156	
GS_MF	20	8	100	100	0.213	0.021	181	155	0.002

¹ CS = conventional strategy; PAR_AS = parentage assignment, the sires of a proportion of females born from multi-sire matings are assigned. GS_M: genomic selection based on a male reference population (all sires); GS_MF: genomic selection based on a male and female reference population (all sires and a proportion of dams).

² AI = Artificial Insemination.

³ NM ♀ = dams born from natural mating.

at random with a maximum number of matings per AI sire dependent on his age. Natural mating sires were used and replaced as in NM. Sire information was always known for lambs born from AI but not always for lambs born from natural mating. For the conventional selection strategy with missing sire information, four NM + AI breeding programs were simulated according to the proportion of inseminated ewes (10, 20 % per year) and the proportion of dams born from natural mating whose sire information was known (0, 25 %). For higher AI levels, only two NM + AI breeding programs were simulated according to the proportion of inseminated ewes (30 or 60 % per year).

Animal insemination-based breeding program with progeny testing

In NM + AI+PT, 1-year-old male candidates were selected as in NM and NM + AI and males for AI were selected as in NM + AI. In their second year, the PT of young AI males was set up via their mating with randomly selected, non-elite dams in the nucleus. In their fourth year, the first records of their daughters were available and thus they were candidates to be selected as elite AI males. Elite AI males were selected among

these candidates and the elite AI males of the previous year. An elite AI male could be used up to four times. Unselected AI males (4 years old and older) were culled. Dams were mated (AI or NM) at most once a year. Dams were ranked according to their EBVs: the best were randomly mated to elite sires and the following dams were randomly mated to young AI males. Other dams and dams that did not conceive to AI were then randomly mated to natural mating males present in their flock. For the conventional selection strategy, three NM + AI+PT breeding programs were simulated according to the proportion of inseminated ewes (30, 60, or 80 % per year) and one breeding program was simulated with missing sire information (AI = 30 % and proportion of dams born from natural mating with sire information = 25 %).

Parentage assignment strategy

For populations with dams with missing sire information, we assessed the usefulness of using parentage assignment based on molecular information (PAR_AS strategy). In the basic situation, the sire was

Table 3

Annual genetic gain and inbreeding rates according to the genomic strategy for meat sheep. Natural mating and AI-based breeding programs (NM + AI), dams with complete sire information.

Strategy ¹	% AI ²	Nb of AI ² ♂ selected per year	% of genotyped ♀	% of NM ♀ ³ with sire information	Annual genetic gain (σ_g/y)				Inbreeding rate ($\Delta F/y$)
					Mean (n = 30)	SD (n = 30)	%	%	Mean (n = 30)
CS	30	8	0	100	0.165	0.022	100		0.004
GS_M	30	8	0	100	0.191	0.020	116		0.003
GS_MF	30	8	25	100	0.230	0.021	140		0.003
GS_MF	30	8	50	100	0.233	0.019	141		0.003
GS_MF	30	8	100	100	0.243	0.018	147		0.003
CS	60	16	0	100	0.158	0.020	96	100	0.002
GS_M	60	16	0	100	0.188	0.016	114	119	0.002
GS_MF	60	16	25	100	0.230	0.014	139	145	0.002
GS_MF	60	16	50	100	0.231	0.015	140	146	0.002
GS_MF	60	16	100	100	0.238	0.015	144	150	0.002

¹ CS = conventional strategy; GS_M: genomic selection based on a male reference population (all sires); GS_MF: genomic selection based on a male and female reference population (all sires and a proportion of dams).

² AI = Artificial Insemination.

³ NM ♀ = dams born from natural mating.

Table 4

Annual genetic gain and inbreeding rates according to the genomic strategy for meat sheep. Natural mating, AI, and progeny testing-based breeding programs (NM + AI+PT), dams with incomplete sire information.

Strategy ¹	% AI ²	Nb of AI ² ♂ selected per year	% of genotyped ♀	% of NM ♀ ³ with sire information	Annual genetic gain (σ_g/y)			Inbreeding rate ($\Delta F/y$)
					Mean (n = 30)	SD (n = 30)	%	Mean (n = 30)
CS	30	10;10	0	25	0.170	0.018	100	
CS	30	10;10	0	100	0.175	0.016	103	
PAR_AS	30	10;10	25	25	0.167	0.018	98	
PAR_AS	30	10;10	50	50	0.171	0.018	100	
PAR_AS	30	10;10	100	100	0.176	0.015	103	0.005
GS_M	30	10	0	25	0.164	0.022	97	
GS_M	30	10	0	100	0.191	0.016	112	
GS_MF	30	10	25	25	0.224	0.018	132	
GS_MF	30	10	50	50	0.232	0.019	136	
GS_MF	30	10	100	100	0.238	0.018	140	0.003

¹ CS = conventional strategy; PAR_AS = parentage assignment, the sires of a proportion of females born from multi-sire matings are assigned. GS_M: genomic selection based on a male reference population (all sires); GS_MF: genomic selection based on a male and female reference population (all sires and a proportion of dams).

² AI = Artificial Insemination. For the CS and PAR strategies, the numbers of young and proven rams are both given.

³ NM ♀ = dams born from natural mating.

unknown for all lambs born from natural mating. Sire information was determined for all 1-year-old males after selection and we tested various proportions of sire assignment (25, 50, 75, or 100 %) for ewe-lambs replacing culled dams. Parentage assignment was based on low-density genotypes (1000 SNPs; genotyping error = 0.5 %) using a likelihood method derived from Tortereau et al. (2017). The quality of the assignment was checked and no errors were observed with this number of markers. In this strategy, the genomic information is not used to predict breeding values and EBVs were computed based on a BLUP animal model.

Genomic selection strategies

For these strategies, as a single step GBLUP was used, all individuals (sires, dams, and candidates) had GEBVs. All animals would end up with genomically enhanced breeding values.

Male reference population

This strategy (GS_M) is based on a male reference population. When a breeding program switches to this GS strategy, all sires (AI and NM) used over the last 10 years are genotyped to initiate the reference population. The following years, male candidates are genotyped in their first year of age and male replacement (both for AI and natural mating) was

based on their GEBVs. Newly selected males entered the reference population. AI males were mated to the dams with the highest GEBVs for 2 years at most and then culled.

Male and female reference population

This strategy (GS_MF) is identical to the previous one for male genotypes, but female genotypes were also considered. When a breeding program switched to using the GS_MF strategy, a proportion (25, 50, or 100 %) of live dams were randomly genotyped. The following years, the same proportion of ewe-lamb replacements was randomly genotyped.

Annual genetic gain and inbreeding rate assessment

The annual genetic gain (resp. inbreeding rate) per replicate was computed as the regression slope of the average true breeding value (resp. pedigree inbreeding coefficient) of first parity dams over a time interval between years 10 and 25. Gains are expressed in genetic standard deviation of the selected trait per year (σ_g/y). Rather than expressing the inbreeding rate per generation which depends on the generation interval, we found that expressing the inbreeding rate per year makes it easier to compare the results. Inbreeding rates were only computed for strategies where the sire information of dams was completely known

Table 5

Annual genetic gain and inbreeding rates according to the genomic strategy for meat sheep. Natural mating, AI, and progeny testing-based breeding programs (NM + AI+PT), dams with complete sire information.

Strategy ¹	% AI ²	Nb of AI ² ♂ selected per year	% of genotyped ♀	% of NM ♀ ³ with sire information	Annual genetic gain (σ_g/y)			Inbreeding rate ($\Delta F/y$)
					Mean (n = 30)	SD (n = 30)	%	Mean (n = 30)
CS	30	10;10	0	100	0.175	0.016	100	0.005
GS_M	30	10	0	100	0.191	0.016	109	0.003
GS_MF	30	10	25	100	0.227	0.014	130	0.003
GS_MF	30	10	50	100	0.235	0.022	134	0.003
GS_MF	30	10	100	100	0.238	0.018	136	0.003
CS	60	20;10	0	100	0.189	0.017	108	0.006
GS_M	60	15	0	100	0.190	0.015	108	0.003
GS_MF	60	15	25	100	0.238	0.017	136	0.003
GS_MF	60	15	50	100	0.240	0.014	137	0.003
GS_MF	60	15	100	100	0.241	0.013	138	0.003
CS	80	26;10	0	100	0.197	0.020	112	0.005
GS_M	80	18	0	100	0.189	0.017	108	0.003
GS_MF	80	18	25	100	0.226	0.014	129	0.003
GS_MF	80	18	50	100	0.233	0.014	133	0.002
GS_MF	80	18	100	100	0.238	0.011	136	0.002

¹ CS = conventional strategy; GS_M: genomic selection based on a male reference population (all sires); GS_MF: genomic selection based on a male and female reference population (all sires and a proportion of dams).

² AI = Artificial Insemination. For the CS strategy, the numbers of young and proven rams are both given.

³ NM ♀ = dams born from natural mating.

and expressed per year. Reported values for gains and inbreeding are averages of 30 replicates.

Results

Natural mating-based breeding programs

The annual genetic gains for NM breeding programs are reported in [Table 1](#) according to the strategy used and the proportion of dams with sire information. For the CS, for which no genomic information was used, the higher the proportion of sire information known, and the higher the annual genetic gain. The increase in gain as a function of the proportion of sire information was not linear and was greater as the pedigree completeness tended to higher values. Moving from the case where none of the dams born from natural mating had a known sire to the case where all those dams had their sire known resulted in +42 % more gain. Using parentage assignment (PAR_AS) provided a higher genetic gain compared with CS for the same proportion of dams with sire information (except for complete pedigrees that gave the same gain) because in the PAR_AS strategy the sires of all 1-year-old males (i.e. candidates) were assigned. With PAR_AS, the increase in gain as a function of the proportion of sire information was linear.

The GS strategy based on a male reference population (GS_M) gave a higher gain than CS for the same proportion of sire information. The annual genetic gain of a GS strategy based on a male and female reference population (GS_MF) was practically independent of the proportion of genotyped dams (0.153–0.161 σ_g/y), and higher than the gain obtained with GS_M strategies (21 % to 48 % depending on the proportion of dams born from natural mating with sire information).

Artificial insemination-based breeding programs without progeny testing

The annual genetic gains for NM + AI programs are reported in [Table 2](#) according to the genomic strategy used for dams with missing sire information. Two “low” levels of AI (% of ewes inseminated per year) were considered: 10 and 20 %. Using parentage assignment had a greater effect when the AI level was low. Compared with CS in which females born from natural mating had no sire information, PAR_AS provided an additional gain, respectively, of +21 % and +10 % for AI levels of 10 % and 20 %.

GS_M gave a lower gain than CS strategies when females born from natural mating had no sire information regardless of the AI level (–6 %, AI = 10 %; –7 %, AI = 20 %). When at least 25 % of females born from natural mating had sire information, GS_M gave a higher gain than CS whatever the AI level (+11 %, AI = 10 %; +15 %, AI = 20 %). Adding female genotypes in the reference population was always beneficial: GS_MF gave similar gains regardless of the proportion of genotyped females (0.180–0.183 σ_g/y , AI = 10 %; 0.213–0.217 σ_g/y , AI = 20 %).

The gains obtained for higher AI levels (30 % and 60 %) are reported in [Table 3](#). In these designs, most of ewe-lamb replacements were born from AI and dam sire information was known. Thus, PAR_AS scenarios were useless and were not considered. Regardless of the AI level, the strategies were ranked as in the pure natural mating programs (CS < GS_M < GS_MF). The benefit of AI depended on the strategy: moving from NM to NM + AI (60 %) gave, respectively, +36 % and +48 % for CS and GS_MF strategies.

Artificial insemination-based breeding programs with progeny testing

The annual genetic gains of NM + AI+PT breeding programs are reported in [Table 4](#) according to the strategy used and the proportion of dams with sire information. Only one level of AI (30 %) was considered because a certain level of AI is needed to ensure correct PT, and higher AI levels would result in complete information of dam sires (all replacement females born from AI). Using PAR_AS to recover missing sires

had very little effect regardless of the completeness of dam sire information (25, 50, or 100 %): from –2 % to +3 % compared with CS.

GS_M gave a lower gain (–3 %) than CS when part of the dams' sire information was missing but a slightly higher gain of +9 % when all dam sires were known (0.191 vs 0.175 σ_g/y). GS_MF provided a much higher gain (+32 to +40 %) than CS, but this gain increased only slightly (0.224 to 0.238 σ_g/y) when the percentage of genotyped females shifted from 25 % to 100 %.

The gains obtained when sire information was complete are reported in [Table 5](#) for three levels of AI (30, 60, and 80 %). Compared with CS, GS_M gave a higher gain at AI = 30 % (+9 %), a similar gain at AI = 60 % and a lower gain at AI = 80 % (–4 %). Regardless of the AI level, the gains obtained with GS_MF increased slightly as the percentage of genotyped females shifted from 25 % to 100 %. GS_MF always gave higher gains than CS but the increase in gain depended on the AI level: with 25 % of genotyped females, GS_MF gave +30 % (AI = 30 %), +26 % (AI = 60 %) and +15 % (AI = 80 %) gain, respectively, compared with CS.

Discussion

In this study, we assessed the benefits of parentage assignment and GS strategies for a set of meat sheep breeding programs meant to reflect a diversity regarding the use of AI and the pedigree completeness. Using a stochastic model, we derived the annual genetic gain of a population under selection with various designs (NM, NM + AI, NM + AI+PT), proportions of known sire information, proportions of inseminated ewes (AI designs only), and proportions of genotyped females for GS strategies.

Benefits of parentage assignment

Parentage assignment was largely beneficial for NM as the increase in genetic gain, compared to a situation where none of the females had a known sire, reached up to +40 %. The benefits were less important for NM + AI (+21 %, %AI = 10 %; +10 %, %AI = 20 %) and low for NM + AI+PT (+3 %) designs. These results confirm the relative advantage of PAR_AS strategies reported in [Raoul et al. \(2016\)](#), depending on the breeding program design. The differences in gain between complete and missing sire information designs for NM and NM + AI are in line with those obtained by [Raoul and Elsen \(2019\)](#) who used a stochastic model but did not model the genomes.

Benefit of a genomic selection strategy based on a male reference population

Switching from CS to GS_M was not always beneficial. The benefits depended on both the proportion of dams with sire information and the design.

For NM designs, GS_M gave a +10 % increase in the gain compared with CS when no sire information was available for dams, and a +15 % to +27 % increase when a proportion of the dams (100 to 25 %) had sire information. When they have known daughters, the estimated breeding values of sires included in the reference population would be more accurate, thus explaining why GS is more favorable.

For NM + AI designs, the benefit depended on the sire information completeness. When at least 25 % of dams born from natural mating had sire information, GS_M was always beneficial regardless of the AI level: from +10 % (AI = 20 %) to +19 % (AI = 60 %). When none of the dams born from natural mating had sire information, GS_M gave a lower gain than CS (–6 %). This means that a reference population that includes natural mating sires with no progeny records (inaccurate information) and AI sires (more accurate information) decreases the accuracy of genomic prediction.

For NM + AI+PT designs, the benefit depended on both the proportion of known sires and the level of AI. When only 25 % of dams born

from natural mating had sire information, GS_M gave a lower gain than CS (−4%). When complete sire information was available for the dams, the benefit of GS_M was positive but low, +9%, for the lower AI level (30%), null for the intermediary AI level (60%), and negative, −4%, for the higher AI level (80%). This means that for lower AI rates, the number of inseminated ewes was too low to benefit from the increase in accuracy provided by PT. In Raoul et al. (2017), in which only the NM + AI+PT design was modeled with complete pedigree information and 50% of ewes were inseminated, GS_M gave +26% increase in gain compared with CS. Contrary to Raoul et al. (2017), the number of AI sires used per year in this study was constant across strategies to take into account constraints due to AI seasonality and the use of fresh semen.

For NM + AI and NM + AI+PT designs, when all females had sire information, the genetic gain nearly reached a plateau, 0.188–0.191 σ_g/y , regardless of the AI level.

Benefit of genomic selection strategy based on a male and female reference population

Regardless the design, the proportion of dams born from natural mating with a sire information, and the AI level, GS_MF was always favorable. In general, the genetic gains expected with 25% of genotyped females were close to those expected with 100% of genotyped females. Compared to CS, the increase in gain when implementing a GS_MF scenario was high to very high for NM (36% to 89%) and NM + AI (36 to 60%). For NM + AI+PT, the increase in gain was also high, 30–36% for AI = 30% and less important as the AI level was high, +26–28% for AI = 60% and +15–21% for AI = 80%.

In these simulations, females to be genotyped were randomly chosen. Different sampling strategies, based on targeted genotyping of female categories as high genetic value females or less related to the male population, might be assessed but previous studies (e.g. Plieschke et al., 2016) show that random sampling gives higher genetic gains.

Comparison across designs

Goddard (1987), Wray and Simm (1990), and Quinton et al. (1992) suggested that selection strategies should be compared at similar levels of inbreeding. The optimum, if defined as the maximum genetic gain of a design for a given inbreeding level, could be determined among a range of values for the main parameters. Nevertheless, applying such an approach to stochastic simulations would be very time-consuming.

For NM designs, the different strategies (CS, GS_M, and GS_MF) were assessed with the same demographic parameters and decision variable selection. The inbreeding levels were low (0.0001 point per year) and similar for all strategies.

For NM + AI designs, the number of AI males used per year has a strong effect on both the genetic gain and inbreeding (Raoul and Elsen, 2019). In the present study, the number of AI males used per year was constant for a given level of AI and across strategies. The values were chosen to reflect real French meat sheep breeding programs. Inbreeding levels, comprised between 0.0002 points per year and 0.0004 points per year, were generally slightly higher for CS than for GS_M and GS_MF but similar for all strategies for a given AI level. As inbreeding levels were different according to the level of AI, caution should be exercised when making comparisons. However, even if input parameters are not identical, the comparison of CS strategies shows that for NM + AI designs, shifting to GS is somewhat more favorable than shifting to NM + AI+PT.

For NM + AI+PT designs, shifting from a conventional selection strategy to GS_M or GS_MF implies substantial changes in terms of the management of male animals. AI males are used younger in GS than in CS, and the variability of the number of doses per AI male is expected to be higher in CS (some AI males are culled after PT and some are

much used as elite reproducers) than in GS. Even if the optimal number of AI sires, for a given AI level, is expected to be lower in GS than in CS, we opted to compare strategies with the same number of AI sires used per year. As in Raoul et al. (2017), GS_M and GS_MF led to lesser increase in the inbreeding rate than CS. We assume that comparing strategies at the same level of inbreeding would have favored genomic strategies.

Benefit of genomic selection for meat traits

In the present study, we only considered the selection of a maternal trait. In France, both meat and maternal traits are selected in meat sheep populations. Each trait is selected separately and no multi-trait index is used. In the present study, we assumed that the selection intensities on meat traits were equal to the currently observed intensities and remained constant across strategies. Selection on meat traits was taken into account as random losses among candidates. We therefore expect that the response to selection on a maternal trait will not be affected by meat trait selection as long as there is no negative genetic correlation between maternal and meat traits. In the GS strategies we modelled, meat phenotypes and genotypes would be available for 1-year-old male candidates. This could result in a more accurate estimation of breeding values for meat traits and enable more balanced selection across maternal and meat traits in the objective. The optimal use of this genomic information for meat traits needs to be considered in further studies.

Practical implementation of GS strategies, economic considerations

In this paper, we show that switching from a CS to a GS strategy (at least to GS_MF strategies) can generate faster genetic progress for all French meat sheep populations. However, genotyping costs have to be considered and a fair comparison would require to assess the different strategies at a similar cost or to take into account costs and revenues associated with each strategy. For NM and NM + AI designs, moving to a GS strategy would not modify sire management practices, so the cost-effectiveness of GS depends on the balance between additional genotyping costs and additional genetic gain. For each breed, the economic benefit of GS depends on how the added economic value linked to the additional genetic gain both within and outside of the nucleus offsets the additional costs of breeders. For NM + AI+PT, switching to a GS strategy would change how AI sires are managed and would lower the related costs. NM + AI+PT designs are then more likely to be able to compensate the additional genotyping costs.

Approximately two times more candidates were genotyped than the number of males selected for natural mating and AI. To implement the GS_MF strategy, at least 25% of dams have to be genotyped. To reduce costs, candidates (and dams) can be genotyped using cheaper low density SNP chips and their 50 K genotypes imputed. Many studies have addressed this possibility in dairy cattle (e.g. Zhang and Druet, 2010), sheep (e.g. Hayes et al., 2012), and other species (e.g. Cleveland and Hickey, 2013). Our simulation (data not shown) indicated that the imputation step has no effect on the genetic gain evaluated in this study as long as sires and candidates (dams) had, respectively, 50 K and at least 3 K SNP genotypes. In some breeds, genomic tests such as parentage certification and parentage assignment (Tortereau et al., 2017), scrapie resistance genetic (Palhière et al., 2004), or hyper-ovulation polymorphism (Martin et al., 2014) are already performed. Additional genotyping costs will be breed-dependent and will decrease if the design of low density SNP chip already includes some of the SNPs required for genomic tests.

Conclusion

In this study, using a stochastic model, we assessed the benefit of GS for a variety of breeding programs that encompass all current French

meat sheep populations. For the current designs with no AI or no PT of AI sires, the benefit of GS based on a male reference population was limited when sire information is missing for dams. For current designs that include PT of AI sires, GS based on a male reference population, and hence a discontinuation of PT, was detrimental compared with conventional selection designs when the AI level was high and favorable when the AI level was low. Regardless of the design, GS based on a male and female reference population was favorable and genotyping 25 % of the females in the nucleus resulted in a significant increase in gain compared with conventional designs.

These results suggest to test GS for breeds that currently implement a PT of AI sires. The reference population would be based on nucleus sires and a part of nucleus dams if dam genotypes are currently available. For breeds with no PT, GS involves additional costs that limit its implementation.

Supplementary materials

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.animal.2020.100040>

Ethics approval

None.

Data and model availability statement

The model was not deposited in an official repository. The Fortran code is available upon request.

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Author Contributions

JR and JME designed the study. JR wrote the simulation program, performed analysis and drafted the manuscript. JR and JME contributed in interpreting the results and revising the manuscript. All authors read and approved the final manuscript.

Declaration of interest

The authors declare no conflict of interest.

Financial support statement

This project has received funding from the European Union's Horizon 2020 research and innovation programme under the Grant Agreement n°772787.

Acknowledgements

We gratefully acknowledge Misztal et al. for making the Blupf90 software available.

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