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Evaluating Selection Strategies Based on Inbreeding Load via Simulation

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ABSTRACT

Inbreeding load is the fraction of the mutation load that is due to recessive action of mutations. This load is only expressed in individual's inbred offspring. As such, inbreeding load contributes to genetic heterogeneity among individuals and can thus be used as a criterion of selection. Future parents could be selected based on their estimated breeding values and their estimated inbreeding load. Here, we evaluated the effectiveness of selection strategies involving inbreeding load in a dairy sheep breeding scheme. We evaluated seven strategies with a stochastic simulation across 15 generations of genetic evaluation and selection. The strategies differed in the criteria of selection (only estimated breeding values, only estimated inbreeding load, both or random) and mate strategies minimising inbreeding load, adjusting estimated breeding values by the expected future inbreeding or random. The strategies were compared in terms of genetic gain, pedigree-based inbreeding coefficients, rate of inbreeding, effective population size, inbreeding depression estimates, and accuracy of selection. Results showed that among the seven strategies, there was no significant difference between the five in which selection was based on estimated breeding values over the 15 years of the simulated dairy sheep breeding scheme. As expected, selection only on the estimated inbreeding load and the random selection and random mating strategy had significantly lower genetic gain than the five strategies in which selection was based on estimated breeding values. To conclude, selecting animals using estimated inbreeding load is feasible. However, the magnitude of inbreeding load effects and its accuracy did not show a clear practical interest. Furthermore, the benefit of using inbreeding load in mate allocation strategies was negligible.

1 | Introduction

Inbreeding load (IL) is the fraction of the mutation load that is due to recessive action of mutations. Individual's IL is hidden in heterozygous condition and can be hence only expressed in their inbred offspring. IL can have a favourable or unfavourable effect on phenotypes of interest, with a positive IL indicating that inbreeding generated by an individual improves the performance of their inbred descendants (Varona et al. 2019). Additionally, IL is a heritable and additive component of each trait (Varona et al. 2019), and the amount of IL will depend on the direction of dominance for loci affecting a trait (Antonios et al. 2025).

Genetic parameters for IL were estimated for growth traits in rabbits (Casellas 2018), pigs (Casellas et al. 2008), and beef cattle (Varona et al. 2019; Hervás-Rivero et al. 2026); for morphological traits in horses (Poyato-Bonilla et al. 2020); and for fertility traits (Perdomo-González et al. 2021) in horses and dairy cattle (Martinez-Castillero et al. 2021). Recently, Antonios et al. (2025) estimated variances due to IL for milk yield in Manech Tête Noire (MTN) and Manech Tête Rousse (MTR) breeds, showing variability significantly different from zero in these breeds.

As demonstrated by Antonios et al. (2025) in their theoretical framework of the single-locus IL concept, the genetic correlation

between the breeding value of a trait and its IL is expected to be negative. In Pirenaica beef cattle it was estimated −0.4 (Varona et al. 2019), while in MTN and MTR sheep breeds, this correlation was shown to be close to zero (~−0.1) for milk yield (Antonios et al. 2025). Such negative correlations indicate that animals with high breeding values contribute to inbreeding depression in their inbred descendants (Varona et al. 2019). However, a small negative estimate (~−0.1) of this correlation in Antonios et al. (2025) suggests that selection for milk yield will not cause a large increase in inbreeding depression in milk yield in inbred animals. For example, by selecting individuals on estimated IL (EIL) for milk yield we could select against recessive alleles that reduce the milk yield in homozygotes. Another possibility could be to use EIL for avoiding undesirable matings. Mate allocation has been used in animal breeding with different purposes, for instance, for exploiting dominance (Toro and Varona 2010; González-Diéguez et al. 2020) or managing genetic defects (Bengtsson et al. 2022). To our knowledge, EIL has not yet been used as a criterion in mate allocation. Thus, matings of individuals with favourable IL for the traits of interest could be prioritised. While matings of individuals with unfavourable IL can reduce performance in inbred offspring, such matings could be avoided, assuming IL is due to the same common ancestor. In this context, there are no studies that explore the possible benefits of involving IL in a selection strategy.

The aim of this study was to evaluate the effectiveness of using the IL for a single trait (milk yield) as a selection criterion in a dairy sheep breeding scheme via stochastic simulations. We deployed seven strategies that differed in the selection criteria: (i) selection only on EBVs, (ii) selection only on EILs, (iii) two selection strategies based on both EBVs and EILs, (iv) selection on both EBVs and EILs coupled with mate allocation, (v) adjusting EBVs by the expected future inbreeding (EFI), and (vi) random selection and random mating strategy (RAND). The strategies were compared in terms of genetic gain, pedigree-based inbreeding coefficients, rate of inbreeding, effective population size, inbreeding depression estimates, and the accuracy of selection.

2 | Materials and Methods

In this study, we used stochastic simulations to evaluate the impact of using IL as a selection criterion on genetic gain, prediction accuracy, and inbreeding parameters in dairy sheep breeding over 15 years. We evaluated seven different strategies that differed in the selection criteria. This section is divided into two parts. The first part describes the simulation of the founder population, and the second part describes the simulation of the breeding scheme and strategies. We provide the complete source code for the simulation at https://github.com/SimonaAntonios/santonios_sheep_idl.

2.1 | Simulation of the Founder Population

We used AlphaSimR (Gaynor et al. 2021) to simulate a realistic dairy sheep breeding scheme, driven by a set of parameters mirroring a French dairy sheep breeding programme.

2.1.1 | Founder Genomes

We used the Markovian coalescent simulator (MaCS; Chen et al. 2009; Gaynor et al. 2021) within the AlphaSimR framework to simulate sheep founder genomes by using recombination rate of 1.5×10^{-8} (Petit et al. 2017) and a mutation rate of 1.5×10^{-8} (Lv et al. 2021). We simulated 26 autosomal chromosomes, each with 0.95×10^{8} base pairs and captured 4000 segregation sites. For simplicity, we assumed that all the chromosomes had the same size. This coalescent simulation mimicked sheep demographic history, that includes a decrease of effective population size (*Ne*) from 7500 at around 10,000 generations ago to the present-day *Ne* of 150 (Rodríguez-Ramilo et al. 2019). Successive reductions of *Ne* were used to reflect early domestication, breed formation, and artificial selection.

2.1.2 | Founder Population

Subsequently, we initiated a founder population of around 62K animals by randomly allocating founder genomes to animals. Founder animals were assigned to different categories (sires of sires, sires of dams, dams of sires, dams of dams, testing sires, natural mating sires, and lambs) to initiate a dairy sheep breeding scheme. We assigned the animals to 237 flocks with a flock size of 320 ± 129 animals, which was constant throughout the simulation.

2.1.3 | Trait Simulation

We simulated a trait mimicking milk yield controlled by 239 additive and dominance quantitative trait loci (QTLs) for the entire genome chosen at random. For practical reasons, we assumed this number of identified and mapped QTLs, obtained from the Animal QTL Database (https://www.animalgenome.org/QTLdb, accessed on 23 April 2023), although the number of truly underlying regions/QTLs is likely to be far higher. The trait was simulated with a heritability of 0.33, an overall population mean of 200 L of milk yield per lactation, and other parameters derived from our early study, such as the additive genetic variance, dominance deviation variance and permanent environment variance as well as flock effect (Varona, Legarra, et al. 2022; Antonios et al. 2025). Individual genetic values for milk yield were simulated by summing the genetic effects at the 239 QTL within AlphaSimR. The additive QTL effects (a) were sampled from a normal distribution with mean of zero and scaled to obtain an additive genetic (breeding value) variance of $\sigma^2_u = 1200$ in the founder population. The dominance QTL effects (d) were generated by multiplying the absolute value of the a with the QTL dominance deviations (δ). Dominance deviations themselves were sampled from a normal distribution with a mean (μ_δ) of 0.48 and variance (σ^2_δ) of 0.06. The values for the μ_δ and σ^2_δ were chosen using altAddTraitAD function in the AlphaSimR package, to generate a dominance variance equal to $0.1\sigma^2_u$ following Aliloo et al. (2017). The IL was not directly simulated, but emerged from the dominance QTL effects.

2.1.4 | Phenotypes

We generated the milk yield phenotypic values only for females. Phenotypic values were generated by summing the genetic value, fixed effects, and additional random effects. The fixed effects included lactation means of 209, 213, 207, and 180 L respectively for the 1st, 2nd, 3rd and 4th lactation, flock, year, and flock-year, sampled from an independent normal distribution $N(0, \sigma_x^2)$, with corresponding variances σ_x^2 obtained from real data respectively as 1200, 1000, and 1000. The random effects were permanent environmental effect, $p \sim N(0, \sigma_p^2)$, and random residual effect $e \sim N(0, \sigma_e^2)$. Values for permanent environmental variance $(\sigma_p^2 = 400)$ and residual variance $(\sigma_e^2 = 1500)$ were obtained from our early study (Antonios et al. 2025).

2.2 | Simulation of the Breeding Scheme

After simulating the founder population, a dairy sheep breeding scheme was initiated and ran for 10 years of conventional pedigree-based EBV selection (the burn-in phase), followed by 15 additional future years of specific strategies (described in the following part). Both the burn-in and the strategies phase were replicated 10 times. The overview of the breeding scheme is presented in Figure 1, with further details given in Figure 2.

At the end of the 25 years, the simulated population included ~483K animals (~420K of them were females) with overlapping generations, mimicking a real dairy sheep breeding scheme.

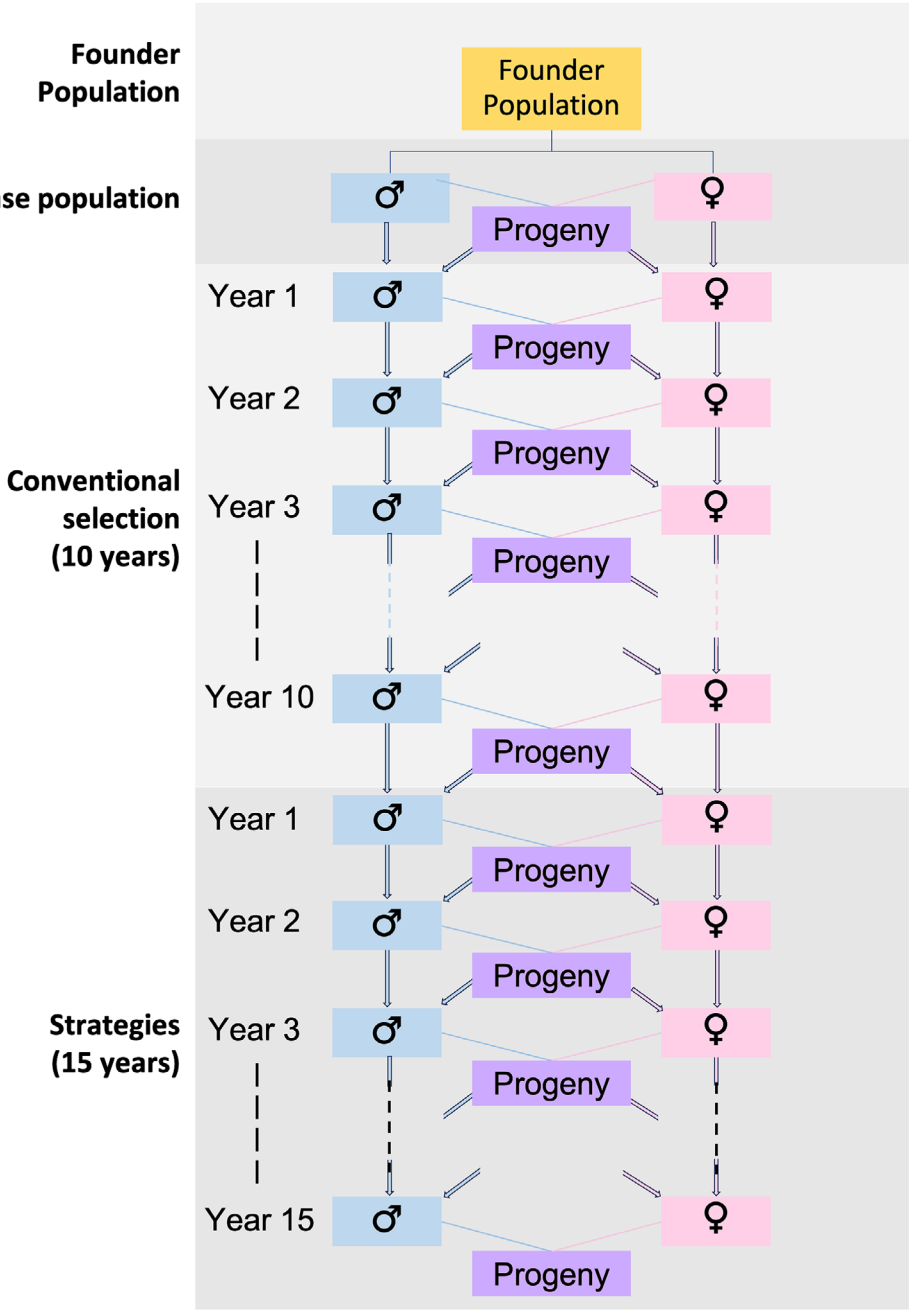

FIGURE 1 | Schematic representation of the whole simulated dairy sheep breeding scheme. Every year of this breeding scheme (Figure 1) is presented in Figure 2. [Colour figure can be viewed at wileyonlinelibrary.com]

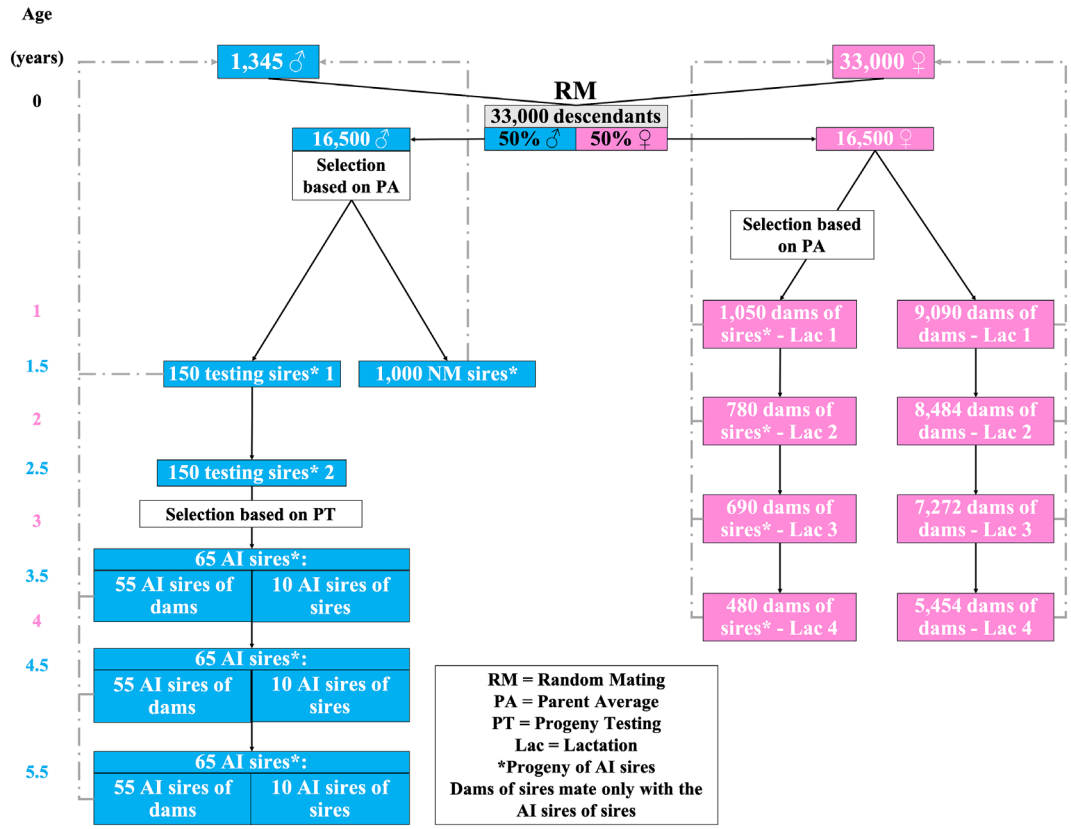

FIGURE 2 | Representation of each year in the simulated sheep breeding scheme. The dashed grey arrows represent the individuals that are participating in mating, the plain black arrows represent selection decisions, and the pink is for females and the blue is for males. [Colour figure can be viewed at wileyonlinelibrary.com]

2.2.1 | Conventional Pedigree-Based EBV Selection (Burn-In)

The aim of the burn-in phase was to provide a common starting point for the future strategies phase and to build up the linkage disequilibrium (LD) due to past selection in the population. In the burn-in phase, selection was based on pedigree-based EBV. We avoided parent-offspring mating and mating between siblings.

Each year, we generated 33K lambs, which mimicked the number of lambs that survive in the real population after lambing, thus accounting for the stillbirths and early deaths. Matings between elite sires (30) and elite dams (3K) produced around 1.5K male lambs. From these, we selected the best 150 males, based on the estimated parent average (EPA), as testing sires to enter the artificial insemination (AI) center in their first year of age. Among the remaining lambs, we selected the best 1K males, also based on their EPA, for natural matings (NM). Testing sires were mated with dams of dams, with each testing sire contributing 30 offspring (Figure 2). After obtaining their daughters phenotypes we selected AI sires at 2.5 years of age based on their EBV. The best 10 testing sires were selected as sires of sires (elite sires) and the next best 55 testing sires as sires of dams. Each AI sire stayed in service for 3 years, so in total, the number of AI sires in each year was ~200. Each sire of sires contributed 144 offspring per year and each sire of dams contributed 33 offspring per year. There were 1K NM sires, which were replaced every year. Each NM sire contributed 19 offspring. These numbers of offspring per sire were based on the real breeding scheme survival rates that were equal to 0.75, a fertility of 0.6 in AI and 0.9 in NM, and a prolificacy of 1.6 in AI and 1.4 in NM (J.M. Astruc, Idele, personal communication).

Approximately 16K female lambs were produced from the matings, with around 7K from AI and around 9K from NM. Out of the female lambs from AI, 1K were selected based on their EPA to become dams of sires and were inseminated by the sires of sires. From the remaining ~15K female lambs, around 9K were randomly selected for either AI or NM. Both groups became dams in their first lactation, and they remained in the simulation for up to four lactations, one per year. This totalled about 33K active dams each year (Figure 2). The best 10% of the dams that were daughters of AI sires were selected as dams of sires (3K) based on their EBV and inseminated by the sires of sires. The rest of the dams were assigned as dams of dams (around 30K). Dams of dams were inseminated randomly by the sires of dams and the testing sires, while the NM sires were used for the other dams of dams (~19K). The replacement rate of the dams was set to around 23%. The simulated prolificacy rate per dam was equal to one, though the number of breeding animals reflected real reproductive parameters. Dams of sires were used in lactation 1 at 35%, 2 at 26%, 3 at 23%, and 4 at 18% (Figure 2). Dams of dams were used in lactation 1 at 30%, 2 at 28%, 3 at 24%, and 4 at 18% (Figure 2).

At the end of the burn-in, we calculated LD as the squared correlation coefficient (r^2) between all pairs of markers

(Hill 1974). The LD decay was measured for increasing distances between markers in cM by calculating the mean r^2 within each distance interval, assuming 1 cM = 1 Mbp. The resulting average LD over replicates was 0.08 ± 0.13 for a distance of < 5 cM, 0.31 ± 0.35 for a distance of < 0.1 cM, and 0.37 ± 0.38 for a distance of < 0.05 cM. These values were in agreement with those reported in Lacaune breed (Baloche et al. 2014) and in five other populations of domestic sheep (Meadows et al. 2008), indicating that the simulation resembled a realistic dairy sheep population.

2.2.2 | Selection Strategies

We evaluated seven different selection strategies that ran for 15 additional years after the burn-in, while the breeding scheme remained unchanged (Figure 2). All strategies used pedigree-based genetic evaluation for milk yield, but differed in the selection criterion (Figure 2): (i) selection based on EBV (EBV), (ii) selection based on EBV and EIL assuming an inbreeding of 1% where we multiplied the EIL of the individuals by 0.01 (EBV-EIL-01); (iii) selection based on EBV and EIL assuming an inbreeding of 10% where we multiplied the EIL of the individuals by 0.1 (EBV-EIL-10); (iv) selection based only on EIL (EIL); (v) selection based on EBV and mate allocation based on the total sum of individuals' common ancestors EIL (EBV-MA; details below); (vi) selection based on EBV adjusted by the expected future inbreeding (EBV-EFI; details below) (VanRaden and Smith 1999), and (vii) random selection and random mating between individuals (RAND). In EBV-EIL-01 and EBV-EIL-10 we respectively assumed an inbreeding of 1% and 10%.

In the EBV-MA strategy, we considered 30 sires of sires and 3K dams of sires as candidates for mating optimisation (90K possible matings), animals were selected based on their EBV in the same way as they were selected in the conventional selection strategy. Optimisation of matings was performed via linear programming (Jansen and Wilton 1985) using the R lpsolve package (Berkelaar et al. 2004). Three constraints were used in the optimisation: (i) each sire mates with 100 dams, (ii) each dam mates only once and gives birth to only one lamb, (iii) mating between parent and offspring as well as mating between siblings is not allowed. We prioritised matings between individuals with no common ancestors. For matings of individuals with common ancestors, we based our selection on the total sum of EIL value across their common ancestors, choosing individuals with the highest (positive) total sum of EIL. Note that we treated all EIL from common ancestors equally, applying no weighting for generational proximity (e.g., grandparents versus distant ancestors). The selection was made in descending order, starting from the highest total sum EIL. For instance, the linear programming function for selecting the highest sum of EIL_{ij} was defined as:

$$f_{\max}\left(EIL_{ij}\right) = \sum_{i=1}^{ns} \sum_{j=1}^{nd} EIL_{ij} \times \theta_{ij},$$

where θ_{ij} are binary decision variables, used to represent whether the mating between sire of sires i and dam of sires j is selected or not. A value of 1 indicates that the mating is selected, while a value of 0 indicates that it is not selected. Thereafter, the constrains for sire of sires i can be written as: $\theta_{i1} + \theta_{i2} + \theta_{i3} + \ \ldots \ + \theta_{i,ns} = 100$ ($i = 1, 2, \ \ldots \ , ns$), and for dam of sires j: $\theta_{1j} + \theta_{2j} + \theta_{3j} + \ \ldots \ + \theta_{j,nd} = 1$ ($j = 1, 2, \ \ldots \ , nd$), where ns and nd are the number of sires of sires (30) and dams of sires (3K), respectively.

In EBV-EFI strategy, all 150 testing sires were considered candidates and 10 bests were selected as an AI sire based on adjusted EBV. For each testing sire, we computed its average relationship with all the contemporary females (3K dams of sires) in order to obtain the EFI (expected future inbreeding) as half the average relationship of this male to the contemporary females. The goal of the EFI is to penalise males with high relatedness with their contemporary females. The calculations were performed using inbupgf90 software (Aguilar and Misztal 2008). The adjusted EBV (aEBV) was equal to $EBV + EFI * \hat{b}$, where $\hat{b}$ is the estimated inbreeding depression parameter per unit of inbreeding obtained using BLUPF90+ software, for each year of the simulation within each replicate.

2.2.3 | Genetic Evaluation Model

Breeding values for milk yield were estimated using single-trait animal model using BLUPF90+ (Lourenco et al. 2022) available at http://nce.ads.uga.edu/wiki/doku.php.

Pedigree-based EBV were obtained using the following model: $y = X\beta + fb + Z_u u + Z_p p + e$, where y is the vector of phenotypic records (milk yield), β is the vector of fixed effects (flock, year, flock-year, and rank of lactation), the term fb models inbreeding depression, where b is the inbreeding depression parameter per unit of inbreeding, and the covariate f is the vector of inbreeding coefficients, u is the vector of breeding values, p is vector of random permanent effects and e is the vector of residuals. The incidence matrices X, Z_u, and Z_p respectively relate records to fixed effects, breeding values, and permanent environmental effects.

In the strategies EBV-EIL-01, EBV-EIL-10, EIL, and EBV-MA, the model included an additional effect, i, the vector of IL. This model can be written as: $y = X\beta + fb + Z_u u + Z_u Ki + Z_p p + e$, where the matrix K is a lower triangular matrix, $K = T(I - P)$, where T contains the partial inbreeding coefficients of all individuals. Those partial inbreeding coefficients account for the identity-by-descent (IBD) contributions derived from the Mendelian decomposition of each individual's inbreeding coefficient. This decomposition of inbreeding splits inbreeding among founders and the Mendelian sampling of the non-founders (Caballero and Toro 2000). I is the identity matrix and the product $Z_u K$ links the phenotypes of animals (rows) to their ancestors (columns) giving rise to inbreeding. The matrix P has 0 on diagonal and 0.5 in row-column positions connecting an individual with its sire and dam. In this model, K is used to reformulate the individual recessive burden due to inbreeding in the individual into a linear model that uses the inbreeding load of its ancestors, and this is possible because the individual pedigree inbreeding can be decomposed as a sum over ancestors of partial inbreeding coefficients. Note that $\begin{pmatrix} u \\ i \end{pmatrix} \sim N\left(\begin{pmatrix} 0 \\ 0 \end{pmatrix}, G \otimes A\right)$; where A is the pedigree-based additive relationship matrix, and

$G = \begin{bmatrix} \sigma_u^2 & \sigma_{u,i} \\ \sigma_{u,i} & \sigma_i^2 \end{bmatrix}$ with σ_u^2 being the breeding value variance, σ_i^2 the IL variance, and $\sigma_{u,i}$ the covariance between breeding value and IL (see Antonios et al. 2025, for a detailed description of the model and inbreeding decomposition). This model gives individual predictions of the inbreeding load genetic effect. For an individual, this value must be understood as the effect expressed on the phenotype (milk yield) of an inbred descendant, with the inbreeding of this descendant coming from the individual under consideration (Antonios et al. 2025). Based on the previous work on French dairy sheep (Antonios et al. 2025), we assumed a low genetic correlation (−0.1) between the EBV and the EIL in the simulation.

The partial inbreeding coefficients were calculated using a Fortran program available at https://github.com/alegarra/getPartialInbreeding, and IL was estimated using BLUPF90+.

2.3 | Measures for Comparison

The selection strategies were compared in terms of genetic gain, average inbreeding coefficient, rate of inbreeding, effective population size (*Ne*), inbreeding depression estimates ($\widehat{b}$), and selection accuracy. To make the breeding strategies comparable, true genetic value and hence genetic gain was centered and standardised to the last year of burn-in (year 10), so that the mean genetic value was 0 and its standard deviation was 1.

For each simulated strategy, the genetic gain for milk yield was estimated from the regression of the genetic value on the year of birth. We also calculated individual pedigree-based inbreeding coefficients using the Meuwissen and Luo (1992) algorithm as implemented in renumf90 program (available at http://nce.ads.uga.edu/html/projects/programs/). We estimated the rate of inbreeding (ΔF_{year}) using the logarithmic regression of $\ln = (1 - F_t)$ on time t (year of simulation), following Pérez-Enciso (1995), where F_t represents the mean inbreeding coefficient at year t across all replicates. We estimated *Ne* as $Ne = \frac{1}{2L\Delta F_{\text{year}}}$, where ΔF_{year} represents the annual inbreeding rate, and L denotes the generation interval. L was defined as the average age of the parents at the birth of their selected offspring. We used $L = 4$, estimated previously for the Pyrenean breeds (Antonios et al. 2023). Inbreeding depression was estimated based on the pedigree-based inbreeding coefficients, expressed by completely inbred (100%) descendants and was compared between strategies. Selection accuracy was measured as the correlation between the estimated and true breeding values in selection candidates. In results we show the average ± standard error across the 10 replicates for each strategy.

3 | Results

3.1 | Genetic Gain

We observed positive genetic gain for milk yield over the fifteen years of selection in all five strategies where selection was based on EBV (EBV, EBV-EIL-01, EBV-EIL-10, EBV-MA, and EBV-EFI) (Figure 3). Comparatively, in the EIL and in the RAND scenarios, we observed a different trend since the EBV was not included in the selection criterion. In the EIL scenario, the genetic trend increased for the first 4 years, followed by a decline. Whereas in the RAND scenario, the genetic trend increased for the first 6 years, followed by no further improvement. This initial gain may be attributed to further dissemination of valuable contributions from ancestors that were previously selected based on their EBVs in the burn-in phase. These animals stayed in the breeding programme for a certain number of years transmitting their relatively high genetic merit to their offspring.

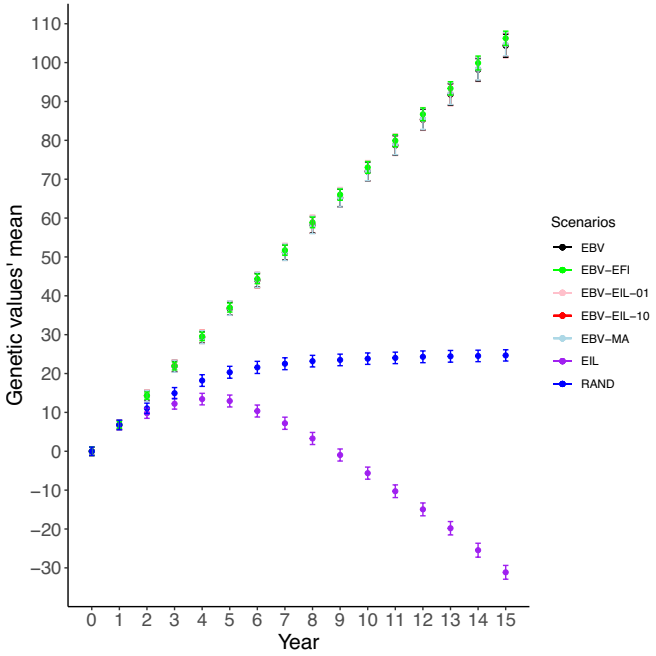

FIGURE 3 | Genetic value trends (mean ± standard error) over the future 15 years of selection with the different strategies. Conventional selection strategy based on estimated breeding values (EBV); EBV-EIL-01: Selection on EBV + 0.01 EIL (EIL: Estimated inbreeding load); EBV-EIL-10: Selection on EBV + 0.1 EIL; EIL: Selection on EIL; EBV-MA: Selection on EBV followed by mate allocation using EIL; EBV-EFI: Selection on EBV adjusted by the expected future inbreeding; RAND: Random selection and mating. [Colour figure can be viewed at wileyonlinelibrary.com]

All the strategies with selection based on EBV had similar rate of genetic gain. In the last year of simulation (Figure 4), the EBV-EFI strategy exceeded the conventional selection strategy (EBV) by approximately 2.8%. The EBV-EIL-01, EBV-EIL-10 and EBV-MA strategies showed gains close to the conventional strategy. The differences between the five strategies were not significant ($p > 0.05$). However, the rate of genetic gain was significantly lower for the EIL and the RAND strategies. EIL strategy had a negative rate of genetic gain, revealing a negative impact of selecting individuals based only on their EIL. RAND strategy had a positive rate of genetic gain, but represented only 18% of that achieved in the conventional selection strategy (EBV).

We were not able to analyse the relationship between the true breeding value and the true IL, because the latter was not

explicitly simulated in this work as mentioned in the Material and Methods' section. Thus, a bivariate plot between EBV and EIL (Figure 5) from the last year of the simulation was analysed and revealed a negative correlation with all strategies.

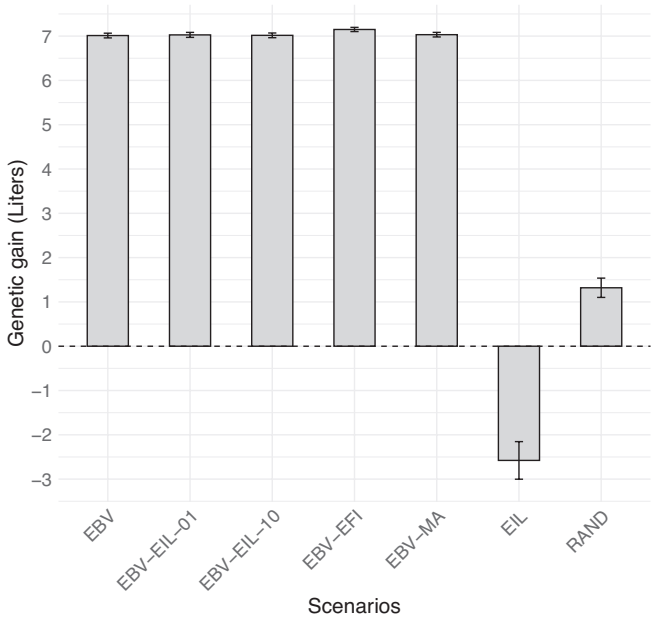

FIGURE 4 | Rate of genetic gain per year for milk yield with the different selection strategies in the last year of simulation. Conventional selection strategy based on estimated breeding values (EBV); EBV-EIL-01: Selection on EBV + 0.01 EIL (EIL: Estimated inbreeding load); EBV-EIL-10: Selection on EBV + 0.1 EIL; EIL: Selection on EIL; EBV-MA: Selection on EBV followed by mate allocation using EIL; EBV-EFI: Selection on EBV adjusted by the expected future inbreeding; RAND: Random selection and mating.

3.2 | Inbreeding Parameters

The increase in mean inbreeding coefficient was similar with all the strategies that included selection on EBVs, increasing to around 1.4% in the last year of simulation (Figure 6). The differences between the five strategies where selection was based on EBV were not significant ($p > 0.05$). On the other hand, mean inbreeding coefficient in the EIL and RAND strategies was significantly lower from the strategies where selection was based on EBV ($p > 0.05$).

To understand the cause for the difference in the mean inbreeding coefficients between the strategies selecting based on either or both EBV and EIL (EBV-EIL-01, EBV-EIL-10, EBV-MA) or only EIL, we analysed the partial inbreeding coefficients and the number of ancestors generating the inbreeding. Three strategies (EBV-EIL-01, EBV-EIL-10, and EBV-MA) had around the same number of ancestors generating inbreeding (around 17K), as indicated by non-zero partial inbreeding coefficients (Table 1), while EIL had a lower number of non-zero partial inbreeding coefficients with a higher number of ancestors generating them (23.9K).

The inbreeding depression estimates ($\hat{b}$ in Table 2) were similar ($p > 0.05$) in all the strategies. The reduction in milk yield ranged between 74 and 79 for 100% of inbreeding, this mean that a 1% of inbreeding would result in a reduction of 0.8 litters in milk.

The ΔF_{year} was similar with all strategies that selected on EBVs ($9.5 \times 10^{-4} \pm 0.1 \times 10^{-4}$) and significantly lower in the EIL strategy (~33% lower than the other strategies) and in the RAND strategy (~45% lower than the other EBVs based strategies) (Table 2). Consequently, *Ne* in the EIL and RAND strategies were higher than the other strategies.

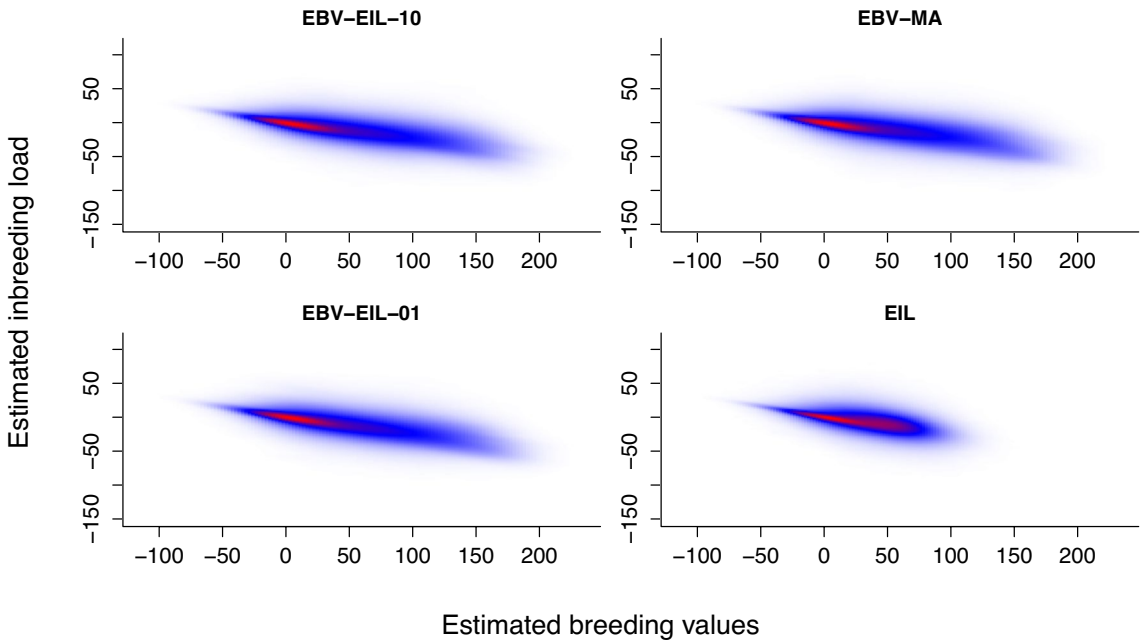

FIGURE 5 | Bivariate plot showing the relationship between estimated breeding values (EBV) and estimated inbreeding load (EIL) in four strategies. EBV-EIL-01: Scenario selecting based on EBV + 0.01 EIL; EBV-EIL-10: Scenario selecting based on EBV + 0.1 EIL; EIL: Scenario selecting based IL; EBV-MA: Scenario implementing mate allocation. [Colour figure can be viewed at wileyonlinelibrary.com]

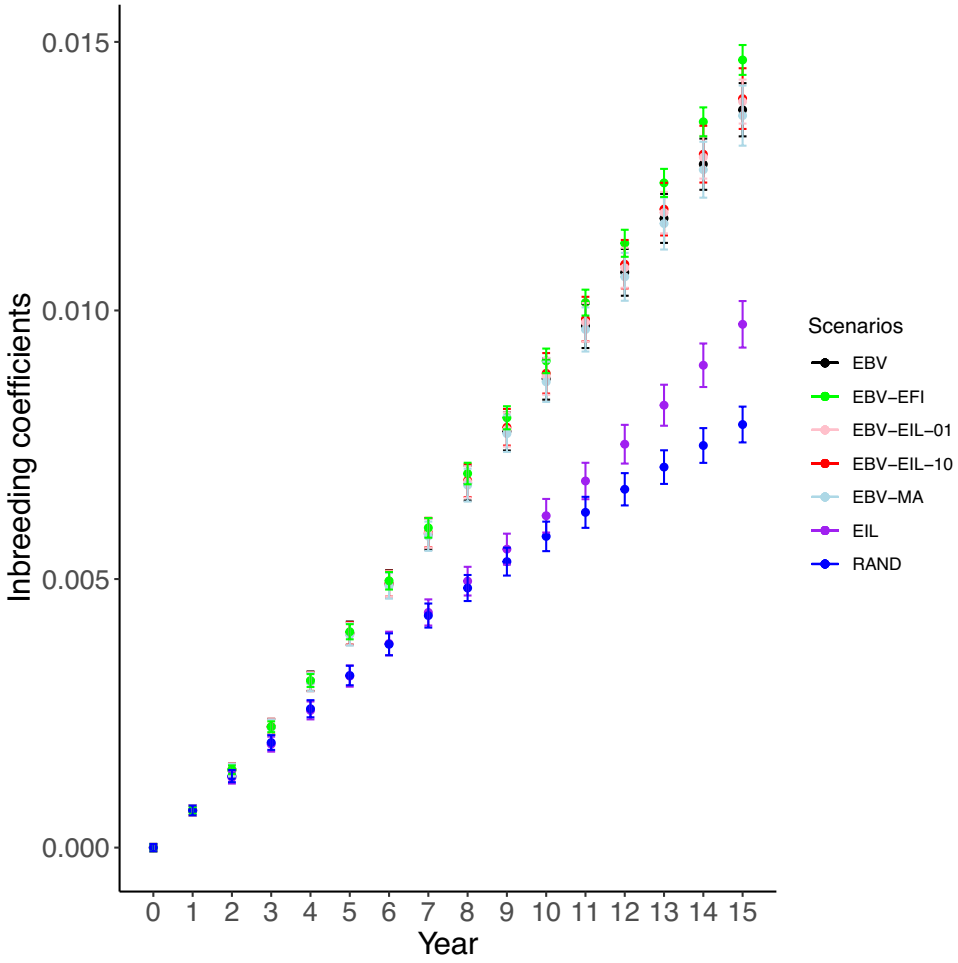

FIGURE 6 | Mean inbreeding coefficient ± standard error during 15 years of selection in the 7 different scenarios. Conventional selection strategy based on estimated breeding values (EBV); EBV-EIL-01: Selection on EBV + 0.01 EIL (EIL: Estimated inbreeding load); EBV-EIL-10: Selection on EBV + 0.1 EIL; EIL: Selection on EIL; EBV-MA: Selection on EBV followed by mate allocation using EIL; EBV-EFI: Selection on EBV adjusted by the expected future inbreeding; RAND: Random selection and mating. [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 1 | Mean and number of non-zero partial inbreeding coefficients and the number of ancestors generating inbreeding in different strategies.

Strategy	Number of PCF ± SE	Number PCF > 0.01 ± SE (%)	Number of AGI ± SE	Average number of PF
EBV-EIL-01	51.8M ± 655.2K	34.0K ± 589 (0.07%)	17.4K ± 162.0	3.0K
EBV-EIL-10	51.2M ± 543.2K	34.0K ± 730 (0.07%)	17.3K ± 234.0	3.0K
EIL	44.6M ± 412.9K	27.4K ± 850 (0.06%)	23.9K ± 161.0	1.9K
EBV-MA	52.0M ± 905.3K	33.7K ± 726 (0.06%)	17.7K ± 266.0	2.9K

Abbreviations: AGI, ancestors generating inbreeding; EBV, estimated breeding value; EBV-EIL-01, scenario selecting based on EBV + 0.01 EIL; EBV-EIL-10, scenario selecting based on EBV + 0.1 EIL; EBV-MA, scenario implementing mate allocation; EIL, estimated inbreeding load; K, $\times 10^3$; M, $\times 10^6$; PCF, partial inbreeding coefficients; PF, partial inbreeding per ancestor; SE, standard error.

3.3 | Accuracy of Selection

All strategies achieved comparable EBV accuracies for the selection candidates of about 0.5. In addition, in all the strategies that included EIL, estimates of inbreeding load effects were not accurate. The low accuracy of EIL is in accordance with other studies on real data showing low accuracy of estimating the IL effects (Varona et al. 2019, Varona, López Carbonell, et al. 2022; Antonios et al. 2025).

4 | Discussion

The objective of this study was to evaluate, through stochastic simulation, the effectiveness of incorporating IL as a selection criterion in a dairy sheep breeding scheme. Overall, selection strategies that included EBVs, either alone or combined with estimated IL, achieved similar outcomes in terms of genetic gain, average inbreeding coefficient, rate of inbreeding, *Ne*, $\widehat{b}$, and selection accuracy over the 15 years of selection. In contrast,

TABLE 2 | Inbreeding depression estimates ($\widehat{b}$), rate of inbreeding per year (ΔF_{year}), and effective population size (*Ne*) for the seven strategies in the last year of simulation.

	EBV	EBV-EIL-01	EBV-EIL-10	EIL	EBV-MA	EBV-EFI	RAND
$\widehat{b}$[1]	−78.8 ± 1.1	−77.6 ± 2.0	−75.9 ± 1.5	−77.7 ± 1.1	−76.7 ± 1.8	−79.0 ± 1.3	−74.5 ± 1.7
ΔF_{year} ($\times 10^{-4}$)	9.4 ± 0.1[a]	9.5 ± 0.1[a]	9.5 ± 0.1[a]	6.4 ± 0.1[b]	9.3 ± 0.1[a]	9.9 ± 0.2[a]	5.2 ± 0.1[c]
Ne	133 ± 2[a]	132 ± 2[a]	131 ± 2[a]	195 ± 2[b]	135 ± 2[a]	125 ± 2[a]	237 ± 5.6[c]

Note: [a,b]Values with different lowercase letters denote statistically significant differences between strategies ($p < 0.05$).
Abbreviations: EBV, scenario selecting based on EBV; EBV-EFI, scenario selecting based on EBV adjusted by the expected future inbreeding; EBV-EIL-01, scenario selecting based on EBV + 0.01 EIL; EBV-EIL-10, scenario selecting based on EBV + 0.1 EIL; EBV-MA, scenario implementing mate allocation; EIL, scenario selecting based EIL; RAND, random selection and mating.
[1]$\widehat{b}$: inbreeding depression estimates expressed by completely inbred (100%) individuals.

selection based exclusively on IL (EIL) and random selection and mating (RAND) strategies resulted in significantly reduced ΔF_{year} and increased *Ne*. However, while the rate of genetic gain in RAND strategy was positive, it represented only 18% of what achieved in the other five EBV based scenarios. Additionally, EIL strategy resulted in a negative genetic gain. Comparing to the EBV based strategies, EIL showed a lower inbreeding coefficient mean through the years (see Figure 6) suggesting that selection based on EIL, effectively decreased the likelihood of high relatedness between mates in later generations, thereby lowering inbreeding in future generations compared to other strategies. This reduction in inbreeding can be attributed to the way EIL strategy selected animals that share fewer common ancestors, which in turn decreases the chances of mating individuals with high relatedness. A key factor contributing to the lower mean inbreeding coefficient with the EIL strategy is the reduced number of non-zero partial inbreeding coefficients per ancestor. These coefficients represent the pathways of IBD from common ancestors, and fewer pathways mean fewer opportunities for IBD alleles to be inherited by the same individual. With the EIL strategy, the smaller number of these pathways effectively limits the mean inbreeding coefficient. This reduction suggests that the EIL scenario is effective reducing relatedness within the population, providing a benefit over more complex strategies (EBV-MA and EBV-EFI), but at the expense of negative genetic gain. By contrast, more complex mating strategies like EBV-MA (which is difficult to implement in practice) and EBV-EFI (which is easier to implement in practice) did not demonstrate any significant advantage in reducing inbreeding when compared to selection based solely EBV. All strategies, excluding EIL and RAND, produced largely comparable results and offered no clear improvement in the reduction of inbreeding compared to the conventional EBV scenario. To evaluate the performance of the EBV-MA and EBV-EFI strategies, they can be compared alongside with optimum contribution selection (OCS) strategy. OCS maximises genetic gain by optimising the genetic contributions of selection candidates while constraining their average coancestry to a predefined value. This dynamic approach has been shown to yield genetic gains significantly higher than standard BLUP-EBV selection at equal rates of inbreeding (Meuwissen 1997). EBV-EFI strategy penalises males based on their average relationship to contemporary females; however, this approach may ignore relationships within a single sex. As noted by Meuwissen (1997), if many highly related individuals are selected as parents, there may be no inbreeding in the immediate offspring, but a large increase in inbreeding occurs in the following generation. OCS is able to control the short and long-term effects of selection on inbreeding. Similarly, the EBV-MA strategy focused on mating optimisation by prioritising matings between unrelated individuals. For individuals sharing common ancestors, mating was only prioritised if the sum of their EIL was positive, and all common ancestors were treated equally. However, EBV-MA did not ensure a long-term reduction in inbreeding. EBV-MA did not fundamentally reduce the long-term rate of inbreeding compared to the EBV scenario because it did not target the genetic contributions of ancestors to future generations. Mating schemes such as minimum coancestry primarily result in a delay of inbreeding of approximately two generations compared to random mating (Sonesson and Meuwissen 2000). Consistently, the annual rate of inbreeding was lower under random selection (RAND) than under the EBV-MA and EBV-EFI strategies. These strategies (EBV-MA and EBV-EFI) may be more effective when they complement OCS to allow for higher selection differentials while maintaining lower level of inbreeding (Sonesson and Meuwissen 2000). This suggests that more effective control of inbreeding requires explicitly targeting the genetic contributions of ancestors to future generations, for example including EIL on an OCS strategy. However, reproduction in dairy sheep breeds is done based on AI with fresh semen, making it difficult to apply OCS methods.

Based on previous research and existing literature (Meuwissen and Woolliams 1994; Harmon and Braude 2010; Leroy 2014), an *Ne* of 50 or higher as we had in our seven strategies (*Ne* > 131) is generally considered sustainable. Meuwissen and Woolliams (1994) highlighted the role of *Ne* in balancing genetic drift and selection pressures, while Leroy (2014) emphasises its importance in conserving genetic variability in managed populations. Furthermore, Harmon and Braude (2010) suggest that in the presence of dominance effects, a sufficiently large *Ne* can mitigate the loss of heterozygosity, thereby preserving overall population fitness. Given these findings, an *Ne* of 131 or greater appears adequate for sustaining genetic health under simulated dominance variation in line with previous studies (Harmon and Braude 2010; Leroy 2014). The current breeding schemes generates limited inbreeding with an *Ne* of around 131 which is considered adequate for maintaining genetic diversity and minimising inbreeding effects.

Few important points should be considered regarding our simulation. First, we simulated effects at a single time point and did not account for new mutations, most of which are likely to be unfavourable. While this limitation is unlikely to affect outcomes over a 15-years selection period, longer-term effects could be more pronounced. However, computational constraints

prevented the extended simulations that would be required to estimate these long-term impacts. Second, IL was not directly simulated, IL emerged from the dominance QTL effects. The inclusion of an optimised function to compute true inbreeding load in AlphaSimR is possible but not straightforward; it is expected for future studies. Third, the number of individuals in the pedigree was lower than in real-world scenarios due to the time-consuming nature of calculating partial inbreeding coefficients, which significantly prolongs a multi-year simulation. Note that we used half the number of females and a full number of males compared to a real population we were aiming to simulate. However, this effect should be small as shown by the expected *Ne* using the Wright's approach to estimating $Ne \sim 4 \times \frac{nM \times nF}{nM + nF}$ based on sex ratio, where *nM* is the number of breeding males and *nF* is the females' number (Wright 1931). With 66,000 females and 1345 males this approach suggests an *Ne* of 5272, while with 33,000 females and 1345 males this approach suggests an *Ne* of 5169. Using the relationship $\Delta F_{\text{generation}} = \frac{1}{2Ne}$, these estimates correspond to the rate of inbreeding per generation ($\Delta F_{\text{generation}}$) of 9.48×10^{-5} and 9.67×10^{-5}, respectively. This result suggests that the reduced number of females did not affect our rate of inbreeding per generation, while it enabled us to reduce simulation time. Forth, in EBV-MA, we were unable to include the entire population because the number of potential matings would be extremely large. For example, even with the current 90,000 possible matings, adding the 165 sires of dams that could mate with 30,000 females would result in 5,040,000 possible matings, excluding the consideration of testing and NM sires. And finally, the use of SNP markers to estimate inbreeding load would likely be more accurate. Varona, López Carbonell, et al. (2022) demonstrated in their study that SNP markers can improve the accuracy of EIL for selection candidates. We did not use SNP markers in this study because genomic selection has been introduced in French dairy sheep breeds in 2016. For improving accuracy of EIL, the number of genotyped animals in these populations is not enough, and most of the genotyped animals are males.

5 | Conclusion

To conclude, we showed that using inbreeding load as a selection criterion is feasible. However, the small accuracy of estimated inbreeding load did not show a clear benefit of including it in genetic evaluation models and subsequent use in selection. Furthermore, the benefit of using inbreeding load in mate allocation strategies was negligible. Our results serve as a reference for further research in other species and traits to explore the possible benefits of selection on inbreeding load, identify strategies in which this would be beneficial, and compare to the alternatives.

Author Contributions

All authors contributed to the study's design and methodology. S.A. performed the statistical analyses and interpreted the results. S.A. drafted the initial version of the manuscript. All authors contributed to the review and editing of the manuscript and approved the final version.

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Ethics Statement

The authors have nothing to report.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available in santonios_sheep_idl at https://github.com/SimonaAntonios/santonios_sheep_idl.

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