# Genomic data enables genetic evaluation using data recorded on LMIC smallholder dairy farms

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## Abstract

**Background:** Genetic evaluation is a central component of a breeding program. In advanced economies, most genetic evaluations depend on large quantities of data that are recorded on commercial farms. Large herd sizes and widespread use of artificial insemination create strong genetic connectedness that enables the genetic and environmental effects of an individual animal's phenotype to be accurately separated. In contrast to this, herds are neither large nor have strong genetic connectedness in smallholder dairy production systems of many low to middle-income countries (LMIC). This limits genetic evaluation, and furthermore, the pedigree information needed for traditional genetic evaluation is typically unavailable. Genomic information keeps track of shared haplotypes rather than shared relatives. This information could capture and strengthen genetic connectedness between herds and through this may enable genetic evaluations for LMIC smallholder dairy farms. The objective of this study was to use simulation to quantify the power of genomic information to enable genetic evaluation under such conditions.

**Results:** The results from this study show: (i) the genetic evaluation of phenotyped cows using genomic information had higher accuracy compared to pedigree information across all breeding designs; (ii) the genetic evaluation of phenotyped cows with genomic information and modelling herd as a random effect had higher or equal accuracy compared to modelling herd as a fixed effect; (iii) the genetic evaluation of phenotyped cows from breeding designs with strong genetic connectedness had higher accuracy compared to breeding designs with weaker genetic connectedness; (iv) genomic prediction of young bulls was possible using marker estimates from the genetic evaluations of their phenotyped dams. For example, the accuracy of genomic prediction of young bulls from an average herd size of 1 ($\mu$=1.58) was 0.40 under a breeding design with 1,000 sires mated per generation and a training set of 8,000 phenotyped and genotyped cows.

**Conclusions:** This study demonstrates the potential of genomic information to be an enabling technology in LMIC smallholder dairy production systems by facilitating genetic evaluations with *in-situ* records collected from farms with herd sizes of four cows or less. Across a range of breeding designs, genomic data enabled accurate genetic evaluation of phenotyped cows and genomic prediction of young bulls using data sets that contained small herds with weak genetic connections. The use of smallholder dairy data in genetic evaluations would enable the establishment of breeding programs to improve *in-situ* germplasm and, if required, would enable the importation of the most suitable external germplasm. This could be individually tailored for each target environment. Together this would increase the productivity, profitability and sustainability of LMIC smallholder dairy production systems. However, data collection, including genomic data, is expensive and business models will need to be carefully constructed so that the costs are sustainably offset.

# Background

The huge increase in milk yield of dairy cattle in advanced economies over the past century is a powerful example of the impact that selective breeding can have on improving livestock productivity. For example, in the US dairy industry, production of milk per cow doubled from an average of 20 litres to 40 litres per day between 1960 and 2000 [1]. Approximately 50% of this improvement can be attributed to breeding. However, despite the potential benefits, similar breeding practices have had poor efficacy and adoption in smallholder dairy production systems in many low to middle-income countries (LMICs). Recent estimates from Kenyan smallholder farms suggest that average productivity per cow is approximately 5 litres per day and there is little evidence of major genetic improvement in recent decades [2–5].

In Kenya and other East African countries, farms with five cows or less account for more than 70% of milk production [6,7], and farms with 10 cows or less account for around 90% of milk production [8]. The low levels of productivity and its economic importance has stimulated renewed efforts to improve dairy cow productivity in LMIC smallholder dairy production systems [6,9–11]. These efforts include new approaches for collecting data from rural farms more effectively and the establishment of effective and penetrant genetic evaluation schemes [10,12–14], breeding programs and dissemination programs [15], all of which have been somewhat intractable to sustain over the long-term in the past.

Genetic evaluation is a central component of a breeding program. The properties of an ideal data set that enables an accurate genetic evaluation include: (i) genetic connectedness between herds or management groups [16]; (ii) sufficient numbers of animals; (iii) sufficiently large herd sizes; and (iv) accurate phenotype collection. Genetic evaluations have been very successful in advanced economies because large data sets are routinely assembled from

74 commercial farms with modest to large herd sizes (e.g., twenty to several thousand cows).
75 Genetic connectedness between herds is high due to the widespread use of artificial
76 insemination (AI). Typically, phenotypes are accurately measured (e.g., automatically on
77 advanced milking machines). Such data enables the genetic and environmental effects of an
78 individual animal's phenotype to be accurately separated. All or many of these features are not
79 present in many LMIC smallholder dairy production systems. For example, smallholder dairy
80 farmers in East Africa have small herd sizes (e.g., herds with one to five cows), a low
81 prevalence of AI (5-10%) [8], and an absence of automated phenotyping systems [17].
82 Traditionally, this has prevented the establishment of effective genetic evaluation systems in
83 these settings.

84 Genomic evaluations use a genomic relationship matrix to capture the realised, rather
85 than expected pedigree-derived relationships between animals [18,19]. The use of genomic
86 information has been transformative for many genetic evaluation systems in advanced
87 economies. For example, the accuracy, which is the square root of reliability, of prediction for
88 milk yield of young bulls increased from 0.62 using pedigree best linear unbiased prediction
89 (PBLUP) to 0.85 for genomic best linear unbiased prediction (GBLUP) [20]. In the context of
90 LMIC smallholder dairy production systems, genomic data could be even more important than
91 it has been in advanced economies. For the first time, genomic data could enable effective
92 genetic evaluation systems based on relatively imprecisely measured phenotypes, collected on
93 cows in very small herd sizes, which have relatively low levels of genetic connectedness. In
94 such a setting, genomic data could capture and utilise information pertaining to haplotypes that
95 are shared by animals in different herds. This information could reveal genetic connectedness
96 that is unseen by pedigree information, which would, in turn, enable more accurate partitioning
97 of the genetic and environmental effects on animal's performance in small herds. This opens
98 up the possibility of an *in-situ* breeding program based on *in-situ* performance data from LMIC

99 smallholder dairy farms. Given that such data reflects the performance of animals within the
100 target management and environment settings, animals produced by such a breeding program
101 would be most suited to the participating smallholder dairy farmers.

102 In genetic evaluations, the herd or management group is usually included in the
103 statistical model to enhance the separation of the genetic and environmental effects of an
104 animal's performance [21–24]. Herds can be modelled as fixed or random effects. Most genetic
105 evaluations in advanced economies model herds as fixed effects because herd sizes are
106 typically large, which leads to fixed and random effects models giving almost equal solutions
107 [22,23]. When herd sizes are small, such as in many LMIC smallholder dairy production
108 systems, modelling herd as a fixed effect leads to inaccurate solutions [25]. Modelling small
109 herds as random effects may reduce this inaccuracy, providing estimated breeding values
110 (EBVs) with higher accuracies. In combination with the use of genomic information, this could
111 enable genetic evaluations to be performed using data recorded, *in-situ*, on LMIC smallholder
112 dairy farms.

113 The aims of this study were to use simulation to quantify: (i) the power of genomic
114 information to enable genetic evaluation based on phenotypes recorded on smallholder dairy
115 farms and, under such conditions, the impact of: (ii) modelling herd as a fixed or random effect;
116 (iii) the genetic connectedness of a breeding population; and (iv) the number of records on the
117 accuracy of EBVs of phenotyped cows and young bulls.

118 Across a range of breeding designs, genomic data enabled accurate genetic evaluation
119 of phenotyped cows using data sets that contained small herds with weak genetic connections
120 (according to pedigree). The genetic evaluation of phenotyped cows using genomic
121 information had higher accuracy compared to pedigree information across all breeding designs.
122 The genetic evaluation of phenotyped cows with genomic information and modelling herd as

123 a random effect had higher or equal accuracy compared to modelling herd as a fixed effect.
124 The genetic evaluation of phenotyped cows from breeding designs with strong genetic
125 connectedness had higher accuracy compared to breeding designs with weaker genetic
126 connectedness. The genomic prediction of young bulls was possible using marker estimates
127 from the genetic evaluations of their phenotyped dams. For example, the accuracy of genomic
128 prediction of young bulls from an average herd size of 1 ($\mu$=1.58) was 0.40 under a breeding
129 design with 1,000 sires mated per generation and a training set of 8,000 phenotyped and
130 genotyped cows. Our results show that genetic evaluations with genomic information can
131 provide a high accuracy of EBVs of phenotyped cows and young bulls when using data from
132 smallholder dairy farms, and would, therefore, enable *in-situ* breeding programs based on
133 performance measured *in-situ*.

134

# Material and methods

Simulations were used to quantify the power of genomic information to enable genetic evaluation based on phenotypes recorded on smallholder dairy farms. Ten replicates of several scenarios were performed with the overall simulation scheme depicted in Figure 1. The simulations were performed using AlphaSimR [26] and were designed to: (i) generate whole genome sequence data; (ii) generate single nucleotide polymorphisms (SNP), quantitative trait loci (QTL) and phenotypes; (iii) generate pedigree structures for LMIC smallholder dairy populations; (iv) vary the population and average herd size; (v) vary the ratios of genetic, herd and environmental variances; and (vi) run genetic evaluations modelling herd as either fixed or random effects. Conceptually, the simulation scheme was divided into historical and evaluation phases.

Each of the 10 replicates consisted of: (i) a burn-in phase shared by all strategies; and (ii) an evaluation phase that simulated breeding with each of a number of different breeding designs. Specifically, the historical component was subdivided into three stages: the first simulated the species' genome sequence; the second simulated founder genotypes for the initial parents; and the third simulated five generations of breeding using phenotypic selection.

The burn-in phase represented historical evolution, under the assumption that livestock populations have been evolving for tens of thousands of years, and historical breeding efforts that were represented by five generations of phenotypic selection. The evaluation phase represented six generations of animal breeding in which animals were selected on their phenotypes. In the evaluation phase, population parameters were varied (i.e., the number of sires mated per generation, large or small population sizes, large or small average herd sizes, and different proportions of the genetic, herd and environmental variances) to resemble a range of possible breeding designs (Figure 1).

**Burn-In: Generation of whole genome sequence data**

For each replicate, a genome consisting of 10 chromosome pairs was simulated for the hypothetical animal species similar to cattle. Sequence data was generated using the Markovian Coalescent Simulator (MaCS) [27] and AlphaSimR [26] for 4,000 base haplotypes for each of ten chromosomes. The chromosomes were each 100 cM in length comprising $10_8$ base pairs and were simulated using a per site mutation rate of $1\times10^{-8}$ and a per site recombination rate of $1\times10^{-8}$. The $N_e$ was set to 1,035 in the final generation of historical simulation, to $N_e$=6,000 (1,000 years ago) to $N_e$=24,000 (10,000 years ago), and to $N_e$=48,000 (100,000 years ago) with linear changes in between [28]. The $N_e$ of 1,035 was chosen to reflect the high genetic diversity found in cattle populations in Africa.

**Burn-In: Founder Genotypes**

Simulated genome sequences were used to produce 2,000 founder animals. These founder animals served as the initial parents in the burn-in phase. Sites segregating in the founders' sequences were randomly selected to serve as 5,000 SNP markers per chromosome (50,000 genome-wide in total) and 1,000 QTL per chromosome (10,000 genome-wide in total).

**Burn-In: Phenotype**

A single trait representing total milk yield for a single lactation was simulated for all animals. The true breeding values (TBVs) were calculated by summing the average effects of the animal's genotype at each QTL. QTL additive effects were sampled from a standard normal distribution, $N(0,1)$, and linearly scaled to produce TBVs in the founder population with a variance ($\sigma_a^2$) of 0.2. Random error was sampled from a normal distribution, $N(0,\sigma_e^2)$. The initial random error variance was set at $\sigma_e^2$=1.8. The TBVs and random error effects were summed to create the phenotypes of the animal. These phenotypes were used for selection during the burn-in and the first 5 years in the evaluation phases of the simulation. Additional

herd effects were added to the phenotypes of the animals, described in a later section, in the final generation of the evaluation phase of the simulation

**Recent (Burn-In) Breeding**

Recent (burn-in) breeding for milk yield was simulated over 5 discrete generations of selective breeding on phenotype. The features of this breeding stage were: (i) 225 sires per generation, (ii) 1,000 dams per generation, and (iii) 2,000 offspring per generation. These numbers were chosen to match the base population $N_e$ of 1,035 following the equation from Charlesworth et al. (2008) that accounts for the variable number of males and females as well as the mean and variance of family size. In the final generation of this stage, 80,000 offspring were generated to enable the full range of scenarios in the evaluation phase of the simulation.

**Evaluation Phase**

The evaluation phase of the simulation modelled breeding using alternative breeding designs. Each design was simulated for an additional 6 generations following the recent breeding burn-in component so that each design could be evaluated with an equivalent starting point. A baseline design was constructed using parameters that are representative of the current smallholder farming system commonly observed in East Africa. We refer to this design as the LMIC design. Alternative breeding designs were modifications that used the LMIC design as a template (Figure 1). The common features across the simulation of all the breeding designs were: (i) all generations of selection produced 80,000 animals of equal sex ratio, (ii) for simplicity selection on sires was based on their phenotype, (iii) no selection was performed on dams. Alternate breeding designs varied: (i) the size of the training set; (ii) the number of sires mated per generation; (iii) the average herd size; and (iv) the proportions of genetic, herd and environmental variances. A schematic for the overall structure of the breeding designs, including the LMIC design, is given in Figure 1 and a detailed description follows.

### *LMIC Design*

The LMIC design was developed to approximate the current smallholder farming system structure commonly observed in East Africa. The training set size was set at 8,000 phenotyped cows and the number of sires mated per generation was set to 1,000. A trait heritability of 0.1 and ratio of 1:4 between genetic and herd effect variance ratios were chosen based upon unpublished data [29].

### Genetic Evaluation Models

Breeding values were estimated using the following basic model:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Zu} + \mathbf{e}, \quad (1)$$

where **y** is a vector of phenotype records measured on cows; **b** is a vector of fixed effects; **u** is a vector of breeding values for which we assumed that with the PBLUP $\mathbf{u} \sim \mathrm{N}(0, \mathbf{A}\sigma_a^2)$ and with the GBUP $\mathbf{u} \sim \mathrm{N}(0, \mathbf{G}\sigma_a^2)$, where **A** is the pedigree numerator relationship matrix based on 5 generations of the pedigree [30] and **G** is the genomic numerator relationship matrix based on 50k SNP chip [31]; **e** is a vector of residuals for which we assumes $\mathbf{e} \sim \mathrm{N}(0, \mathbf{I}\sigma_e^2)$; **X** and **Z** are the incidence matrices linking phenotype records respectively to **b** and **u**. We have conducted three analyses with the basic model in relation to a herd effect: (i) we excluded it, which gave us the basic model with intercept as the only fixed effect; (ii) we modelled it as a fixed effect; and (iii) we modelled it as a random effect for which we assumed $\mathbf{h} \sim \mathrm{N}\left(0, \mathbf{I}\sigma_h^2\right)$. We assumed that the variance of herd effects $\sigma_h^2$, breeding values $\sigma_a^2$ and residuals $\sigma_e^2$ were known and set them to the simulated values of the LMIC design. Only the last generation of phenotype data was used in model 1 to mimic the recent introduction of phenotype, pedigree and genomic data recording.

PBLUP evaluations were run using the WOMBAT software [32]. GBLUP evaluations were run using the AlphaBayes software [33]. Three genetic evaluation models were fit: (i) excluding herd effects; (ii) herds modelled as fixed effects; and (iii) herds modelled as random effects. All models modelled the animal IDs as random effects. All other parameters were held constant at the values used in the LMIC design.

**Genetic Connectedness and Herd Size**

Genetic connectedness was varied across different breeding designs in two ways; (i) herd connectivity – the distribution of related animals within and across different herds, and (ii) the recent $N_e$ of the breeding design. The herd connectivity was varied by simulating different average herd sizes. To generate datasets with a range of different average herd sizes, the realised herd sizes were sampled from a Poisson distribution with a lambda of 1 ($\mu = 1.58$, $\sigma^2 = 0.66$), 2 ($\mu = 2.32$, $\sigma^2 = 1.60$), 4 ($\mu = 4.06$, $\sigma^2 = 3.78$), 8 ($\mu = 8$, $\sigma^2 = 8$), 16 ($\mu = 16$, $\sigma^2 = 16.19$) and 32 ($\mu = 32$, $\sigma^2 = 31.92$). The recent $N_e$ of the breeding design was varied using four different numbers of sires mated per generation: 100, 250, 1,000 and 5,000 sires. The number of dams per generation remained constant at 40,000. All other parameters were held constant at the values used in the LMIC design.

**Size of Training Set**

The size of the training set used in the genetic evaluations was varied across different breeding designs using four different numbers of records: 2,000, 8,000, 16,000 and 32,000 phenotyped cows. Phenotyped cows were sampled evenly across the population, to ensure the genetic connectedness was maintained. All other parameters were held constant at the values used in the LMIC design.

## Trait Heritability and Herd Effect

To produce the final phenotype records, the TBVs were standardized and re-scaled, and herd and random error effects were sampled from a normal distribution with corresponding variances. In addition to the LMIC design, which had a trait with a narrow sense heritability of 0.1 and herd effect variance ratio of 0.4, we simulated two other scenarios: (i) a trait with a narrow sense heritability of 0.3 and herd effect variance ratio of 0.4; and (ii) a trait with a narrow sense heritability of 0.5 and herd effect variance ratio of 0.4. For each of the three scenarios, the TBVs, herd effects and random errors were summed to create the final phenotypes of the cows. All other parameters were held constant at the values used in the LMIC design.

## Generation of young bull population

For each scenario we generated an additional generation of offspring to produce a validation set of 2,000, 8,000, 16,000 and 32,000 selection candidates, the young bulls that would have been genomically tested. Young bulls had no phenotypes recorded and as such served as forward validation of the model 1 fitted on phenotyped cows.

## Comparison of Breeding Designs

The various breeding designs resulted in 288 different scenarios which enabled multiple comparisons. The breeding designs were compared based upon the accuracy and bias of EBVs separately for each scenario and replicate – we report mean and 95% interval of estimates over replicates. Accuracy was measured as the Pearson's correlation coefficient between the EBVs and TBVs. The bias of genomic prediction was measured as the slope of the regression of the TBVs on the EBVs.

# Results

The various breeding designs resulted in 288 different scenarios which enabled multiple comparisons. Across a range of breeding designs, genomic data enabled accurate genetic evaluation of phenotyped cows using data sets that contained small herds with weak genetic connections. The main trends observed in our results show: (i) the genetic evaluation of phenotyped cows using genomic information had higher accuracy compared to pedigree information across all breeding designs; (ii) the genetic evaluation of phenotyped cows with genomic information and modelling herd as a random effect had higher or equal accuracy compared to modelling herd as a fixed effect; (iii) the genetic evaluation of phenotyped cows from breeding designs with strong genetic connectedness had higher accuracy compared to breeding designs with weaker genetic connectedness; (iv) the genomic prediction of young bulls was possible using marker estimates from the genetic evaluations of their phenotyped dams. For example, the accuracy of young bulls from an average herd size of 1 ($\mu$=1.58) was 0.40 under a breeding design with 1,000 sires mated per generation and a training set of 8,000 phenotyped and genotyped cows. The accuracies of genomic prediction of young bulls followed similar trends to those observed in the evaluation of phenotyped cows, with a reduction of ~0.1 in overall accuracy.

To ease the presentation, we break the results into 5 sections: (i) LMIC design; (ii) impact of herd effect modelling; (iii) impact of genetic connectedness and heritability; (iv) impact of training set size; and (v) prediction of young bulls.

## LMIC Design

The accuracy of genetic evaluation of phenotyped cows, from small, weakly genetically connected herds was quantified under the LMIC design. Genetic evaluation with phenotyped cows from intermediate and large average herd sizes had a higher accuracy than genetic

297 evaluation with phenotyped cows from small average herd sizes. Increases in average herd size
298 had a diminishing effect on increases in accuracy of genetic evaluation of phenotyped cows.
299 The genetic evaluation of phenotyped cows using genomic information had higher accuracy
300 compared to pedigree information across all breeding designs. Table 1 reports the accuracy of
301 EBVs of phenotyped cows with both genetic evaluation methods as average herd size was
302 changed. The accuracies reported correspond to models with the herd modelled as a random
303 effect. At an average herd size of 1 ($\mu$=1.58), phenotyped cows had an accuracy of EBVs of
304 0.40 with the PBLUP and 0.50 with the GBLUP (an increase of 0.10). At all other average herd
305 sizes, the increase in accuracy of GBLUP compared to PBLUP was between 0.11 and 0.12. In
306 what follows, results will only be presented for the GBLUP.

307 **Table 1. The impact of genetic evaluation method on EBV accuracy**

| ***Method*** | | ***Size of Herd*** | | | | | |
|---|---|---|---|---|---|---|---|
| | | ***1*** | ***2*** | ***4*** | ***8*** | ***16*** | ***32*** |
| ***PBLUP*** | ***Accuracy*** | *0.40* | *0.41* | *0.43* | *0.44* | *0.45* | *0.46* |
| ***GBLUP*** | ***Accuracy*** | *0.50* | *0.53* | *0.54* | *0.56* | *0.57* | *0.57* |

308
309 *Comparison of the accuracy of genetic evaluation method under the LMIC design with different*
310 *average herd sizes and using the PBLUP or GBLUP method. Herd is modelled as a random*
311 *effect. Standard error was 0.01 or less.*
312

313 **Impact of herd effect modelling**

314 Genetic evaluations were run using three models: (i) excluding a herd effect, (ii) herd
315 modelled as a fixed effect, and (iii) herd modelled as a random effect. The genetic evaluation
316 of phenotyped cows that included a herd effect had higher accuracies across all breeding
317 designs. The genetic evaluation of phenotyped cows with genomic information and modelling
318 herd as a random effect had higher accuracy compared to modelling herd as a fixed effect at

low average herd sizes. However, the accuracies of the two modelling approaches converged once a herd size of 8 was reached. Figure 2 plots the average herd size against the accuracy for each of the three evaluation models. Figure 2 shows that excluding a herd effect gave an accuracy of 0.48, averaged across all herd sizes. At average herd sizes of 1.58 and 2.32, modelling herd as a random effect increased the accuracy by 0.10 and 0.05, compared to modelling herd as a fixed effect. At an average herd size of 8, the accuracies from the two modelling approaches had practically converged.

**Impact of genetic connectedness and trait heritability**

In the simulations we varied genetic connectedness between herds in two ways; (i) herd connectivity – varied by simulating different average herd sizes; and (ii) the recent $N_e$ of the breeding design - varied using different numbers of sires mated per generation. The genetic evaluation of phenotyped cows from breeding designs with strong genetic connectedness had higher accuracy compared to breeding designs with weaker genetic connectedness. Figure 3 plots the average herd size against the accuracy of EBVs of phenotyped cows for each of the four breeding designs with different numbers of sires mated per generation. Figure 3 shows that at an average herd size of 1 ($\mu$=1.58), a decrease in the number of sires mated per generation from 5,000 to 1,000, 250 and 100 increased the accuracy from 0.46 to 0.50, 0.55 and 0.62, respectively. This shows the individual impact of the number of sires mated per generation on the accuracy. With 1,000 sires mated per generation, an increase in the average herd size from 1.58 to 32, increased the accuracy from 0.50 to 0.58. This shows the individual impact of the average herd size on the accuracy. An increase in the average herd size from 1.58 to 32, and a decrease in the number of sires mated per generation from 1,000 to 100, increased the accuracy from 0.50 to 0.68. This shows the combined impact of the genetic connectedness of the breeding design on the accuracy.

The genetic connectedness of the breeding design also showed interactions with the heritability of the trait. Across all trait heritabilities, the EBVs of phenotyped cows had lower accuracy in breeding designs that had weak genetic connections. The lower accuracy due to an increase in the number of sires mated per generation in the breeding design became more prominent at lower heritabilities. The lower accuracy due to a decrease in the average herd size of the breeding design was more prominent at higher heritabilities. Figure 4 plots the average herd size against the accuracy of EBVs of phenotyped cows for two of the four different numbers of sire mated per generation (100 and 1,000 sires). The three panels correspond to the heritability under the different breeding designs. Figure 4 shows that the highest accuracy (0.94) was achieved for a high heritability trait (0.5) and when genetic connectedness was strong (100 sires mated per generation and an average herd size of 32). A decrease in the average herd size from 32 to 1.58, reduced the accuracy by 0.07. An accuracy of 0.68 was achieved for a low heritability trait (0.1) and when genetic connectedness was strong (100 sires mated per generation and an average herd size of 32). An increase in the number of sires mated per generation to 1,000 sires mated per generation, reduced the accuracy by 0.10.

**Impact of Training Set Size**

Genetic evaluation of phenotyped cows with a larger number of records had higher accuracies for all average herd sizes. Figure 5 plots the average herd size against the accuracy of EBVs of phenotyped cows for the four different training set sizes. Figure 5 shows an increase in the number of records in the training set increased the accuracy across all of the average herd sizes. At an average herd size of 1 ($\mu$=1.58), an increase in the number of records in the training set from 2,000 to 8,000, 16,000 and 32,000 records increased the accuracy from 0.41 to 0.50, 0.59 and 0.68, respectively.

366 **Prediction of young bulls**

367 Genomic prediction of young bulls was possible using marker estimates from the
368 genetic evaluations of their phenotyped dams. The accuracies of young bulls followed similar
369 trends to those observed in the evaluation of phenotyped cows, with a reduction of ~0.1 in
370 overall accuracy. Genomic prediction of young bulls with a larger number of records in the
371 training set had higher accuracies. The accuracy of genomic prediction of young bulls from an
372 average herd size of 1 ($\mu$=1.58) was 0.40 under a breeding design with 1,000 sires mated per
373 generation and a training set of 8,000 phenotyped and genotyped cows. Figure 6 plots the
374 accuracy of EBVs of candidate young bulls against the average herd size for the four different
375 training set sizes. Figure 6 shows that an increase in the number of records in the training set
376 increased the accuracy across all of the average herd sizes. At an average herd size of 1
377 ($\mu$=1.58), an increase in the number of records in the training set from 2,000 to 8,000, 16,000
378 and 32,000 records increased the accuracy from 0.28 to 0.40, 0.51 and 0.62, respectively.

379 The accuracy was also affected by an interaction between the heritability of the trait
380 and the genetic connectedness of the breeding design. The genetic connectedness of the
381 breeding design was less important for traits with a higher heritability. Figure 7 plots the
382 accuracy against the average herd size for two of the four different numbers of sire mated per
383 generation (100 and 1,000 sires). The three panels correspond to the different trait heritabilities
384 in the breeding designs. Figure 7 shows that an increase in the average herd size did not recover
385 the loss of accuracy due to lower genetic connectedness (100 vs 1,000 sires mated per
386 generation). This is different from what was observed with the accuracy for phenotyped cows.
387 Figure 7 shows that for a high heritability trait (0.5) and an average herd size of 32, increasing
388 the number of sires mated per generation from 100 to 1,000 sires mated per generation reduced
389 the accuracy of young bulls by 0.04.

# Discussion

In this paper, we demonstrated that genetic evaluation using genomic information can provide accurate EBVs when using data recorded on smallholder farms across a range of breeding designs. Therefore, genetic evaluations using genomic information could enable *in-situ* data recorded on smallholder farms to be used to drive *in-situ* genetic improvement programs and genetic importation programs to improve animal performance on such smallholder farms. This capacity would enable tailored improvement and importation of genetics for smallholder farms. The results of our study highlight three main points for discussion: (i) factors that impact the accuracy of genomic evaluations; (ii) limitations of the simulation; and (iii) prospects for animal breeding in LMIC smallholder dairy production systems.

## Factors that impact the accuracy of genomic evaluations

### *Impact of Herd Size*

The herd or management group is usually included in the statistical model of genetic evaluations to enhance the partitioning of the genetic merit of an individual from the non-genetic effects underlying its phenotype [21–24]. Herds can be modelled as fixed or random effects. One of the reasons underlying the great success of genetic evaluations in advanced economies is that large data sets are routinely assembled from commercial farms with large herd sizes. This data structure is suited to modelling herd as a fixed effect. This data structure also enables accurate separation of genetic and environmental effects and reduces potential bias due to a difference in management effects between different herds.

However, LMIC smallholder dairy farms often have small herd sizes, typically between one and five cows. With herd sizes as small as this, LMIC smallholder dairy datasets sit at one extreme of the bias-variance trade-off [34]. Modelling herd as a fixed effect provides unbiased

414 estimates. However, when herd sizes are small, these estimates of herd effect may have large
415 variance. Therefore, modelling herd as a fixed effect in the LMIC smallholder dairy genetic
416 evaluations may lead to herd effect estimates with high variance and a reduced ability to
417 correctly rank individuals by genetic merit [25]. This could lead to a decreased accuracy of
418 EBVs. An alternative approach in such settings would be to model herds as random effects.
419 Modelling herd as a random effect looks to minimize the variance of estimates, but the resulting
420 estimates are inherently biased due to shrinkage applied during estimation. However, the
421 shrinkage process allows phenotypes recorded in small herds to partially and proportionately
422 contribute to the genetic evaluation. This is essential for LMIC smallholder dairy genetic
423 evaluations with herd sizes typically between one and five cows. The results from our study
424 support this and showed that when data is collected from herds between one and four cows,
425 genomic evaluations modelling herd as a random effect outperformed modelling herd as a fixed
426 effect. In the case of genomic evaluations using data from an average herd size of 1 ($\mu$=1.58),
427 modelling herd as a random effect increased the accuracy of EBVs of phenotyped cows by 0.10
428 compared to modelling herd as a fixed effect. It was only when the average herd size was 8 or
429 more that the accuracy of EBVs of phenotyped cows from the two models converged. Overall
430 our results demonstrate that modelling herd as a random effect in LMIC smallholder dairy
431 genetic evaluations: (i) increases the accuracy of genetic evaluations; (ii) enables phenotypes
432 recorded in all herds to partially and proportionately contribute to the genetic evaluation; and
433 (iii) enables the breeding values of all animals (even those in single cow herds) to be calculated.
434 However, as is discussed later, modelling herd as a random effect may increase accuracy but
435 bias may be generated when non-random associations between the genetic value of cattle and
436 the herd management exist within the training set.

*Impact of GBLUP as a tool to increase connectedness between herds*

Sufficient genetic connectedness between herds is important for accurate genetic evaluations [16,35]. In dairy production systems in advanced economies, large herd sizes and widespread use of artificial insemination creates strong genetic connectedness between herds that enables accurate separation of genetic and environmental effects. Because strong genetic connectedness between herds is already established in dairy production systems in advanced economies, GBLUP has primarily increased the accuracy of EBVs compared to PBLUP by capturing and exploiting deviations from expected relationships between cattle caused by Mendelian sampling [36–38]. For example, the accuracy, which is the square root of reliability, of prediction for milk yield of young bulls have increased from 0.62 using pedigree best linear unbiased predictions (PBLUP) to 0.85 for genomic best linear unbiased predictions (GBLUP) [20]. We say "primarily" because most training populations are comprised of bulls that were progeny tested across a large number of herds. In this situation, modelling both the genetic and herd effects jointly is less of a concern. The single-step GBLUP method and the recent rise of cow genotyping will also enable improvements by jointly modelling of genetic and herd effects. In LMIC smallholder dairy production systems the benefit using GBLUP will be both due to exploiting deviations from expected relationships caused by Mendelian sampling and due to implicit increases of genetic connectedness between herds.

Generating sufficient genetic connectedness between herds is especially difficult and important in LMIC smallholder dairy production systems because herd sizes are often small, farms are geographically dispersed, and artificial insemination is not widely used [8]. In such production systems, the genetic and environmental effects are likely to be partially or fully confounded. This is most obvious in the case of a single cow herd where we cannot separate the genetic effect of the cow from the herd effect of the farm. However, a range of levels of confounding could also arise in small herds composed of cows sharing the same pedigree-

462 derived relatedness, with the recent common ancestor or ancestors only used in that herd. In
463 both of these circumstances, PBLUP has limited ability to partition a cow's phenotype into its
464 genetic and environmental components. In contrast, GBLUP can achieve this partitioning,
465 because it is capable of tracking the different permutations of haplotypes shared between cattle
466 in different herds. During a genetic evaluation, GBLUP implicitly estimates the effects of these
467 haplotypes and from this also the EBV of each animal. This allows phenotypic records from
468 cows with shared haplotypes in different herds to contribute to the implicit estimation of
469 haplotype effects and the estimates of those haplotype effects allows the partitioning of those
470 cow's phenotypes into their genetic and herd environment components. Furthermore, through
471 this implicit increasing of genetic connectedness between herds, GBLUP increases the number
472 of herds and cows that contribute useable information to the genetic evaluation compared to
473 PBLUP. All of these interlinked factors that underlie the advantages of GBLUP, firstly make
474 genetic evaluations using data recorded *in-situ* on smallholder herds possible, and secondly,
475 work to make those genetic evaluations more accurate than those of PBLUP. In our study, the
476 increase in genetic connectedness provided by GBLUP resulted in genetic evaluations with
477 approximately 0.1 higher accuracy of EBVs compared to PBLUP, independent of herd size.
478 This result probably overestimates the power of PBLUP in such settings. We used five
479 generations of error-free pedigree records in PBLUP. In reality, limited pedigree recording
480 takes place in LMIC smallholder dairy production systems. We should emphasise though that
481 LMIC smallholder dairy data structures likely do not enable very accurate estimation of
482 individual haplotype effects and that the dataset size will continue to be an important factor.

483 Another benefit of the increased genetic connectedness of training sets provided by
484 GBLUP, not assessed in our study, may be the mitigation of the bias of EBVs. In LMIC
485 smallholder dairy production systems, natural sire mating is prevalent, pedigree recording is
486 limited, herd sizes are often small and farms are geographically dispersed. This structure is

likely to lead to isolated family clusters in pedigrees. Therefore, when using PBLUP in LMIC smallholder dairy genetic evaluations, most of the information used to calculate the EBV for any particular individual will be provided by close relatives captured by this poorly connected pedigree. This may result in only a very small number of herds contributing effective information to the genetic evaluation of an animal or group of related animals. This becomes a problem if confounding exists between the environment and the genetics in the isolated clusters of herds. Confounding can occur when the same natural service bull is used by a cohort of farmers with farms that have a better or worse than average herd environment. This may lead to biased breeding values under PBLUP. In contrast, haplotypes are likely to be dispersed across more herds. Therefore, GBLUP could accumulate effective information from more herds and more cows and thus be less prone to having haplotypes confounded with the environment.

**Limitations of the simulation**

Our simulations did not model the full complexity that would arise in practical genetic evaluations for LMIC smallholder dairy production systems. In this section we discuss three limitations of our simulations: (i) high genomic selection accuracy; (ii) a simplified distribution of animals across farms; and (iii) a simplified breeding goal.

*Impact of high genomic selection accuracy*

The accuracies of EBVs of phenotyped cows and young bulls observed in these simulations are likely higher than what may be expected in practical genetic evaluations for LMIC smallholder dairy production systems. Several simplifications of the simulation are likely to have caused this, including the absence of genotyping and pedigree errors, additive genetic architecture, homogeneity of environment and a single breed. Also, fixed variance components were used in the estimation of EBVs. In practical LMIC genetic evaluations, the

511 estimation error of variance components may result in lower accuracies of EBVs. However,
512 we believe that the main conclusion from this study (i.e., that GBLUP is more powerful than
513 PBLUP in LMIC smallholder production systems for several reasons) would still hold for more
514 realistic simulations or real data. For decades it has been difficult to sustain widespread
515 recording and use of pedigree to drive genetic evaluations in LMIC dairy production systems.
516 GBLUP, for the reasons we outline, offers a route to overcoming this problem.

517 *Impact of simplified distribution of animals across farms*

518 The distribution of cattle across herds in the population impacts the choice of modelling
519 herd as a fixed or random effect in genetic evaluations. Bias, detected in this study as an
520 inflation or deflation of EBVs, can be generated when a non-random association between herd
521 management and genetic potential of cattle exists. Such non-random associations can be
522 generated, for example, by well-resourced farmers who use better management practices also
523 being able to afford semen of higher genetic merit sires, or by the restriction of natural mating
524 sires to herds in specific regions. As discussed previously, modelling herd as a fixed effect
525 estimates the herd effects independently for each herd. When herd sizes are large, such as in
526 advanced economies, this can reduce bias caused by differences in the genetic means of
527 different herds. Herd sizes are not large in LMIC smallholder dairy production systems. In such
528 circumstances, modelling herd as a random effect in genetic evaluations allows phenotypes
529 recorded in small herds to partially and proportionately contribute to the genetic evaluation.
530 This benefit extends to small herds composed of cows of varying relatedness, with the ancestral
531 haplotypes only present in that herd. This is important in an LMIC smallholder dairy
532 production systems context, with more than 70% of milk in Kenya produced by herds of one
533 to five cows [6,7]. However, the choice between modelling herd as a random effect should
534 consider the bias-variance trade-off [34]. This choice is particularly important if correlations
535 between herd management and the genetic value of cows exist. Under this scenario, if the

differences in genetic means across herds are not accounted for, the herd effect of an animal may be partially assigned to the genetic effect when herd is modelled as a random effect. In our study, cattle were assigned to herds at random and no correlation between herd management and the genetic value of cows existed. Therefore, significant bias effects were only detected in genetic evaluations modelling herd as a fixed effect with an average herd size of one (results not shown). There is another impact of the simulation not modelling the full complexity of the distribution of cattle and its genetic effects across farms. The training sets likely had an increased genetic connectedness compared to practical genetic evaluations in LMIC smallholder dairy production systems. This resulted in accuracies of EBVs that are likely to be higher than expected in practical genetic evaluations in LMIC smallholder dairy production systems. However, our study also did not capture the full complexity of the interaction between genetic connectedness and herd size. Therefore, our results likely underestimated the benefits of GBLUP to increase genetic connectedness and more accurately separate the genetic and environmental components of each cow's phenotype in small herds in practical genetic evaluations in LMIC smallholder dairy production systems. With the projected increases in data recording, we expect that these effects will diminish or that the scale of the data will enable at least reasonably high accuracy to stimulate genetic progress.

*Impact of simplified breeding goal*

The breeding program examined in this simulation only considered a single quantitative trait that did not interact with the environment. The breeding goal for practical LMIC smallholder dairy production systems would be much more complex in practice. It would comprise of several correlated traits (e.g., milk yield, milk components, fertility, feed requirements, heat tolerance, disease resistance) many of which would interact with the environment. The single quantitative trait with 10,000 QTL that we simulated is representative of such an index with a few additional assumptions: all traits are measured on all animals, all

561 traits are pleiotropic, and economic merit is linear. This study simulated a simplified genetic
562 architecture without considering dominance, epistasis and gene by environment interaction.
563 This will likely decrease the absolute values of accuracy reported in this study but the main
564 conclusions of our study (i.e., that GBLUP is more powerful than PBLUP in LMIC smallholder
565 dairy production systems for several reasons) will still hold.

566 **Prospects for animal breeding in LMICs**

567 Our motivations for undertaking this study were to contribute to the enabling of the
568 sustained and long-term use of animal breeding to improve agricultural productivity and
569 sustainability in LMIC smallholder dairy production systems. Breeding has been hugely
570 successful for improving animals and plants in advanced economies and for improving plants
571 in LMICs. Breeding has had limited success in improving animals in LMICs. We believe that
572 for animal breeding to be successful in LMIC smallholder dairy production systems it must be
573 driven by data recorded *in-situ* on animals from such farms. We believe that the limited success
574 of animal breeding in these contexts is due to the infrastructure and data structures that are
575 prevalent in these systems, which make genetic evaluation using pedigree difficult, if not
576 impossible. Specifically, the infrastructure required to record pedigree over long periods of
577 time is typically absent in LMIC smallholder dairy production systems. The lack of widespread
578 use of AI and the small herd sizes result in a data structure that has insufficient genetic
579 connectedness between herds to facilitate genetic evaluations based on pedigree. We believe
580 that genomic data offers a route to overcome these problems and the results of our study show
581 this. However, our study did not quantify the long-term impacts of genomic data in LMIC
582 smallholder dairy breeding programs. As an example, our study demonstrated that the EBVs
583 of young bulls from an average herd size of 1 ($\mu$=1.58) could be predicted with an accuracy of
584 0.40. However, as well as increasing the accuracy of selection, genomic evaluations also offer
585 an opportunity to reduce the generation interval of breeding programs. These reductions in the

586 generation interval have been the primary driver of the gain in the rate of genetic improvement
587 in dairy breeding programs in advanced economies because they have approximately halved
588 the generation interval, thereby doubling the rate of genetic gain [20]. In LMIC breeding
589 programs, it is difficult to estimate the reductions in the generation interval that genomic
590 evaluations could provide. This is due to the lack of pedigree recording and infrastructure for
591 the widespread use of AI, already discussed. However, it is possible to say that genomic
592 evaluations will allow LMIC breeding programs to drive the generation interval to near the
593 biological and economic minimum for that system. The impact of this, and the other results
594 from our study, on the long-term genetic gain of LMIC smallholder dairy breeding programs
595 will need to be explored further.

596 Genomic data is expensive and its requirement may create a new cost barrier to the
597 success of animal breeding in LMIC smallholder dairy production systems. New business
598 models are needed to overcome this barrier in a self-sustaining way. One such model could
599 involve establishing an intertwined breeding and dissemination program for a target
600 environment. The cost of operating the breeding program would need to be proportionate to
601 the market that it would serve via its dissemination program. The breeding program could
602 comprise an informal set of nucleus animals distributed across many small herds within the
603 target environment. These nucleus animals could be genotyped and phenotyped and this data
604 used for a genetic evaluation using GBLUP. The best animals from this nucleus could be
605 disseminated via artificial insemination (with or without a subsequent progeny testing scheme),
606 as natural service sires, or as heifers. Further, the genomic prediction equation calculated for
607 the genetic evaluation could be used to select any external animals that would be imported into
608 the region. To reduce the costs of data recording in the nucleus and to increase the value of
609 what would be disseminated a whole range of additional technologies and services could be
610 bundled together. For example, nucleus herds could also serve as demonstration herds and the

611 dissemination program could provide additional extension services (e.g., a text message for a
612 small fee with management or market information). Or improved animal genetics could be
613 packaged together with other technology (e.g., improved seeds) which may have higher
614 adoption rates. Overall, a business model could be constructed that bundles technology, data
615 recording, extension services, and a marketplace for LMIC smallholder farmers. This type of
616 self-sustaining platform would maximize the benefits and cost-efficiency of any component
617 (e.g., the genotyping and phenotyping of animals). This business model could leverage the
618 successes of established technologies and practices to drive adoption of those that have been
619 traditionally more intractable. The Africa Dairy Genetic Gains [14], the Public Private
620 Partnership for AI Dissemination [15] projects and the emerging social enterprises (e.g., One
621 Acre Fund [39], and electronic marketplaces for agricultural products in LMICs (e.g.,
622 Livestock 247 [40]) show that many components of such a model are already in place.

# Conclusions

This study has demonstrated the potential of genomic information to be an enabling technology in LMIC smallholder dairy production systems by facilitating genetic evaluations with *in-situ* records collected from farms with herd sizes of four cows or less. Across a range of breeding designs, genomic data made it possible to accurately predict EBVs of phenotyped cows and young bulls using data sets that contained small herds that had weak genetic connections. The use of *in-situ* smallholder dairy data in genetic evaluations would establish breeding programs to improve *in-situ* germplasm and, if required, would enable the importation of the most suitable external germplasm. This could be individually tailored for each target environment. Together this would increase the productivity, profitability and sustainability of LMIC smallholder dairy systems. However, genomic data is expensive and business models will need to be carefully constructed so that the costs are sustainably offset.

# Declarations

## Ethics approval and consent to participate

Not applicable.

## Consent for publication

Not applicable.

## Availability of data and material

The simulated data and materials are availailable upon request.

## Competing interests

The authors declare that they have no competing interests

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## Author's contributions

JMH conceived the study. JMH and OP designed the study. OP performed the analysis. OP and JMH wrote the manuscript. RM, RCG, MJ and GG helped interpret the result and refined the manuscript. All authors read and approved the final manuscript.

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# Figures

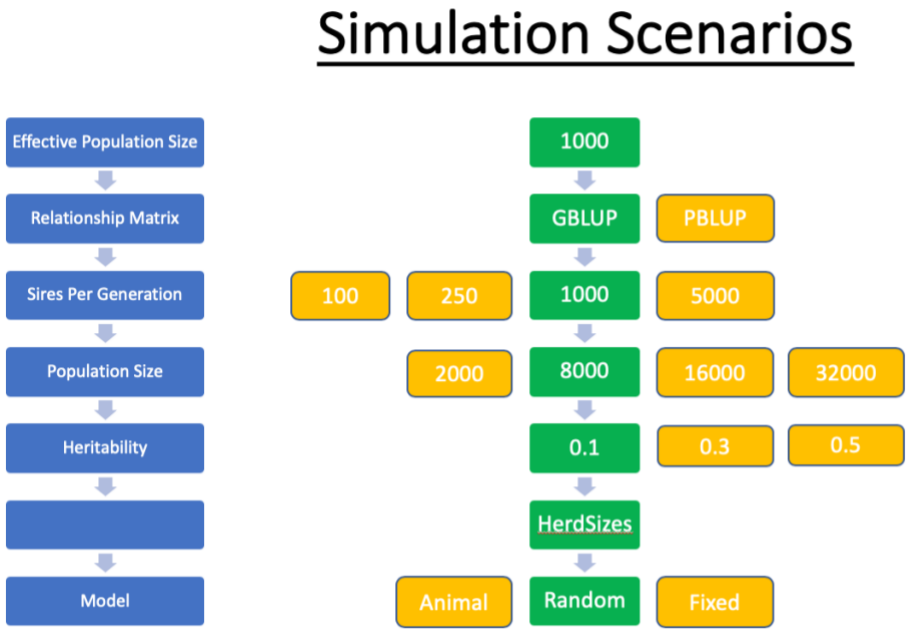



*Figure 1.* ***Simulation scenarios.*** *The conventional breeding design is highlighted in green. Breeding designs were compared for each design parameter individually (horizontally), while keeping all other design parameters fixed at the values of the conventional breeding design.*

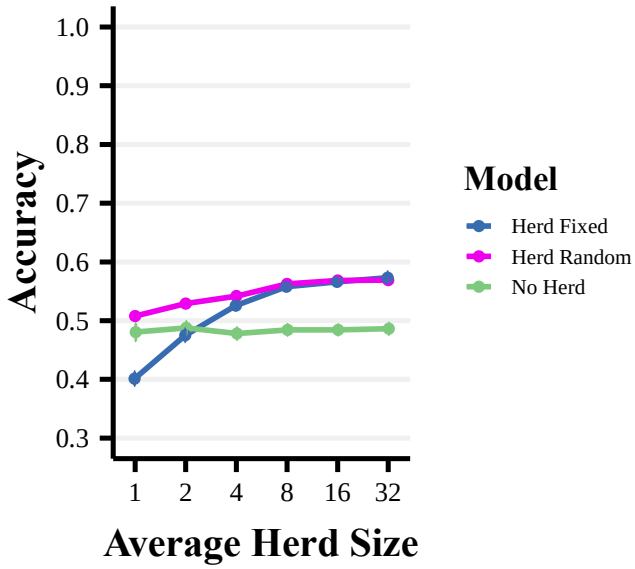
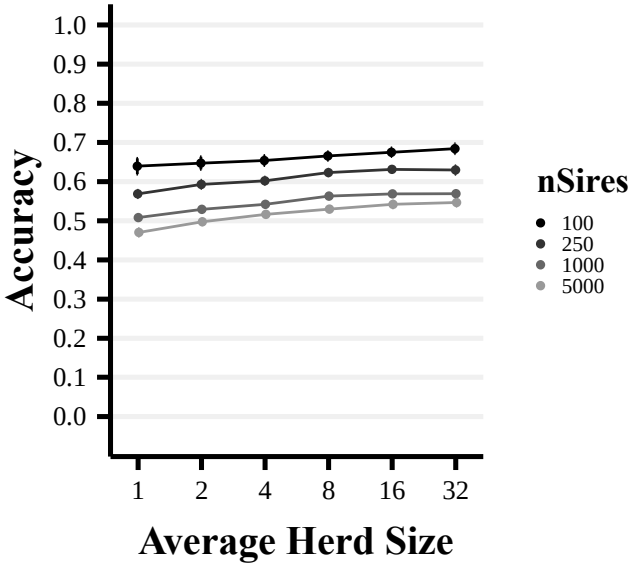



*Figure 2.* ***The impact of the model on EBV accuracy of cows****. Comparison of the statistical modelling of herd under the LMIC design with GBLUP. The accuracy of estimated breeding values as a function of average herd size (1-32) and the herd effect (i) excluded from the model (*[Symbol]*), (ii) modelled as a fixed effect (*[Symbol]*) and (iii) modelled as a random effect.*

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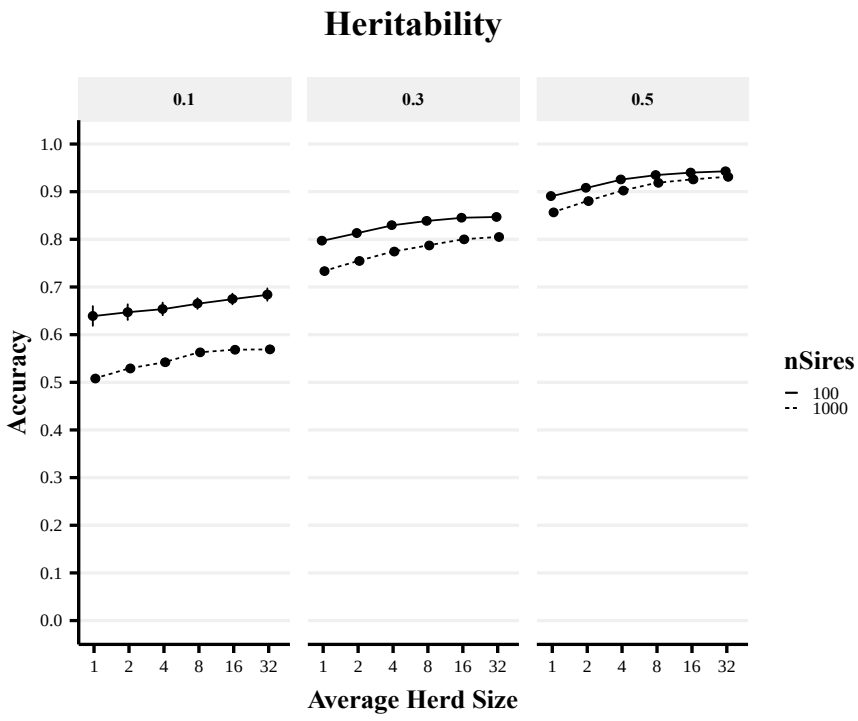
783 *Figure 3.* ***The impact of genetic connectedness on EBV accuracy of cows****. Comparison of genetic*
784 *connectedness of the training set with GBLUP. The accuracy of estimated breeding*
785 *values are presented as a function of average herd size (1-32) and the number of sires (100, 250, 1000*
786 *& 5000). The number of records in the training set is 8000. Herd is modelled as a random effect.*




787

788 *Figure 4.* ***The impact of genetic connectedness and heritability on EBV accuracy of cows.***
789 *Comparison of the heritability of the trait and genetic connectedness with GBLUP. The accuracy of*
790 *estimated breeding values as a function of average herd size (1-32) and the genetic connectedness of*

*the training set (100 & 1,000 sires per generation). The three panels correspond to the heritability of the trait (0.1, 0.3 & 0.5). Herd is modelled as a random effect.*

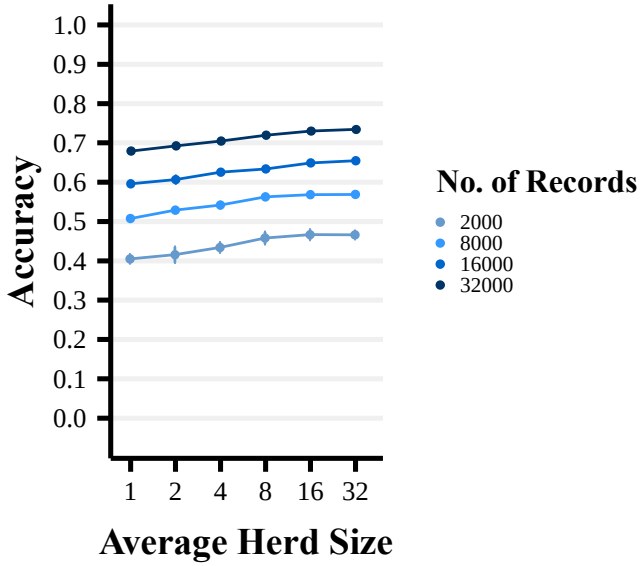



*Figure 5.* ***The impact of training set size on EBV accuracy of cows.*** *Comparison of the number of records in the training set with GBLUP. The accuracy of estimated breeding values of cows as a function of average herd size (1-32) and the number of records in the training set (2000, 8000, 16000 & 32000). Herd is modelled as a random effect.*

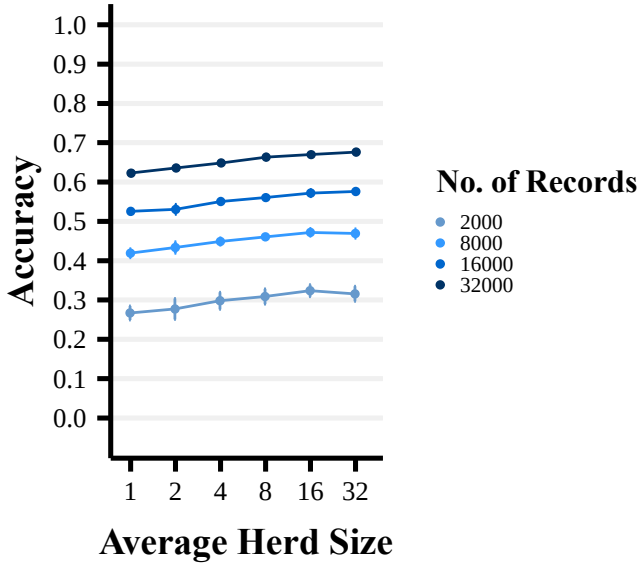
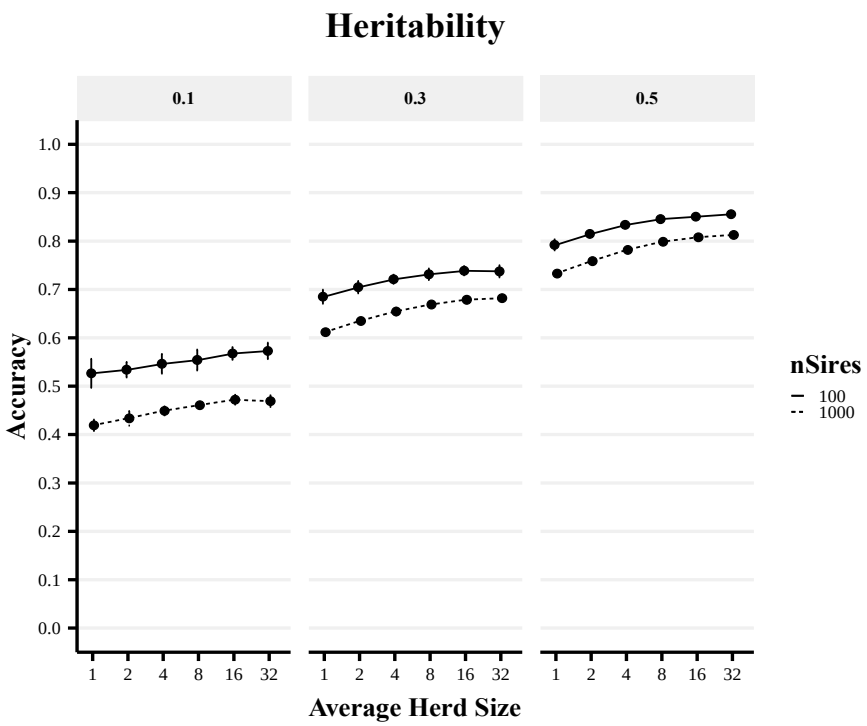



*Figure 6.* ***The impact of training set size on EBV accuracy of young bulls.*** *Comparison of the number of records in the training set and genetic connectedness with GBLUP. The accuracy of genomic estimated breeding values of young bulls as a function of average herd size (1-32) and the number of records in the training set (2000, 8000, 16000 & 32000. Herd is modelled as a random effect.*

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804 *Figure 7.* ***The impact of genetic connectedness and heritability on EBV accuracy of young bulls.***

805 *Comparison of the heritability of the trait with GBLUP. The accuracy of genomic estimated breeding*

806 *values of young as a function of average herd size (1-32) and the genetic connectedness of the*

807 *training set (100 & 1,000 sires per generation). The three panels correspond to the heritability of the*

808 *trait (0.1, 0.3 & 0.5). Herd is modelled as a random effect.*

809