Genetic parameters, predictions, and rankings for semen production traits in a Thailand multi-breed dairy population using genomic-polygenic and polygenic models

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ABSTRACT

The objectives were to compare estimates of variance components, genetic parameters, prediction accuracies, and rankings of bulls for semen volume (VOL), number of sperm (NS), and motility (MOT) using genomic-polygenic (GPRM) and polygenic repeatability models (PRM). The dataset comprised 13,535 VOL, 12,773 NS, and 12,660 MOT from 131 bulls collected from 2001 to 2017 in the Semen Production and Dairy Genetic Evaluation Center of the Dairy Farming Promotion Organization of Thailand. Genotypic data encompassed 76,519 actual and imputed SNP from 72 animals. The three-trait GPRM and PRM included the fixed effects of contemporary group, ejaculate order, age of bull, ambient temperature, and heterosis. Random effects were animal additive genetic, permanent environmental, and residual. Variance components and genetic parameters were estimated using AIREMLF90. GPRM heritabilities were slightly greater than PRM for MOT (0.27 compared with 0.24), and slightly less for VOL (0.11 compared with 0.12), and NS (0.17 compared with 0.19). Repeatabilities were slightly less for GPRM than PRM (0.44 compared with 0.45 for MOT, 0.26 compared with 0.28 for NS, and 0.20 compared with 0.21 for VOL). Additive genetic correlations were high between NS and MOT (GPRM: 0.76, PRM: 0.78), moderate between VOL and NS (GPRM: 0.43, PRM: 0.55), and near zero between VOL and MOT (GPRM: -0.13, PRM: 0.04). Rank correlations between GPRM and PRM estimated breeding values (EBV) were high for all traits. The similarity between GPRM and PRM results suggested that SNP data from the small number of genotyped animals had a minimal impact on genetic predictions in this population.

Keywords: Dairy bull; Genomic; Polygenic; Semen production; Tropical

1. Introduction

Artificial insemination (AI) is an essential technique for genetic improvement of milk production traits in Thailand dairy population. Holstein frozen semen from countries with high-producing Holstein populations (Canada, USA, Australia, Japan; Department of Livestock Development, 2015) has been introduced to genetically improve these traits in Thailand. Crossbreeding was initially used to combine the high milk producing capacity of Holstein with the desirable fertility and tropical adaptability of local cattle. These crossbred animals, however, could not produce enough milk to meet Thailand's demand. Thus, a national upgrading system was implemented to produce animals with a greater Holstein percentage breeding while retaining tropical adaptability. Both purebred and crossbred Holstein sires were used. The outcome of this mating system was a multi-breed dairy population composed of animals of a variety of percentages of Holstein and various other breeds (Brown Swiss, Jersey, Red Dane, Brahman, Red Sindhi, Sahiwal and Thai Native; Koonawootrittriron et al., 2009).

Semen traits are economically important for dairy producers because female AI conception rates are highly dependent on semen quantity and quality (Swanson and Herma, 1944; Seidel and Schenk, 2008). Quantity and quality of semen are assessed through semen volume (VOL), number of sperm (NS), and motility (MOT). Heritabilities for these traits ranged from moderate to high and the genetic correlations ranged from low to high in temperate regions (Taylor et al., 1985; Druet et al., 2009; Karoui et al., 2011; Atagi et al., 2017). Currently, there is neither a genomic-polygenic nor a polygenic evaluation for semen traits in the Thailand dairy multi-breed populations. There, however, is historical information available on VOL, NS, and MOT at the Semen Production and Dairy Genetic Evaluation Center of the Dairy Farming Promotion Organization of Thailand (DPO). This information could be used to obtain the estimates of variance components and genetic parameters needed to predict genetic values and rank sires for selection and mating purposes. Further, assessing the impact of genomic

information on the accuracy of genomic-polygenic relative to polygenic predictions and bull rankings also needs to be determined. Thus, the objectives of this research were 1) to estimate variance components, genetic parameters, and genetic predictions for VOL, NS, and MOT using genomic-polygenic and polygenic repeatability models, and 2) to compare the rankings of genomic-polygenic and polygenic EBV for VOL, NS, and MOT from AI sires in the top 5%, 10%, 15%, 20% and all sires in the DPO dataset.

2. Materials and methods

2.1. Data, animals and traits

Data were collected by the Semen Production and Dairy Genetic Evaluation Center of the DPO (Muaklek, Saraburi province, in Central of Thailand, 14º38′24.7″ latitude North, 101º11′57.2″ longitude East] from October 2001 to July 2017. Semen traits were: volume (VOL, ml), number of sperm (NS; million), and motility (MOT, %). Semen volume was the quantity of semen per ejaculation as measured in a scaled tube. Number of sperm per ejaculate was calculated by multiplying semen volume by sperm concentration. Sperm motility referred to the percentage of active motile sperm (average of two repeated measures of percentage of spermatozoa moving forward) analyzed with an optical microscope by a single trained technician. Bull identification, collection date and time, ejaculation number, ambient temperature (ºC), and collector's name were recorded at each semen collection. The phenotypic data file contained records from 131 bulls (13,533 VOL, 12,773 NS, and 12,660 MOT). Bulls were the progeny of 62 sires and 112 dams. The pedigree file included 304 bulls, sires, and dams. Numbers of records, means, SD, minima, and maxima for VOL, NS, and MOT are presented in Table 1.

Most bulls in the DPO dataset were Holstein crossbreds (95%), and the remaining 5% were purebred H. Bull Holstein percentage ranged from 62.5% to 100% (average = 92%). Bull

non-Holstein fractions were composed of various percentages of other breeds (Brown Swiss, Jersey, Red Dane, Brahman, Red Sindhi, Sahiwal and Thai Native breeds; Koonawootrittriron et al., 2009). Young bulls were trained for semen collection when bulls were between 10 and 18 mo of age. Semen was collected to produce frozen semen when bulls were older than 18 mo, once a week for bulls younger than 60 mo, and twice a week for bulls 60 mo or older. Semen continued to be collected from each bull until 25,000 doses of frozen semen were produced or when a bull reached approximately 108 mo of age.

2.2. Climate, nutrition and management

Weather in Central of Thailand is influenced by the southwestern (May to October) and northeastern monsoons (October to February). The average temperature during the years of the study was 22.3 ^{o}C (average minimum = 15 ^{o}C and average maximum = 34 ^{o}C), the average relative humidity (RH) was 69.3% (average minimum = 33% and average maximum = 97%), and the average rainfall was 1,243.1 mm (average minimum = 934 mm and average maximum = 1,615 mm). Monthly average temperatures, relative humidity, and rainfall were 24.3 ^{o}C, 63.3%, and 19.6 mm in January, 24.6 ^{o}C, 63.2%, and 29.3 mm in February, 30.9 ^{o}C, 67.2%, and 207.9 mm in March, 32.4 ^{o}C, 70.5%, and 304.4 mm in April, 31.4 ^{o}C, 75.5%, and 378.0 mm in May, 30.4 ^{o}C, 74.8%, and 317.2 mm in June, 27.6 ^{o}C, 74.5%, and 706.7 mm in July, 27.1 ^{o}C, 76.8%, and 852.3 mm in August, 26.6 ^{o}C, 81.4%, and 677.1 mm in September, 26.2 ^{o}C, 79.3%, and 691.9 mm in October, 25.6^{o}C, 71.3%, and 31.5 mm in November, and 23.7 ^{o}C, 65.1%, and 13.5 mm in December (Thai Meteorological Department, 2018).

Bulls were kept in open barn stalls until they were assessed to be ready for semen collection. Bulls were fed 4 to 6 kg/d of concentrate (16% of CP, 2% fat, 14% fiber, and 13% moisture; Charoen Pokphand Foods, Bangkok, Thailand) and 50 to 60 kg/d of roughage. Green roughage (Guinea grass; *Panicum maximum,* Ruzi grass; *Brachiaria ruziziensis,* Napier grass;

106 *Pennisetum purpureum,* and Para grass*; Brachiaria mutica*) was cut and transported to bull
107 stalls. When green roughage was limited (November to June), bulls were provided hay and
108 silage (Guinea and Ruzi grass). A mineral supplement was available throughout the year. Bulls
109 were dewormed and vaccinated against Foot and Mouth Disease and Tuberculosis every 6
110 months (Department of Livestock Development, 2011).
111
112 *2.3. Genotypic data*
113 Genotypes obtained from semen samples of 61 of 131 bulls with phenotypic records,
114 and from blood samples of 11 dams of sires available from previous research (Jattawa et al.,
115 2016) were used in this study. Briefly, DNA extraction from tissue samples (semen and blood),
116 and genotyping were as follows. The DNA was extracted from frozen semen with a GenElute™
117 Mammalian Genomic DNA Miniprep kit (Sigma®, USA), and from blood samples with a
118 MasterPure™ DNA Purification kit (Epicentre® Biotechnologies, USA). The quality and
119 quantity of extracted genomic DNA were measured with a NanoDrop™ 2000
120 spectrophotometer (Thermo Fisher Scientific Inc., Wilmington, DE, USA). Samples with a
121 DNA concentration of 15 ng/µl and an absorbance ratio of 1.8 at 260/280 nm were genotyped
122 with GeneSeek Genomic Profiler (GGP) chips (GeneSeek Inc., Lincoln, NE, USA). The 61
123 bulls were genotyped with GGP80K and the 11 dams of sires were genotyped with GGP9K.
124 The numbers of SNP were 76,694 for bulls genotyped with GGP80K and 8,590 for dams
125 genotyped with the GGP9K. Dams genotyped with GGP9K were imputed to GGP80K using
126 FImpute version 2.2 (Sargolzaei et al., 2014), as part of a previous study (Jattawa et al., 2016).
127 Imputation was conducted with the complete genotype dataset of the Thailand multi-breed
128 population that contained 2,661 genotyped animals (1,412 cows with GGP9K, 570 cows with
129 GGP20K, 540 cows with GGP26K, and 89 sires and 50 cows with GGP80K; Jattawa et al.,

2016). The SNP genotypes with a call rate of less than 0.9 or a minor allele frequency of 0.04 were discarded, resulting in an edited genotype file with 76,519 SNP markers per animal.

2.4. Estimation of variance components and genetic parameters

Variance and covariance components for VOL, NS, and MOT were estimated using the three-trait genomic-polygenic (GPRM) and polygenic repeatability models (PRM). With the GPRM, a single-step procedure was utilized that combined pedigree, phenotypic, and genotypic information (Legarra et al., 2009; Aguilar et al., 2010), whereas with the PRM only pedigree and phenotypic data were used. The three-trait GPRM and PRM were as follows:

$$\mathrm{y} = \mathrm{Xb} + \mathrm{Z_a a_a} + \mathrm{Z_p p_p} + \mathrm{e},$$

where y was a vector of bull VOL, NS, and MOT records, b was a vector of fixed effects that included contemporary group (year-month of collection), ejaculate order (first or second), age of bull (mo), ambient temperature (^{o}C), and heterosis as a function of heterozygosity ([sire Holstein fraction × dam O fraction] + [sire O fraction × dam Holstein fraction], where O = other breeds; Koonawootrittriron et al., 2009), a_a was a vector of random animal additive genetic effects, p_p was a vector of random permanent environmental effects, and e was a vector of random residuals. Incidence matrices X, Z_a, and Z_p related VOL, NS, and MOT records to elements of vector b, a_a, and p_p, respectively. Vector a_a was distributed with mean zero and variance equal to H $\otimes$ V_a for GPRM and to A$\otimes V_a$ for PRM, where V_a was a 3 × 3 matrix of additive genetic variances and covariances among VOL, NS, and MOT, and $\otimes$ was the Kronecker product. Vector p_p was distributed with mean zero and variance equal to I $\otimes$ V_{p_p}, where V_{p_p} was a 3 × 3 matrix of permanent environment variances and covariances among semen traits. Similarly, vector e was distributed with mean zero and variance equal to I $\otimes$ V_e, where V_e was a 3 × 3 matrix of residual variances and covariances among semen traits. The genomic-polygenic relationship matrix H (Legarra et al., 2009) was equal to,

155 $$H = \begin{bmatrix} A_{11}+A_{12}A_{22}^{-1}(G_{22}-A_{22})A_{22}^{-1}G_{21} & A_{12}\,A_{22}^{-1}G_{22} \\ G_{22}\,A_{22}^{-1}A_{21} & G_{22} \end{bmatrix},$$

156 where, A_{11} was the matrix of additive relationships among non-genotyped animals, A_{12} was the
157 matrix of additive relationships between non-genotyped and genotyped animals, A_{22}^{-1} was the
158 inverse of the matrix additive relationships among genotyped animals, G_{22} was the matrix of
159 genomic relationships among genotyped animals, $G_{22} = ZZ'/2\sum p_j\left(1-p_j\right)$, where p_j = frequency
160 of Allele 2 in Locus j, and the z_{ij} were equal to $(0 - 2p_j)$ for homozygous genotype 11 in locus
161 j, $(1 - 2p_j)$ for heterozygous genotypes 12 or 21 in Locus j, and $(2- 2p_j)$ for homozygous genotype
162 22 in Locus j (VanRanden, 2008; Aguilar et al., 2010). Matrix G_{22} was constructed using the
163 default weight factors (tau =1, alpha = 0.95, beta = 0.05, gamma = 0, delta = 0 and omega = 1),
164 and scaled using the default restrictions (mean of diagonal elements of G_{22} = mean of diagonal
165 elements of A_{22}, and mean of off-diagonal elements of G_{22} = mean of off-diagonal elements
166 ofA_{22}) defined by PREGSF90 of the BLUPF90 Family of Programs (Misztal et al., 2018).

167 The GPRM and PRM variance and covariance components for VOL, NS, and MOT
168 were estimated by restricted maximum likelihood (REML) using an Average-Information
169 algorithm with program AIREMLF90 (Tsuruta, 2014). Priors for genetic, permanent
170 environmental, and residual variances were estimated using single-trait analyses with the same
171 GPRM and PRM models described above. Priors for covariances were set to 10^{-5}. GPRM and
172 PRM heritabilities and repeatabilities for VOL, NS, and MOT as well as genetic, permanent
173 environmental, temporary environmental, and phenotypic correlations among these traits were
174 computed using the corresponding GPRM and PRM variance component estimates.

175

176 *2.5. Estimation of genomic-polygenic and polygenic breeding values and rank correlations*

177 Estimated breeding values (EBV) for VOL, NS, and MOT for all animals were obtained
178 with the three-trait GPRM and PRM described above using variance components obtained at

179 convergence for each model. Accuracies of EBV were calculated as $\left(\sqrt{1 - PEV/\widehat{\sigma_a^2}}\right) * 100$,

180 where PEV was the prediction error variance and $\widehat{\sigma_a^2}$ was the REML estimate of the additive
181 genetic variance. Associations between rankings of bull EBV for VOL, NS, and MOT computed
182 with GPRM and PRM were tested using Spearman's rank correlations using the Correlation
183 procedure of SAS (SAS, 2011). Spearman rank correlations between GPRM and PRM EBV for
184 the three semen traits were computed for the top 5% (n = 7), 10% (n = 11), 15% (n = 17), 20%
185 (n = 24), all bulls (n = 131), and only genotyped bulls (n = 61) to assess changes in rank at
186 various prediction levels.
187
188 **3. Results and discussion**
189 *3.1. Heritabilities and repeatabilities*
190 Estimates of additive genetic, permanent environmental, temporary environmental, and
191 phenotypic variance and covariances for VOL, NS, and MOT from genomic-polygenic
192 repeatability model (GPRM) and polygenic repeatability model (PRM) are reported in Table 2.
193 Estimates of additive genetic, permanent environmental, temporary environmental and
194 phenotypic variances were similar across models. The GPRM additive genetic variances were
195 2.3% less, permanent environmental variances were 6.0% greater, temporary environmental
196 variance were 5.5% greater, and phenotypic variances were 3.8% greater than those from PRM.
197 These GPRM and PRM variance components resulted in slightly lesser values of heritabilities
198 (-2.1%) and repeatabilities (-4.7%) for GPRM than for PRM (Table 3). This indicated that the
199 genotypic information from the 72 animals in this study had a small negative impact on the
200 estimates of variance components for these traits. This outcome, however, may change in the
201 future as additional phenotypic and genotypic information become available in the DPO dataset.
202 Heritability estimates and the SD for all traits from GPRM and PRM are presented in
203 Table 3. The heritability estimates for MOT were slightly greater when genotypic information

was used (0.27 for GPRM and 0.24 for PRM). Conversely, heritabilities for VOL and NS were slightly less when genotypic information was included in the model (VOL: 0.11 for GPRM and 0.12 for PRM; NS: 0.17 for GPRM and 0.19 for PRM). This indicated that GPRM accounted for additive genetic relationships among animals in this population more accurately resulting in greater heritabilities for MOT than from PRM. The GPRM and PRM heritabilities for VOL, NS, and MOT were within the range of values reported for various countries. The VOL heritabilities here were less than estimates from Holstein populations in France (0.22 of VOL; Druet et al., 2009), Spain (0.22 of VOL; Karoui et al., 2011), Poland (0.26 for VOL; Suchocki and Szyda, 2015) and Japan (0.42 for VOL; Hagiya et al., 2017). Conversely, the heritabilities for NS and MOT here were greater than estimates for Japanese Black bulls in Japan (0.09 for NS and 0.15 for MOT; Nishimura et al., 2010) and Nellore bulls in Brazil (0.11 for MOT; Silveira et al., 2012). Heritability values in a large Canadian Holstein dataset (5,644 records from 137 mature and 2,023 records from 61 young bulls) were greater than values in the present study for all three traits (VOL = 0.24 in young bulls and 0.44 in mature bulls; NS = 0.38 in young bulls and 0.54 in mature bulls; MOT = 0.31 in young bulls and 0.01 in mature bulls; Mathevon et al., 1998a). Heritability estimates for VOL, NS, and MOT in the present study were greater than values from Hereford data collected in the United States (0.09 for VOL and 0.22 for MOT; Kealey et al., 2006), Angus in the United States (0.13 for MOT; Knights et al., 1984; 0.05 for MOT; Garmyn et al., 2011), Herefords in the US (0.14 for NS; Neely et al., 1982), young Simmental in Croatia (0.04 for VOL; Kaps et al., 2000) and Brahman and Tropical composite bulls in Northern Australia (0.24 and 0.15 for MOT; Corbet et al., 2013). The large differences of heritability estimates for semen traits among studies may reflect differences in breed composition, numbers of animals in the study, environmental conditions, and methods of estimation of variance components. The lesser heritability values for VOL than for NS and MOT in the present study indicated that this trait was affected to a greater extent by environmental

229 factors (housing, nutrition, climate, health care) than the other two traits. All three traits,
230 however, could be included in selection programs to improve semen traits in this population
231 (greater selection responses would be expected for MOT and NS than for VOL). Selection for
232 these traits would be expected to positively affect bull fertility and semen production in the DPO
233 population. Further, selection of AI bulls based on genetic capacity to produce semen may also
234 lead to increases in the number of doses of frozen semen per bull (Mathevon et al., 1998a).

235 Repeatabilities for semen traits from GPRM and PRM were of a pattern similar to that
236 of heritabilities for VOL, NS, and MOT, however, values were greater due to the contribution
237 of permanent environmental variances (Table 3). Repeatabilities were high for MOT (0.44 ±
238 0.03 for GPRM and 0.45 ± 0.03 for PRM), and moderate for NS (0.26 ± 0.03 for GPRM and
239 0.28 ± 0.02 for PRM), and VOL (0.20 ± 0.02 for GPRM and 0.21 ± 0.02 for PRM). Repeatability
240 estimates for semen traits were from 47% to 88% larger than heritabilities indicating that
241 permanent environmental effects were important for semen traits in this population. The
242 repeatabilities for VOL, NS, and MOT from GPRM and PRM were within the range of estimates
243 of polygenic repeatabilities from various cattle populations. Repeatabilities for VOL (0.32 to
244 0.49) and NS (0.31 to 0.34) were moderate in French Montbéliard bulls (Mathevon et al.,
245 1998b). Similar moderate estimates of repeatability were estimated in US Holstein bulls (0.23
246 for VOL and 0.26 for NS; Taylor et al., 1985), and in Austrian dual-purpose Simmental bulls
247 (0.29 for VOL, 0.24 for NS; Gredler et al., 2007). Greater repeatabilities than values in the
248 present study, however, were estimated for VOL (0.57 to 0.59), NS (0.56 to 0.57), and MOT
249 (0.52 to 0.55) in Swedish Red-White and Swedish Friesian breeds (Stälhammar et al., 1989).
250 Repeatability values indicated that MOT would be more similar across semen samples of a bull
251 than NS and VOL, and that temporary environmental effects (seasonal changes, management,
252 nutrition) had a greater influence on these traits than additive genetic and permanent

environmental effects. This emphasizes the desirability of collecting several records per bull to decrease temporary environmental effects and help improve EBV accuracies for these traits.

3.2. Additive genetic, permanent environmental, and phenotypic correlations

Estimates of additive genetic, permanent environmental, temporary environmental, and phenotypic covariances for VOL, NS, and MOT from GPRM and PRM are shown in Table 2, and the corresponding correlations are presented in Table 3. The GPRM additive genetic covariances between VOL and NS, and NS and MOT were 12.6% less, permanent environmental covariance were 17.5% greater, temporary environmental correlations were 9.1 % greater, and phenotypic correlations were 5.9 % greater than those from PRM. Additive genetic, permanent environment, temporary environment, and phenotypic correlations between VOL and MOT were close to zero. Differences between GPRM and PRM correlations between VOL and NS, and between NS and MOT were of a similar pattern as differences between covariances. GPRM additive genetic correlations between VOL and NS, and NS and MOT were 12.2% less than PRM, GPRM permanent environmental correlations were 13.7% greater than PRM, GPRM temporary environmental correlations were 2.8% greater than PRM, and GPRM phenotypic correlations were 1.6% greater than PRM (Table 3).

Additive genetic correlations were positive and high between NS and MOT (0.76 ± 0.13 for GPRM and 0.78 ± 0.16 for PRM), positive and moderate between VOL and NS (0.43 ± 0.35 for GPRM and 0.55 ± 0.42 for PRM), and near zero between VOL and MOT (-0.13 ± 0.39 for GPRM and 0.04 ± 0.38 for PRM; Table 3). The positive GPRM and PRM additive genetic correlations between VOL and NS and between NS and MOT indicated that bulls with a greater NS tended to have a greater VOL and MOT and vice versa. Estimates of permanent environmental, temporary environmental and phenotypic correlations were of similar patterns as values for GPRM and PRM (i.e., positive and high between VOL and NS; from 0.66 ± 0.43

for PRM to 0.83 ± 0.44 for GPRM), positive and moderate between NS and MOT (from 0.46 ± 0.01 for PRM to 0.48 ± 0.01 for GPRM), and near zero between VOL and MOT (from -0.01 ± 0.49 for PRM to 0.20 ± 0.48 for GPRM; Table 3).

The GPRM and PRM aadditive genetic correlations between semen traits in the present study were within the range of estimates of polygenic additive genetic correlations in dairy and beef cattle breeds residing in locations where temperate environmental conditions prevail. Similar to results in the present study, additive genetic correlations between VOL and MOT were low in Canadian Holstein (0.14; Diarra et al., 1997), Normandes in France (-0.17 to 0.03; Ducrocq and Humblot, 1995), and Holsteins in Japan (0.16; Atagi et al., 2017), but moderate in Japanese Blacks (0.44; Atagi et al., 2017). Additive genetic correlations between NS and MOT in US Polled Herefords were greater (0.87), however, in Holsteins and Japanese Blacks in Japan were less (0.21 and 0.55; Atagi et al., 2017) than estimates in the DPO dataset. The additive genetic correlation between VOL and NS in the present study was comparable to Holsteins (0.48) in Japan and less than in Japanese Blacks (0.69; Atagi et al., 2017), and Holsteins in Poland (0.82; Suchocki and Szyda, 2015).

3.3. Accuracies and animal rankings

The EBV accuracies for VOL, NS, and MOT computed with GPRM and PRM are shown in Fig. 1 for all bulls (n = 131) and only for genotyped bulls (n = 61) in Figure 2. Mean EBV accuracies for all bulls tended to be greater for NS (82% for GPRM and 84% for PRM), followed by MOT (83% for GPRM and 79% for PRM), and the least accurate were those for VOL (70% for GPRM and 73% for PRM). Similarly, the greatest mean EBV accuracies for genotyped bulls only were those for NS (84% for GPRM and 84% PRM), followed by those for MOT (84% for GPRM and 82% for PRM), and lastly those for VOL (74% for GPRM and 73% for PRM). Mean GPRM EBV accuracies for only genotyped bulls were slightly greater than those for all bulls

303 (84% compared with 82% for NS, 84% compared with 83%, and 74% compared with 73% for
304 VOL). Mean GPRM EBV accuracies for all bulls were either slightly less (-2% for VOL and -
305 3% for NS) or slightly greater (4% for MOT) than mean PRM EBV accuracies, whereas mean
306 GPRM EBV accuracies for only genotyped bulls were either slightly greater than (1% for VOL
307 and 2% for MOT) or equal to (for NS) mean PRM EBV accuracies.

308 Prediction accuracies for semen traits were unavailable in the literature. The comparable
309 GPRM and PRM EBV accuracies in the present study are not consistent with the greater EBV
310 accuracies obtained for genomic-polygenic relative to polygenic models for milk production
311 traits in the Thailand dairy multi-breed population (5.2% to 7.2%; Jattawa et al., 2015) and in
312 North American Holsteins (23% to 29%; VanRaden et al., 2009; Schenkel et al., 2009).
313 Accuracy of genomic prediction is expected to increase as the number of genotyped animals
314 increases (Goddard, 2009; VanRaden et al., 2009). The marginal effect of genotypic information
315 on GPRM EBV accuracies was likely due to the small number of animals genotyped (72)
316 compared to the number of animals represented in these other studies (2,661 in Jattawa et al.,
317 2015; 5,335 in VanRaden et al., 2009; and 12,913 in Schenkel et al., 2009). Thus, as the number
318 of genotyped animals increases in future years, the advantage of GPRM over PRM in terms of
319 greater EBV accuracies may become more apparent.

320 Table 4 contains Spearman rank correlations between GPRM and PRM EBV rankings
321 for VOL, NS, and MOT in the top 5% (n = 7), 10% (n = 11), 15% (n = 17), 20% (n = 24), all
322 bulls (n = 131), and only genotyped bulls (n = 61). Rank correlations between GPRM and PRM
323 EBV for all bulls were slightly greater for NS (0.99) than for VOL and MOT (0.97). Rank
324 correlations for bulls in the top 5%, 10%, 15%, 20%, and only genotyped bulls tended to be
325 greater for NS than for VOL and MOT. Rank correlations between GPRM and PRM EBV across
326 traits ranged from 0.83 to 0.96 in the top 5% of bulls, from 0.90 to 0.98 in the top 10%, from
327 0.85 to 0.93 in the top 15%, from 0.84 to 0.91 in the top 20%, and from 0.94 to 0.99 for only

genotyped bulls. Rank correlations between GPRM and PRM EBV all bulls were more similar to those for only genotyped bulls than those for bulls in the top 5%, 10%, 15%, 20%, perhaps largely due to the greater percentage of bulls represented in these two groups of bulls as compared with the other four groups. These rank correlations indicated that the selection response would be largely similar when choosing bulls based on GPRM and PRM EBV rankings. As the number of genotyped animals increases in future years, however, differences between GPRM and PRM EBV for semen traits will likely become larger and favor the use of GPRM, making it the model of choice to optimize genetic progress for these traits in the DPO population. Further research with larger phenotypic, pedigree, and genotypic information needs to be conducted to verify these aspects as results may differ with additional future information.

4. Conclusions

Genomic-polygenic and polygenic repeatability models yielded comparable estimates of variance components and genetic parameters (heritabilities, repeatabilities, correlations). Mean GPRM EBV accuracies for all bulls were either slightly lesser or greater, but for only genotyped bulls were these either greater or equal to PRM EBV accuracies. Rank correlations between EBV from genomic-polygenic and polygenic repeatability models were high for all traits, indicating that selection response with both models would be similar. As genotypic information accumulates over time, however, the accuracy of genomic-polygenic EBV as well as selection response are expected to increase, making it the model of choice for the DPO population.

Conflict of interests

The authors declare that they have no conflicts of interest.

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Table 1

Descriptive statistics for semen volume, number of sperm, and motility

Traits	*n*	Mean	SD	Min	Max
Semen volume (ml)	13,535	5.8	2.0	1.5	12.0
Number of sperm (million)	12,773	6,012	2,175	1,600	11,000
Motility (%)	12,660	47.2	13.9	30.0	80.0

Table 2

Additive genetic, permanent environmental, temporary environmental, phenotypic variances and covariances for semen volume (VOL), number of sperm (NS), and motility (MOT) computed using two repeatability models

Variance component	Model[a]			
Additive genetic	GPRM	SE	PRM	SE
Var (VOL), ml^2	3,983	1,919	4,515	1,953
Cov (VOL, NS), ml*million	34,029	23,397	45,147	23,156
Cov (VOL, MOT), ml*%	-430	1,242	249	1,310
Var (NS), $million^2$	1,176,300	348,330	1,285,700	346,270
Cov (NS, MOT), million*%	62,449	19,973	62,797	20,779
Var (MOT), $\%^2$	5,777	1,635	5,098	1,741
Permanent environment	GPRM	SE	PRM	SE
Var (VOL), ml^2	3,592	1,767	3,122	1,724
Cov (VOL, NS), ml*million	41,766	21,148	31,012	19,687
Cov (VOL, MOT), ml*%	744	1,108	16	1,173
Var (NS), $million^2$	616,310	277,240	508,250	260,220
Cov (NS, MOT), million*%	29,720	15,727	29,652	16,524
Var (MOT), $\%^2$	3,550	1,348	4,344	1,547
Temporary environment	GPRM	SE	PRM	SE
Var (VOL), ml^2	30,105	284	28,547	271
Cov (VOL, NS), ml*million	318,420	2,044	292,200	1,917
Cov (VOL, MOT), ml*%	1,904	143	1,306	138
Var (NS), $million^2$	5,117,200	179	4,685,700	172
Cov (NS, MOT), million*%	116,660	1,937	106,870	1,815
Var (MOT), $\%^2$	11,605	146	11,386	143
Phenotypic	GPRM	SD	PRM	SD
Var (VOL), ml^2	37,688	1,093	36,194	1,102
Cov (VOL, NS), ml*million	394,420	13,776	368,560	13,870
Cov (VOL, MOT), ml*%	2,229	821	1,580	829
Var (NS), $million^2$	6,913,600	246,950	6,483,400	247,410
Cov (NS, MOT), million*%	209,030	15,150	199,520	15,193
Var (MOT), $\%^2$	20,941	1,248	20,839	1,259

[a]GPRM = Genomic-polygenic repeatability model; PRM = Polygenic repeatability model; SE = standard error; SD = standard deviation from 5,000 samples (Meyer and Houle, 2013)

Table 3

Estimates of heritabilities, repeatabilities, and correlations for semen volume (VOL), number of sperm (NS), and motility (MOT) computed using two repeatability models

Parameter	Model[a]			
	GPRM	SD [b]	PRM	SD
Heritability (VOL)	0.11	0.05	0.12	0.05
Heritability (NS)	0.17	0.05	0.19	0.05
Heritability (MOT)	0.27	0.07	0.24	0.08
Repeatability (VOL)	0.20	0.02	0.21	0.02
Repeatability (NS)	0.26	0.03	0.28	0.03
Repeatability (MOT)	0.44	0.03	0.45	0.03
Additive genetic correlation (VOL, NS)	0.43	0.35	0.55	0.42
Additive genetic correlation (VOL, MOT)	-0.13	0.39	0.04	0.38
Additive genetic correlation (NS, MOT)	0.76	0.13	0.78	0.16
Permanent environmental correlation (VOL, NS)	0.83	0.44	0.66	0.43
Permanent environmental correlation (VOL, MOT)	0.20	0.48	-0.01	0.49
Permanent environmental correlation (NS, MOT)	0.62	0.37	0.61	0.46
Temporary Environmental correlation (VOL, NS)	0.81	0.01	0.80	0.01
Temporary Environmental correlation (VOL, MOT)	0.10	0.01	0.07	0.01
Temporary Environmental correlation (NS, MOT)	0.48	0.01	0.46	0.01
Phenotypic correlation (VOL, NS)	0.77	0.01	0.76	0.01
Phenotypic correlation (VOL, MOT)	0.08	0.03	0.06	0.03
Phenotypic correlation (NS, MOT)	0.55	0.02	0.54	0.02

[a]GPRM = Genomic-polygenic repeatability model; PRM = Polygenic repeatability model

[b]SD = standard deviation from 5,000 samples (Meyer and Houle, 2013)

489 **Table 4**

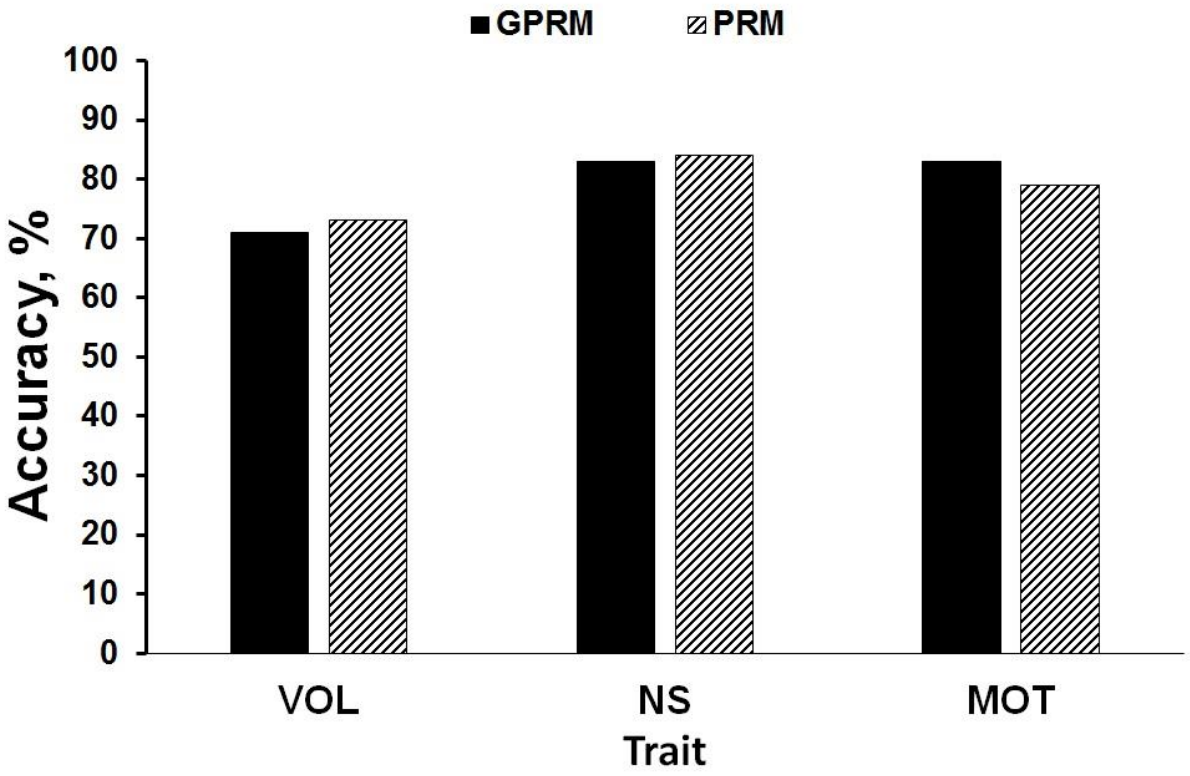
490 Spearman rank correlations between EBV for semen volume (VOL), number of sperm (NS),
491 and motility (MOT) computed using two repeatability models

492

Trait	Bulls[a]	GPRM, PRM[b]
VOL	Top 5% (7)	0.83
	Top 10% (11)	0.91
	Top 15% (17)	0.85
	Top 20% (24)	0.84
	100% (131)	0.97
	Genotyped only (61)	0.98
NS	Top 5% (7)	0.96
	Top 10% (11)	0.98
	Top 15% (17)	0.93
	Top 20% (24)	0.90
	100% (131)	0.99
	Genotyped only (61)	0.99
MOT	Top 5% (7)	0.86
	Top 10% (11)	0.90
	Top 15% (17)	0.88
	Top 20% (24)	0.91
	100% (131)	0.97
	Genotyped only (61)	0.94

493 [a]Numbers in brackets are percentages of animals in common between GPRM and PRM

494 [b]GPRM = Genomic-polygenic repeatability model; PRM = Polygenic repeatability model



495

496 **Fig. 1.** Mean EBV accuracy for semen volume (VOL), number of sperm (NS) and motility
497 (MOT) for all bulls (*n* = 131) evaluated with a genomic-polygenic repeatability model (GPRM)
498 and a polygenic repeatability model (PRM)

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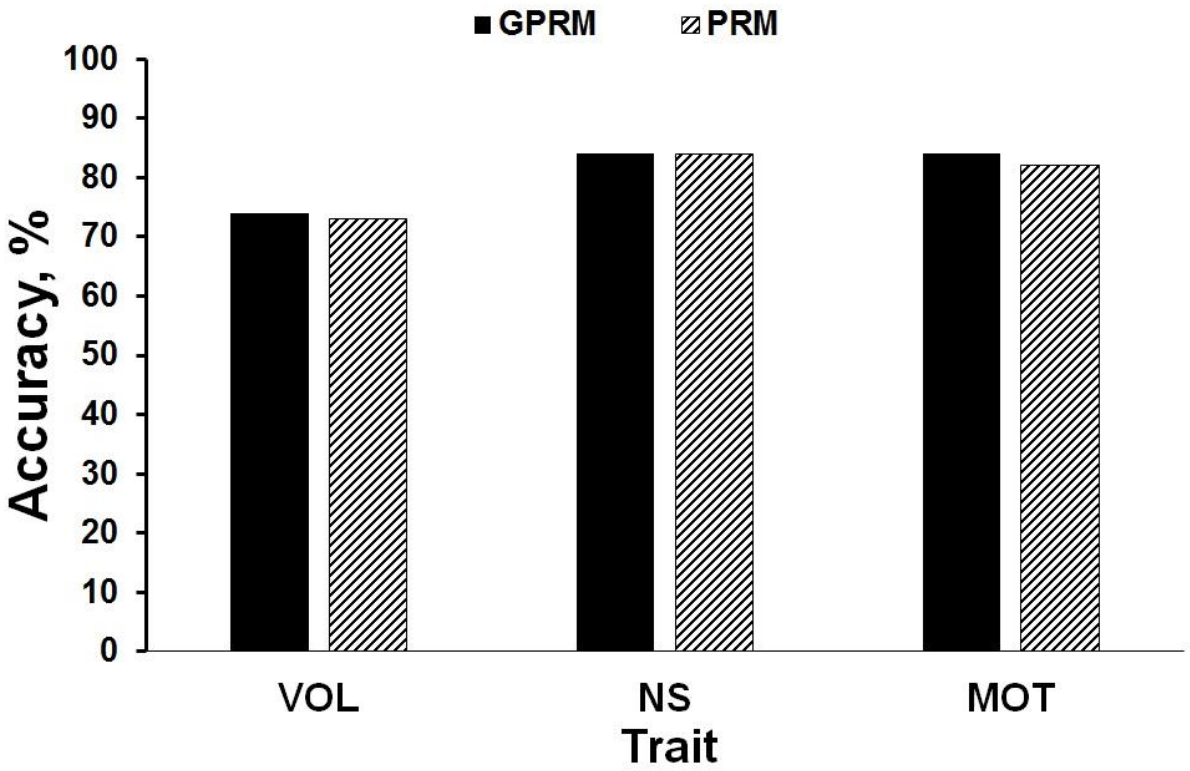

500

501 **Fig. 2.** Mean EBV accuracy for semen volume (VOL), number of sperm (NS) and motility
502 (MOT) for only genotyped bulls (n = 61) evaluated with a genomic-polygenic repeatability
503 model (GPRM) and a polygenic repeatability model (PRM)

504