Use of insemination data for joint evaluation of male and female fertility in predominantly seasonal-calving dairy herds

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ABSTRACT

Conception in dairy cattle is influenced by the fertility of the cow and the bull and their interaction. Despite genetic selection for female fertility in many countries, selection for male fertility is largely not practiced. The primary objective of this study was to quantify variation in male and female fertility using insemination data from predominantly seasonal-calving herds. Nonreturn rate (NRR) was derived by coding each insemination as successful (1) or failed (0) based on a minimum of at least 25 d. The NRR was treated as a trait of the bull with semen (male fertility) and the cow that is mated (female fertility). The data (805,463 cows that mated to 5,776 bulls) were used to estimate parameters using either models that only included bulls with mating data or models that fitted the genetic and permanent environmental (PE) effects of bulls and cows simultaneously. We also evaluated whether fitting genetic and PE effects of bulls as one term is better for ranking bulls based on NRR compared with a model that ignored genetic effect. The age of cows that were mated, age of the bulls with semen data, season of mating, breed of cow that mated, inbreeding of cows and bulls, and days from calving to mating date were found to have a significant effect on NRR. Only about 3% of the total variance was explained by the random effects in the model, despite fitting the genetic and PE effects of the bull and cow. The 2 components of fertility (male and female) were not correlated. The heritability of male fertility was low (0.001 to 0.008), and that of female fertility was also low (~ 0.016). The highest heritability estimate for male fertility was obtained from the model that fitted the additive genetic relationship matrix and PE component of the bull as one term. When this model was used to calculate bull solutions, the differ-

ence between bulls with at least 100 inseminations was up to 19.2% units (-9.6 to 9.6%). Bull solutions from this model were compared with bull solutions that were predicted fitting bull effects ignoring pedigree. Bull solutions that were obtained considering pedigree had (1) the highest accuracy of prediction when early insemination data of bulls, and (2) improved model stability (i.e., a higher correlation between bull solutions from 2 randomly split herds) compared with the model which fitted bull with no pedigree. For practical purposes, the model that fitted genetic and PE effect as one term can provide more accurate semen fertility values for bulls than the model without genetic effect. To conclude, insemination data from predominantly seasonal-calving herds can be used to quantify variability between bulls for male fertility, which makes their ranking on NRR feasible. Potentially this information can be used for monitoring bulls and can supplement efforts to improve herd fertility by avoiding or minimizing the use of semen from subfertile bulls.

Key words: male fertility, female fertility, evaluation, cross-validation

INTRODUCTION

In dairy cattle the successful selection for milk production traits has led to a decline in female fertility due to the unfavorable genetic correlation between fertility and production traits (e.g., Lucy, 2001; Berry et al., 2014; Ma et al., 2019). As a result, dairy cattle genetic improvement programs have expanded their breeding goals to include female fertility, which has subsequently led to an improvement in female fertility. However, fertility is a complex trait that is influenced by both female and male fertility and their interaction. The contribution of male fertility has been given less attention, presumably on the assumption that the AI industry can properly screen and standardize the quality of semen before it is widely distributed. However, the economic effect of even a small difference in semen fertility between bulls is likely to be large because nor-

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mally one bull is mated to thousands of females, and the benefit of using bulls with better semen fertility is immediate and has a direct effect on overall herd fertility.

In most countries, bull fertility is a phenotypic evaluation used to rank bulls (e.g., Carrick et al., 2000; Kuhn and Hutchison, 2008; Berry et al., 2014). With the recent shift in the dairy industry toward the intensive use of young genomically selected bulls, exploring causes of variation in bull fertility early has become an emerging area of research (Taylor et al., 2018; Haile-Mariam and Pryce 2019). The renewed interest in assessing the extent of genetic variation in male fertility is partly because of the potential to carry out genomic-enabled screening of bulls before extensive use for semen collection and mating (Abdollahi-Arpanahi et al., 2017; Rezende et al., 2020).

Furthermore, recent genome-wide association studies have identified SNPs, or chromosome regions, that affect both male and female fertility (Peñagaricano et al., 2012; Fortes, et al., 2013). As expected, some of the regions associated with male fertility could be affected by selection for milk production (Peñagaricano and Khatib, 2012; Ma et al., 2019). This suggests a possible unfavorable genetic correlation between male fertility and milk production (Khatib et al., 2010; Lan et al., 2013), similar to the relationship between female fertility and milk production (Lucy, 2001; Berry et al., 2014; Haile-Mariam and Pryce 2019). From this, it might be tempting to hypothesize that male and female fertility may be genetically correlated. If the genetic correlation is high, then information on male fertility, which can be available on young bulls before their progeny are born, can be used to screen bulls for female fertility. Literature estimates of genetic correlations between male and female fertility vary from -0.51 (e.g., Varona and Noguera, 2001) to near zero (e.g., Meyer et al., 1991; David et al., 2007) to 0.73 (e.g., Johnston and Moore 2019; Piles et al., 2005) and may differ between breeds in addition to purpose (i.e., dairy versus beef).

The objectives of this study were (1) to explore the quality of the nonreturn rate (**NRR**) data from predominantly seasonal-calving herds in Australia by estimating fixed effects and comparing the solutions with results in the literature; (2) to quantify the extent of genetic variation in male and female fertility by analyzing NRR as a trait of both the bull with semen (male fertility) and the cow (female fertility) by fitting the genetic effect of the bull and the cow and the permanent environmental effect of the bull and the cow; and (3) to test whether fitting the permanent environmental (**PE**) and genetic effect of AI bulls as one term can help to improve prediction of yet-to-be observed insemination of bulls, compared with fitting bull only, which is the

current approach for predicting semen fertility value of bulls in Australia (Carrick et al., 2000).

MATERIALS AND METHODS

Data and Deriving Nonreturn Rate Measure

For this study we accessed data that are routinely used for evaluation of NRR of AI bulls, which is published as semen fertility value (**SFV**) by DataGene Ltd., Melbourne, Australia. DataGene has been using these data to calculate SFV, which is a phenotypic evaluation of AI bulls for fertility of their semen (Carrick et al., 2000). The SFV for Jersey bulls from Australia and the service bull conception rate from the United States were jointly used for genomic evaluation of male fertility recently by Rezende et al. (2020). The NRR of bulls collected between 2004 and 2019 were used for this study. About 73% of the insemination data used in this study were from seasonal or split (twice yearly) calving herds and 27% from year-round calving herds.

In Australia, 25-d NRR is used to rank bulls on success of their insemination data (Carrick et al., 2000). A 25-d NRR is shorter than that used in most other countries (e.g., Clay and McDaniel, 2001; Cassell et al., 2003) and is assumed to be more suitable for calving systems dominated by seasonal or split calving, because natural service bulls are normally introduced before the end of the mating season to maximize the number of cows that get pregnant in the shortest possible time. The research that developed the methodology for evaluation of SFV of bulls in Australia (Carrick et al., 2000) found that a period shorter than 25 d would incorrectly classify more cows as pregnant, whereas a period longer than 25 d would also mean that the outcome of most inseminations would be unknown and would reduce the amount of usable data. In seasonal-calving herds with a strict AI mating period, NRR is valid if there is an opportunity to observe cows for at least 25 d before the end of the AI mating season following a previous insemination. Therefore, cows that were mated toward the end of the mating season that were not observed for at least 25 d and inseminations that took place after 150 d from calving for the first time in seasonal-calving herds were excluded. For year-round calving herds, such restrictions were assumed to be unnecessary. In all cases, any information (mating or insemination) that indicates that an insemination has failed was used if available at the time of data extraction. This means that any insemination or natural mating that occurred anytime within the lactation was used to change a successful insemination (1) to a failed insemination (0).

For this study, the service date of all AI bulls that were mated to cows where the outcome of the mating

Table 1. The structure of data used for analyses

Item	All data	Holstein (bull and cow)
No. of records	2,069,915	1,445,525
No. of bulls with mating data	5,776	4,159
No. of cows with mating data	805,463	575,291
No. of sires of cows with data	18,898	12,950
No. of bulls that are sire of cows with mating	4,395	3,264
No. of herds	1,836	1,701
Mean NRR ¹ (%)	50.47 (50.00) ¹	48.59 (49.98) ¹

¹NRR = nonreturn rate. Standard deviation given in parentheses.

could be coded as not returned (1) or returned (0) were used. Inseminations of virgin heifers were excluded, because the use of sexed semen and insemination following synchronization were more common in heifers than in cows and currently this information is not recorded. For each cow, within a mating season (i.e., lactation) only the first 3 inseminations were considered. For cows with more than 3 inseminations, the third insemination is coded as failed (0), and all subsequent inseminations were ignored. Inseminations recorded in the first 12 parities were considered. Inseminations were valid if they were performed at least 15 d after calving. When 2 inseminations occurred less than 10 d apart, only the second insemination was assumed to be valid. For this study we accessed data of 5,576 bulls that mated to 805,463 cows in 1,836 herds (see Table 1) from the DataGene database, Melbourne, Australia. In total, close to 2.2 million inseminations (matings) were used in this study (Table 1), and the number of inseminations per bull varied from 10 to a maximum of 43,075. In these data, about 79% of the inseminations were carried out by farmers (also called DIY inseminations) and the rest by AI technicians.

Statistical Analyses

Fixed effects and variance components for random effects were estimated using a mixed linear model in ASReml (Gilmour et al., 2015). The response variable was NRR, coded as 100 (not returned) and 0 (returned). For this study the insemination data of all breeds of bulls [e.g., Holstein (**Hol**), Jersey (**Jer**), Red breeds, Brown Swiss] and cows (e.g., Hol, Jer, Red breeds, Brown Swiss, crossbreeds), were used.

The fixed effects fitted included the age of the cow (in years), which was highly correlated with parity of cow, mating number, month of mating, cow breed, the data processing center that provided the data, age of the bull at insemination (in years), days from calving to AI date, days from mating date to the end of the AI period of the herd-year, and inbreeding (**F**) of the cow and of the bull. Age of cow, age of bull, days from calv-

ing to AI date, and days from insemination to end of AI period were fitted as covariates (linear and quadratic regression). Days from insemination date to end of AI date was fitted for seasonal-calving herds where the start and end of the AI period could be determined. Inbreeding of the cow and of the bull were fitted both as a linear regression or as classification variables. A contemporary group effect based on the combination of herd-year of insemination for herds that performed their own (DIY) AI and herd-year-AI technician for inseminations performed by AI technician was also fitted. Heterosis and bull breed were not part of the final model because they did not have significant effect.

The following random effects were fitted depending on the model used: (1) the PE effect of the bull with semen and (2) the PE effect of cow that was mated, (3) the genetic effect of the bull with additive relationship matrix (**A**), and (4) the genetic effect of the cows with **A**. Mainly we tested 4 models, which are a subset of the models fitted by David et al. (2007). In this study we tested model 1 and model 2, which treated NRR data as the trait of the bull (male fertility) and the trait of the cow (female fertility), respectively. In model 3 NRR was treated as both the trait of the bull and of the cow without estimating covariance. Model 4 is the same as model 3 but allowed for estimation of covariance between them.

The most complete statistical model (model 4) in matrix notation can be written as

$$\mathbf{y} = \mathbf{X}\mathbf{b} + \mathbf{W}_1\mathbf{bullpe} + \mathbf{W}_2\mathbf{cowpe} + \mathbf{Z}_1\mathbf{bullped} + \mathbf{Z}_2\mathbf{cowped} + \mathbf{e}, \quad [1]$$

where **y** is the vector of observations (NRR), **b** is the vector of fixed effects; **bullpe** is the vector of the random PE effect of the bull with semen; **cowpe** is the vector of the random PE effect of the cow that was mated; **bullped** is the vector of the additive genetic effect of the bull with semen; **cowped** is the vector of the additive genetic effect of the cow that was mated; **e** is the vector of random residual effect; **X**, **W**₁, **W**₂, **Z**₁, and **Z**₂ are incidence matrices that associate ob-

servation to levels of fixed effects, bull and cow PE effects, and the additive genetic effects of both bulls and cows through numerator relationship, respectively. Assumptions about the expectation of the model were as follows: $E(y) = Xb$, $E(\text{bullpe}) = 0$, $E(\text{cowpe}) = 0$, $E(\text{bullped}) = 0$, $E(\text{cowped}) = 0$, and $E(e) = 0$; and assumptions about the variances were $\text{Var}(\text{bullpe}) = \text{bullpe} \otimes \mathbf{I}_1$, $\text{Var}(\text{cowpe}) = \text{cowpe} \otimes \mathbf{I}_2$, and $\text{Var}(e) = e \otimes \mathbf{I}_e$, where $\mathbf{I}_1$, $\mathbf{I}_2$, and $\mathbf{I}_e$ are identity matrices. The residual error variance was assumed to be normally and independently distributed.

With regard to the genetic effects, it was assumed that

$$\begin{matrix} \text{bullped}_1 \\ \text{cowped}_2 \end{matrix} \sim MVN(0, \mathbf{G} \otimes \mathbf{A}), \quad \text{where}$$

$$\mathbf{G} = \begin{bmatrix} \sigma_{\text{bull}}^2 & \sigma_{\text{bull,cow}} \\ \sigma_{\text{cow,bull}} & \sigma_{\text{cow}}^2 \end{bmatrix}. \quad \text{The } \mathbf{G} \text{ matrix becomes diagonal when the covariance between male and female genetic effect is ignored; } MVN \text{ is multivariate normal distribution; } \mathbf{A} \text{ is additive relationship matrix; and } \otimes \text{ is the Kronecker matrix product.}$$

In addition, we tested model 1a, which fitted the random bull and cow effects, and model 1b, which fitted the genetic and PE effect of the bull as one term with $\mathbf{A}$ and the random effect of the cow. Model 1a is the model currently used by DataGene to calculate SFV for bulls (Carrick et al., 2000), and model 1b is an alternative model tested in this study. The pedigree data for forming $\mathbf{A}$ included all animals and their parents from the master pedigree of DataGene.

Effect of Genomic Selection on Variation in Semen Fertility of Bulls. To assess whether the intensive use of young genomically selected bulls for a short time before adequate screening has increased genetic variance in NRR of bulls (e.g., Taylor et al., 2018), the NRR data of bulls born before 2012 (i.e., 2004 to 2011) and after 2011 (i.e., 2012 to 2018) were also analyzed separately using model 1 and model 1b.

Comparison of Models for Predicting SFV of Bulls. This was performed by predicting bull solutions using 2 models and 2 validation approaches. The 2 models were (1) the current model, which is used by DataGene for calculating SFV (i.e., model 1a); and (2) model 1b, which fitted the genetic and PE effect of bulls as one term with $\mathbf{A}$. For the first validation approach, the entire mating data set was split into 2 random sets (even or odd herds), and bull solutions were predicted using each data set. Then the correlations between bull solutions from the 2 herd groups were compared for each model. In the second validation approach, we used early data (i.e., mating data up to 2016, or 75% of the total data) to predict bull solutions of the future data (mating data of 2017 to 2019) based

on the 2 models. The main aim of the first approach was to assess the stability of the models, and that of the second approach was to compare the predictive ability of 2 models (i.e., cross-validation). Correlations between bull solutions based on different number of inseminations were calculated using each model, assuming that a higher correlation between bull solutions from the 2 randomly grouped herds is an indicator of model stability. Similarly, for bulls with mating data in the 2 time periods, correlations between bull solutions based on early and future data were compared for the 2 models.

Bull Solutions for Male and Female Fertility.

The mean and the standard deviation (SD) of bull solutions for male and female fertility were tabulated to demonstrate the extent of variability. Because bull solutions from different models of the current analyses were similar, bull solutions from model 1b (the genetic and PE effects were fitted as one term) and model 4 (both female and male fertility were jointly analyzed, considering genetic correlation between them) are tabulated. Presence of any undesirable phenotypic (NRR) or genetic trend in male fertility and female fertility was assessed using data from this study. Genetic trends for male (by year of birth of bulls with insemination data) and female fertility (by birth of sires of cows with mating data) from both model 4 and phenotypic trend (based on year of mating) adjusted for all fixed effects are plotted.

RESULTS

Mean NRR and Fixed Effects

The mean NRR of the data of all breeds was 50.5%, with SD of 50.0%, and that of the Hol breed only (both Hol bulls and cows) was lower at 48.9% (Table 1). The effect of month of insemination, which had a significant effect on NRR, is shown in Figure 1, with the proportion of inseminations that were carried out each month. The NRR was lower in the first 3 mo of the year (the summer months) than in the winter and spring months in Australia. In the first part of the year between January and April, the number of inseminations recorded were also fewer compared with the rest of the year.

The effect of age of cow and bull at insemination on NRR is shown in Figure 2. The NRR decreased with age of cow, where the difference between 2-yr-old cows and the oldest cows (15 yr old) was over 26%. The age of a bull when its semen is used for mating has a small but significant curvilinear relationship with the success of inseminations, where NRR increased up to about 4 yr of age and stabilized and started to decline (Figure 2). Repeated insemination of cows also increased NRR,

Figure 1. Solution (Sol) of nonreturn rate (NRR) for month of mating and proportion (Prop) of matings by the month.

where the difference between the first mating and the third mating was as high as 11.8%, but only 5% of the cows were mated for the third time. Days from calving to mating date had a curvilinear relationship with NRR, where the lowest NRR was observed when cows were mated early relative to calving, and NRR increased up to approximately the mean interval of 90 d and started to decline thereafter. However, as the effects of days to mating date and number of insemina-

tions are somewhat confounded, these results should be interpreted with caution. Days from mating to the end of AI period had a less pronounced curvilinear relationship with NRR. As expected, cows that were observed for a shorter period (~ 25 d) showed higher NRR than cows that were observed for longer period. This relationship can be approximated by a regression line (-0.01% NRR per day of increase in time from mating to the end of the AI period) with an R^2 of 0.78.

Figure 2. Effect of age of cow and bull at mating, in years, on nonreturn rate (NRR).

When the effect of inbreeding (F) was fitted in the model as covariate, F of the cow and of the bull were highly significant ($P > 0.0001$) and significant ($P > 0.05$) on NRR, respectively. This was despite the higher F levels in bulls (mean 4.25%) than in cows (mean 2.63%). In cows NRR decreased by $-0.72 \pm 0.34\%$ for every 1% increase in F. When the F of cows and bulls were fitted as class variables [0% F (level 1) to 10% F and above (level 11)], the greatest reduction in NRR was observed in cows with 7 and 8% F compared with noninbred cows. The NRR for cows with 7 and 8% F were $-2.78 \pm 0.36\%$ and $-3.00 \pm 0.51\%$ lower, respectively. In the case of bulls' F, significant declines relative to noninbred bulls were observed after F reached 6% (-1.27 ± 0.40), and the maximum decline of -1.56 ± 0.57 was for bulls with F of 10% and more.

The breed of the bull used for insemination did not have a significant effect on NRR, but the breed of the cow that was mated had a significant effect. Relative to Jer cows, the NRR of Hol cows was ($-3.56 \pm 0.25\%$), and that of Australian Red breeds cows was ($1.42 \pm 0.51\%$; i.e., higher than that of Jer cows). The NRR of 3/4-Hol 1/4 Jer crosses (-2.76 ± 0.32) were closer to those of Hol cows than to those of Jer cows. We found that F₁ Jer-Hol crosses had higher NRR (1.58 ± 0.28) if their sire breed was Jer than if their sire breed was Hol (-0.22 ± 0.38).

Variance Components and Genetic Parameters

Table 2 shows the variance components estimated using several models. In comparing the models using likelihood ratio tests, model 4 was not better than model 3. We also found little difference in model fit between models 1a and 1b. Both models 3 and 4, which included both female (cow) and male (bull) genetic effects with PE effects of the cow and the bull, fitted the data better than all the other models. The proportion of the total variance explained by the random effects of the models was between 2.6 and 2.9% (Table 2). The sum of the cow genetic and PE variance components accounted for about 2.26% of the total variance. The variance explained by the bull was close to 0.5% when the genetic and PE effects were fitted with A of the bulls as one term. Heritability and repeatability for male and female fertility from the different models were very similar (Table 2). The genetic correlation estimate between male and female fertility was effectively zero (Table 2).

For practical purposes, if the interest is to assess male fertility joint analyses with female using a genetic model, model 3 or model 4, in our case, produced similar results to the model that did not account for the genetics of the cow provided the random cow effect

Table 2. Number of levels and variance components and their SE, based on all breeds' data with complete pedigree using model 1 (bull fertility),¹ model 2 (cow fertility), model 3 (bull and cow fertility jointly ignoring genetic correlation), and model 4 (bull and cow fertility jointly accounting for genetic correlation)

Random effect	Level	Model 1 estimates	Model 1a estimates	Model 1b estimates	Model 2 estimates	Model 3 estimates	Model 4 estimates
Bull or permanent (PE)	5,576	8.99 ± 0.69	11.54 ± 0.49	—	11.51 ± 0.49	8.95 ± 0.72	8.89 ± 0.73
Cow permanent (PE)	804,938	47.96 ± 1.51	47.93 ± 1.51	47.94 ± 1.51	18.52 ± 1.88	18.59 ± 1.88	15.99 ± 1.89
Bull genetic	24,483	2.75 ± 0.69	—	14.94 ± 0.67	—	2.76 ± 0.80	2.85 ± 0.82
Cow genetic	1,398,276	—	—	—	34.17 ± 1.60	34.17 ± 1.60	35.18 ± 1.62
Residual variance (σ_e^2)		2,196.42 ± 2.60	2,196.45 ± 2.60	2,196.62 ± 2.60	2,194.11 ± 2.59	2,194.04 ± 2.59	2,194.98 ± 2.60
Prop. var. explained ²		0.026 ± 0.001	0.026 ± 0.001	0.028 ± 0.001	0.028 ± 0.001	0.029 ± 0.001	0.028 ± 0.001
Prop. bull var. ³		0.005 ± 0.000	0.005 ± 0.000	0.007 ± 0.000	0.005 ± 0.000	0.005 ± 0.000	0.005 ± 0.000
Prop. cow var. ³		0.021 ± 0.001	0.021 ± 0.001	0.021 ± 0.001	0.015 ± 0.001	0.023 ± 0.001	0.023 ± 0.001
h^2 bull ⁴		0.001 ± 0.000	—	0.007 ± 0.000	—	0.001 ± 0.000	0.001 ± 0.000
h^2 cow ⁵		—	—	—	0.016 ± 0.001	0.015 ± 0.001	0.016 ± 0.001
Genetic correlation bull and cow		—	—	—	—	—	-0.058 ± 0.074

¹Models 1a and 1b fitted bull effect and both permanent environmental (PE) and genetic (G) effects jointly, as PE and G effects, respectively.

²Proportion of variance explained by all random effects.

³Bull and cow effects (PE and or G) of the total variance.

⁴Heritability of bull = $\sigma_{\text{bull genetic}}^2 / (\sigma_{\text{bull genetic}}^2 + \sigma_{\text{bull PE}}^2 + \sigma_e^2)$.

⁵Heritability of cow = $\sigma_{\text{cow genetic}}^2 / (\sigma_{\text{cow genetic}}^2 + \sigma_{\text{cow PE}}^2 + \sigma_e^2)$.

Table 3. Variance components and genetic parameters ($\pm$ SE) of pre- and postgenomic bulls, using 2 models (model 1¹ and 1b²)

Item	Pregenomic		Postgenomic	
Mean NRR ³ (SD)	51.22 (49.99)		49.35 (50.00)	
Number of bulls	3,531		2,045	
	Model 1	Model 1b	Model 1	Model 1b
Bull genetic variance	2.36 $\pm$ 0.92	13.52 $\pm$ 0.80	3.24 $\pm$ 1.29	15.64 $\pm$ 1.10
Bull PE	8.80 $\pm$ 0.93	—	9.63 $\pm$ 1.27	—
Cow variance (PE)	44.95 $\pm$ 2.08	44.91 $\pm$ 2.08	41.51 $\pm$ 3.37	41.59 $\pm$ 3.37
Residual variance	2,185.0 $\pm$ 3.34	2,185.00 $\pm$ 3.34	2,204.57 $\pm$ 4.99	2,204.71 $\pm$ 4.99
Bull ratio	0.005 $\pm$ 0.000	—	0.006 $\pm$ 0.000	—
Cow ratio	0.020 $\pm$ 0.001	0.020 $\pm$ 0.001	0.018 $\pm$ 0.001	0.018 $\pm$ 0.001
Male h ²	0.001 $\pm$ 0.000	0.006 $\pm$ 0.000	0.002 $\pm$ 0.001	0.007 $\pm$ 0.001

¹Fitted the permanent environmental (PE) effect of bull and cows and the genetic effect of the bull.²As model 1, but fitted PE and the genetic effects as one term.³NRR = nonreturn rate.

is included (model 1). Similarly, if the objective is to quantify the genetic effect of female fertility, only fitting the bull with insemination data should be considered (model 2 versus 3). Fitting both PE and the genetic effect of bulls as one term with **A** (model 1b) captured about 29% more variance than fitting the bull effect only (model 1a) and about 27% more variance than fitting the PE and genetic effects each separately in the same model (model 1, Table 2).

Effect of Genomic Selection on Genetic Variation in Semen Fertility

The variance components and parameters estimates based on 2,045 bulls born after the introduction of genomic selection (i.e., born after 2011) and 3,531 bulls born before the introduction of genomic selection (i.e., born between 2002 and 2011) are shown in Table 3. The genetic variance captured by the bull (male fertility)

has increased by up to 37% in the postgenomic era compared with the pregenomic era (Table 3).

Comparison of Models for Predicting SFV of Bulls

Table 4 shows that the correlation between bull solutions estimated using odd and even herds was more stable under model 1b (genetic and PE effect fitted as one term with **A**) than model 1a (fitting bull effect). Even for bulls with at least 400 matings (i.e., the publication criterion of DataGene), using model 1b was better than model 1a in terms of model stability. For bulls with at least 1,000 inseminations (Table 4), the correlation between bull solutions from the 2 models were nearly identical.

Table 5 shows that accuracy measured as the correlation between bull solutions of early and yet-to-be-observed data using model 1b is consistently better than model 1a (by 0.04 to 0.05 units).

Table 4. Correlations between bull solutions when predicted based on mating data from even and odd herds using model 1a¹ and model 1b²

No. of bulls	Minimum no. of matings per bull	Correlation of bull solutions of even with odd herds ¹	Correlation of bull solutions of even with odd herds ²	Correlation between bull solutions from models 1a and 1b
5,018	All	0.19	0.25	0.90
3,759	40	0.21	0.26	0.91
2,215	100	0.25	0.29	0.93
1,097	200	0.28	0.32	0.95
486	400	0.41	0.46	0.97
220	800	0.42	0.46	0.97
161	1,000	0.55	0.58	0.98
66	2,000	0.78	0.80	0.98

¹Fitting bull effect (model 1a).²Fitting bull genetic and permanent environmental effect as one term (model 1b). Minimum of number of matings per bull in odd herds.

Table 5. Correlations between bull solutions predicted based on early mating data (before 2017) with solutions predicted based on late data (2017 to 2019) using model 1a and model 1b

No. of bulls	Minimum no. of matings per bull ¹	Model 1a ²	Model 1b ³	Bull solutions from models 1a and 1b (later data)
1,690	1_1	0.121	0.171	0.857
1,135	10_10	0.148	0.199	0.894
689	40_40	0.193	0.236	0.921
536	100_50	0.212	0.256	0.929
369	100_100	0.226	0.266	0.949

¹Number of matings in periods 1 and 2, respectively.²Fitting bull effect.³Fitting bull genetic and permanent environmental effect as one term.

Mean Solutions for Male and Female Fertility and Their Correlation With Other Economic Traits

Table 6 shows the mean and SD of solutions for bulls with at least 40 inseminations based on model 4 and model 1b. Overall, the SD of male fertility (bull solutions) when estimated using model 1b was about half the SD for female fertility. The variation among bulls, when estimated based on the fitting the genetic effect after accounting for PE (i.e., model 4), was about half that where both were fitted as one term (model 1b). The variation among bulls based on their average NRR (unadjusted) was twice that of female fertility.

The correlation between bull solutions based on a genetic model that considered genetic and PE effects as one term and that which accounted for PE was high (0.84). All other correlations between bull solutions from the models that fitted genetic and PE effect separately (i.e., models 3 and 4) were close to 1. Similarly, correlations between bull solutions for female fertility were close to 1. When bull solutions for male and female fertility were estimated using the same model (model 4), then the correlation between them was effectively 0 (~0.02–0.06). Correlations of bull solutions for male fertility with some selected economic traits, including Best Performance Index (the economic index in Australia), were also effectively zero. The correlation

between bull solutions for female fertility from models 2 or 3 or 4 (which had a correlation of more than 0.98 with each other) with female fertility EBV from the routine national genetic evaluation was 0.73.

The genetic trends for male and female fertility and the phenotypic trend for NRR are shown in Figure 3. The genetic trend for male fertility by birth year of bulls was slightly positive, whereas the phenotypic trend, which was the mean solution for year of mating, was negative until 2015. By contrast, female fertility, which was based on year of birth of bulls with daughters in this data, showed a positive genetic trend over time (Figure 3).

DISCUSSION

One of the objectives of this study was to assess whether male fertility can be used to improve genetic evaluation for female fertility. The results show that the correlation between male and female fertility is effectively zero, so there is little benefit of joint genetic evaluation of female and male fertility. Thus, if the aim is to calculate bull solutions using insemination data, the simplest model that fitted the random effect of the cow is adequate. Similarly, if the aim is to use the mating data to evaluate female fertility, ignoring the genetic effect of bulls has little effect on the evaluation of female fertility. These results agree with those reported by David et al. (2007), who tested up to 8 different models.

The other objective of this study was to quantify the extent of variance in male fertility that is captured by the bulls with insemination data and to assess whether there are practical benefits of fitting the genetic effect of bulls, compared with fitting bull effect only, when evaluating bulls for semen fertility. Based on model comparisons, fitting of the genetic and PE effects as one term was better than fitting bull without genetic effect in terms of model stability and predictive ability. Despite this, the genetic variance captured by the bull

Table 6. Mean (SD) and range in bull solutions for male and female fertility (%) from the model that considered genetic correlation (male and female fertility) and male fertility that jointly fitted genetic and permanent environmental (PE) effects

Trait	Mean (SD)	Minimum	Maximum
Male fertility genetic ¹	−0.22 (1.12)	−5.77	3.42
Female fertility ¹	−1.28 (4.43)	−20.13	15.41
Male genetic ignoring PE ²	−0.61 (2.17)	−18.09	9.65
Average raw NRR ³ (%)	51.29 (8.54)	11.11	96.61

¹Model 4.²Model 1b.³NRR = nonreturn rate.

Figure 3. Genetic trend based on bull solutions by birth year and phenotypic trend by year of mating. NRR = nonreturn rate; fert = fertility.

and the heritability of male fertility is still small, and improving male fertility through selection will remain difficult. Nevertheless, the selective use of bulls with better NRR could have an immediate effect on herd fertility. For example, bull solutions generated from the model that fitted the genetic and PE effect as one term (model 1b) can supplement information on semen parameters when screening and monitoring bulls by AI companies. When sourcing semen from different bulls, farmers could also consider bull solutions as additional screening criteria and use this information to avoid or minimize the use of semen from subfertile bulls.

Mean NRR and Fixed Effects

The mean NRR in the current study was lower than the mean of 56% reported by Carrick et al. (2000), who used data from Australian herds that were mated between 1994 and 1998. The mean NRR in the current study are similar to the 51% reported for Irish herds, including several breeds (Berry et al., 2011). The slightly higher NRR in Jer (51%) compared with Hol cows (48%) observed in the current study is similar to the those reported by Cassell et al. (2003) based on US data.

The significant fixed effects in this study had considerable similarity to comparable effects in other studies (e.g., Cassell et al., 2003; Clay et al., 2004; Kuhn et al., 2008; Kuhn and Hutchison, 2008; Berry et al., 2011), suggesting that the insemination data from mostly

seasonal-calving herds in Australia is of reasonably good quality. The lower NRR observed in the summer months in Australia agree with results observed in the United States, where the lowest conception rates were in July and August (Kuhn et al., 2008). The decrease in NRR with age of cow observed in the current study also agreed with literature (e.g., Cassell et al., 2003; Clay et al., 2004; Kuhn et al., 2008; Berry et al., 2011).

The observation that age of bull has a curvilinear relationship with NRR agrees with the findings of Kuhn and Hutchison (2008). As in the present study, Berry et al. (2011) also observed an increased NRR with the increase in the number of matings. The curvilinear relationship that was observed between NRR and days calving to mating date observed in the current study agrees with Haile-Mariam et al. (2004) working on 25-d first service NRR data of Australian dairy cattle.

Cows with 7 to 8% inbreeding (F) had around 3% lower NRR than noninbred cows, but bulls with inbreeding of 10% or more had 1.6% lower NRR. The effect of F of cows and bulls observed in this study is similar to that reported by Cassell et al. (2003) for Jer and Hol cows in US herds. Despite the higher F levels in bulls than in cows, our finding that the effect of bull F on NRR was less important and less consistent is in agreement with Cassell et al. (2003).

Kuhn et al. (2008) reported that the conception rate of bulls was affected by the milk yield of the cow they were mated to. Similarly, in this study we found that NRR of bulls that mated to cows with high milk yield

was lower than that of bulls that mated to cows with low milk yield. In this study, fitting milk yield or omitting it from the model had no effect on the proportion of variance explained by the bull (results not shown) and the bull solutions (correlation between bull solutions of ~ 0.99). Because of this we chose to analyze the mating data of more cows, including those without milk yield data. This is because about 15% of the cows with NRR data did not have milk yield data.

Variance Components and Genetic Parameters

The analyses of NRR data of Australian dairy cattle to quantify the variance explained by bulls and cows showed that a large proportion of the variance remained unexplained. The observation that the proportion of variance explained by the models is low agrees with other studies that have analyzed similar data in dairy cattle (Cassell et al., 2003) and in sheep (David et al., 2007). The heritability estimate of female fertility from this study is low and agrees with findings from other studies (e.g., Cassell et al., 2003; Haile-Mariam et al., 2004; David et al., 2007).

The heritability of male fertility, which is even lower than female fertility, agrees with several other studies (David et al., 2007; Kuhn and Hutchison, 2008; Berry et al., 2011). However, heritability estimates for male fertility are affected by several factors. First, in this and several other studies (e.g., Berry et al., 2011; Kuhn et al., 2008), the adjustment for nuisance factors that affect male fertility could not be performed to the same extent as for female fertility. For example, the age of the bull at the time of mating and the F of the bull are the only fixed effects for which a correction could be made. The age of bulls when semen is collected and information on volume, concentration, dilution rate, and batch of semen, which are known to affect semen fertility (e.g., Mathevon et al., 1998), were not available. Our inability to correct for these variables is likely to have affected the accuracy of the parameters estimated. Second, the modeling of male fertility in some of the models used in this study (e.g., models 1, 3, and 4) and other studies which fit the genetic and PE effects of the bull (e.g., David et al., 2007; Berry et al., 2011) as separate components could be less than optimal and lead to low genetic variance of the bull. Modeling similar traits such as gestation length or calving ease, where direct genetic (equivalent to mated bull) and maternal (equivalent to the mated cow) genetic effects are fitted, does not separate the PE from the direct genetic effect. For example, analyses of calving ease data by Eaglen and Bijma (2009), where sire-maternal grandsire or animal models were used, fitted only the sire of the

calf or the calf itself with **A** without PE effects, respectively. In this study, when the bull with mating data was fitted as one term, the variance attributable to the bull increased by up to 5 times, from 2.75 (model 1) to 14.94 (model 1b, Table 2).

Third, when modeling male fertility using NRR data, the outcome of the mating is considered to be the trait of the bull in a sire model formulation, and the expectation is that the variance has to be multiplied by 4 to convert to an animal-model equivalent, particularly in the situation where the mating is successful, because it is actually the trait of the fetus. However, when the insemination fails and there is no fetus, this is not clear. To demonstrate this, we re-analyzed the data fitting a sire-maternal grandsire model (i.e., bull with mating data and the sire of the cow that mated) to estimate the variance captured by male and female fertility fitting the genetic and PE as 2 terms and fitting the genetic effect only (i.e., ignoring PE). Results from these analyses are presented in Appendix Table A1 for comparison. For both male and female fertility, the bull solutions from these analyses (Table A1) were similar to results shown in Table 2. When the sire (i.e., bull) variances are multiplied by 4 and converted to additive genetic variance and the bull solutions and their SD are multiplied by 2 and converted to EBV scale, the difference in SD between male and female fertility was reduced (Table A1). After such modifications, the SD of the EBV for male fertility from the model where the genetic (i.e., bull) and PE effects are fitted as one term (model 1b) was close to that of female fertility (Table A1). However, this rescaling does not change bull rankings.

Effect of Genomic Selection on Genetic Variation in Semen Fertility

That the genetic variance for male fertility in the postgenomic era increased by 9 to 37% compared with the pregenomic era agrees with Taylor et al. (2018), which suggests that these need to be monitored as more data from genomically tested bulls accumulates. However, the change in mean NRR is small (51 versus 49%), which agrees with results from Amann and De Jarnette (2012), who observed that the AI industry has continued to provide quality semen to the dairy industry during the genomic selection era.

Comparison of Models for Predicting SFV of Bulls

With regard to model stability, model 1b is better than model 1a by up to 20%, suggesting that model 1b will rank bulls more consistently. Similarly, the predic-

tion of masked future data is more accurate using model 1b than model 1a by up to 33%. That bull solutions predicted from the model fitted with the genetic and PE bulls as one term improved the accuracy prediction of bull solutions for NRR, compared with a model that ignored the genetic effect, is in general agreement with several recent studies (e.g., Abdollahi-Arpanahi et al., 2017; Rezende et al., 2020).

In addition to better model accuracy and stability, another benefit of model 1a is that bull solutions can be generated through relationships for animals without their own insemination data. When we calculated the correlation between bull solutions based on early data (i.e., pedigree) and bull solutions based on the later data (masked data), the accuracy for bulls with at least 40 inseminations in the later period was 0.094. This low accuracy could be because the evaluation relies on the male side of the pedigree, which could be incomplete for some bulls. An alternative is to use genomic-enabled evaluation (e.g., Peñagaricano et al., 2012; Abdollahi-Arpanahi, et al., 2017; Rezende et al., 2020), as most bulls have genotype data. Genomic-enabled predictions of bull fertility so far are based on 2-step genomic evaluation models using the service sire conception rate or SFV as response variable (e.g., Abdollahi-Arpanahi et al., 2017; Rezende et al., 2020). It would be interesting to assess the accuracy of genomic prediction from models that use the raw NRR and genotype data in a single-step genomic prediction model.

Mean Solutions for Male and Female Fertility and Their Correlation With Other Economic Traits

The genetic correlation between male and female fertility, which is estimated to be near zero, is within the range of most recent literature estimates (Clay et al., 2004; David et al., 2007). Berry et al. (2011) reported a slightly stronger positive correlation between male and female fertility based on bull solutions. The observation that the correlation between bull EBV from different models for both male and female are high is in agreement with results from David et al. (2007). The correlation between bull solutions that DataGene published as SFV and the bull solutions from the current analyses, where the genetic and PE were fitted as one term (model 1b), was high (0.93) for bulls with at least 400 inseminations. However, the SD of the bull solutions from the current analyses is 45% higher, which shows more spread and provides more opportunity for selection or screening. In the current analyses, the random effect of bull by year of mating (bull-year) was significant in most analyses, but correlation between bull rankings that ignored bull-year and that accounted for bull-year effect was high (0.98). The difference between

the worst and the best bull was reduced by almost 60% when bull-year effect was fitted, and most recent genomically tested bulls are used for a short time; thus, for practical purposes, the benefit of fitting bull-year effect may be small if any.

That the genetic correlation between bull solutions for male fertility and other economic traits is near zero agrees with findings by Clay and McDaniel (2001). When NRR data are treated as the trait of the bull (male fertility) and the cow (female fertility), the sire EBV for female fertility (from model 3 or 4) were highly correlated (0.73) with female fertility from the national genetic evaluations, expressed as 6-wk in-calf rate (largely based on calving interval). This suggests that the national genetic evaluation is improving both components of fertility [i.e., conception rate (NRR) and showing estrus early after calving].

CONCLUSIONS

The use of insemination data to evaluate male and female fertility, by treating the data as the trait of the bull and cow that are mated, respectively, showed genetic variability for both. Lack of genetic correlation between male and female fertility shows that prediction of bull solutions for male or female fertility can be performed using a simpler model. Estimates of bull solutions for male fertility considering pedigree and PE effect as one term were better in terms of model stability and predictive ability than the model ignoring the genetic effect. However, correlations between bull solutions for male fertility from different models are above 0.90 for bulls with over 400 inseminations. Overall insemination data from predominantly seasonal-calving herds can be used to quantify variability between bulls for male fertility. Potentially this can be used for monitoring bulls and making early decisions to avoid using semen from subfertile bulls.

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APPENDIX

Table A1. Genetic parameters for male and female fertility ($\pm$ SE) when analyzing nonreturn rate of all breed data using sire-maternal grandsire (mgs)

Item	Genetic and PE ¹ effect	Genetic and PE as one term
Male h^{22}	0.006 $\pm$ 0.001	0.026 $\pm$ 0.001
Female h^{23}	0.016 $\pm$ 0.001	0.021 $\pm$ 0.001
Total male variance	2,209.15 $\pm$ 2.87	2,212.23 $\pm$ 2.90
Total female variance	2,249.29 $\pm$ 2.46	2,249.53 $\pm$ 2.46
Male genetic variance, σ_M^2	12.40 $\pm$ 3.09	57.66 $\pm$ 2.78
Female genetic variance, σ_F^2	34.76 $\pm$ 2.68	45.18 $\pm$ 1.94
Ratio of cow to total female variance	0.023 $\pm$ 0.001	0.020 $\pm$ 0.001
Ratio of bull to total male variance	0.004 $\pm$ 0.000	—
SD of EBV (2 times progeny transmitting ability)		
Males (bulls with mating data)	1.48	4.28
Females (sires of cows)	4.21	4.21

¹PE = permanent environmental. Male additive genetic variance $\sigma_M^2 = 4\sigma_{bull}^2$; the mated female additive genetic variance $\sigma_F^2 = 4\sigma_{mgs}^2 + \sigma_{bull}^2 - 4\sigma_{bull,mgs}$, was derived as described by Eaglen and Bijma (2009) from the variances and covariances matrix of sire-(bull)-maternal grandsire (sire of the mated cow) models.

²Male h^2 = male genetic variance/total male variance.

³Female h^2 = female genetic variance/total female variance.