RANDOM REGRESSION FOR MODELING SEMEN FERTILITY IN HF PUREBRED AND CROSSBRED BULLS USING A BAYESIAN FRAMEWORK

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ABSTARCT

Data on insemination records of Holstein Friesian (HF) purebred (n=45,497) and crossbred (n=58,497) collected from the BAIF Research Foundation were utilized. The conception rate was modeled as a binary trait, using linear repeatability models. Random regression models (RRM) were used to obtain the trajectory of variance components across age of the bulls. Legendre Polynomials up to order of fit of 4 were used for the random effects of additive genetic and permanent environmental effects. 200,000 Gibbs samples were generated with a burn-in of 20,000 and thinning interval of 50 using the THRGIBBS1F90 program. Heritability estimates were very low (<0.1) in both breeds but peaked at the extreme ages. Heritability and repeatability estimates ranged between 0.038 (8 years) to 0.627 (10 years) and 0.060 to 0.809 respectively in purebreds. Narrower ranges of 0.010 (4 years) to 0.087 (11 years) and 0.532 to 0.832 for heritability and repeatability respectively, were obtained in crossbreds. Effect of permanent environment was low in purebreds compared to the crossbreds. The study using RRM was able to provide genetic parameter estimates of fertility for all ages throughout the productive lifespan of bulls.

Keywords: Conception rate, Gibbs sampling, heritability, Legendre polynomials

INTRODUCTION

India has the world's largest cattle population but the average milk yield per cow is lower compared to other developed countries which could be attributed to the lack of genetically superior animals. To increase India's milk production, several dairy development programs were implemented for crossbreeding and grading up indigenous and non-descript cattle. The most important biotechnological tool used is artificial insemination (AI) which allows the dissemination of a large number of semen doses from genetically superior bulls.

Most dairy development programs only incorporate milk production traits where the bulls are selected based on their dams' milk-producing ability. Semen production traits are

negatively correlated with the milk production traits (Hagiya *et al.*, 2018) which can lead to a decline in fertility that reduces the genetic gain and profitability in the long term.

The conception rate is measuring the non-return rate (NRR) after 56 to 76 days of the first AI service (Murray *et al.* 1983; Kuhn and Hutchison, 2008; Norman *et al.*, 2008). This can be used as a measure of male fertility which provides an index for genetic prediction of AI bulls. The outcome of an insemination event depends on male as well as female fertility (Averill *et al.*, 2006) but the correlation between male and female fertility is low which emphasizes the study of bull (male) fertility independently (Butler *et al.*, 2020). Directly measuring the conception rate provides a combined estimate of the manifestation of several semen traits. Haugan *et al.* (2005) demonstrated the superiority of elite bulls over ordinary bulls which reiterates the importance of the study of bull fertility.

Conception rate estimates collected at the field level (farmers' herds) are an important indicator of bull fertility, which depends on the semen quality. The main advantage of this study was these records of insemination that were available from the field level. This not only provides insights into the differences in fertility for purebreds and crossbreds but also helps us to understand the effects of various factors affecting fertility under practical situation of cattle rearing.

These insemination records are repeatable in nature and thus, random regression models can be beneficial for understanding the trajectories of underlying (co)variance structures over the age of the bulls. There are no studies available that have used random regressions for modeling conception rates and understanding the variability in bull fertility over the age of the bulls is important. This study is also unique as it compares two different genetic groups of purebred and crossbred Holstein Friesian bulls.

With this background, this study was undertaken to obtain the trajectories for conception rate over the productive lifespan of the bulls as well as to understand the differences between HF purebred and crossbred bulls.

MATERIALS AND METHODS

Semen collection

Semen collection was done at two semen stations located at Uruli Kanchan (Pune, Maharashtra) and Dharouli (Jind, Haryana). The frozen semen station at Uruli Kanchan is

situated at 18.5° N and 73.8° E at an altitude of 559 m above sea level and at Dharouli is situated at 29.2° N and 76.2°E at an altitude of 227 m above sea level.

Semen collection was done using a teaser bull in an artificial vagina when the bulls were sufficiently stimulated after 2 to 3 false mounts. The time between the two mounts differed between the bulls. 1 or 2 ejaculates were collected in a glass tube and stored at 37° C. Ejaculate volume was recorded directly and sperm concentration was estimated using a digital photometer (IMV technologies). Initial motility was assessed subjectively after semen dilution after which 0.25 ml straws with 20×10^6 spermatozoa per straw were prepared. Sealed and printed semen straws were then cooled to 4° C for 3 hours followed by stepwise cooling to reach -140° C over a span of 7 to 8 minutes and then immersion stored in liquid Nitrogen at -196° C using a programmable freezer (IMV technologies). Post-thaw motility was also assessed subjectively 24 hours post-freezing using a phase-contrast microscope. The ejaculates which did not fulfill the minimum standards (https://www.nddb.coop) were discarded though the records have been included in the analysis.

Artificial insemination

Data on conception rate was collected from the field where AI was done by Bharatiya Agro Industries Foundation's (BAIF) 170 cattle breeding stations. This included regions from Uttar Pradesh (Etah, Unnao, Bareilly, and Meerut districts), Bihar (Chhapra, Chhapra-Siwan, Siwan, Samastipur, and Vaishali districts), and Maharashtra (Jalgaon and Beed districts) states. AI service is provided at the farmer's doorstep when they contact the AI technician after which the pregnancy diagnosis is done trans-rectally 60 to 70 days later. All the information about the cow as well as the farmer maintaining it is recorded by the AI technician at the time of AI.

Data structure

The fertility trait of interest in the present study was the conception rate which was recorded as a binary trait with 1 (conceived) and 0 (not conceived). This is done to include all the information available and take into account all the factors that could affect male and female fertility to reduce bias (Averill *et al.,* 2004). 45,497 HF purebred and 58,497 HF crossbred insemination records from 87 purebred and 78 crossbred bulls were utilized for the study.

Factors included

Different factors that could affect the conception rate were identified from the data available. Berry *et al.* (2011) reported the importance of including these systematic factors in

the mixed models as they influence the ranking of bulls for their fertility. Fixed factors included in the analysis were the location of semen station (Pune, Jind), breed of the cow (HF purebred, HF crossbred), breed of the cow (exotic, indigenous, non-descript), the season of semen collection (summer- March to June, monsoon- July to October, winter- November to February), the year of semen collection (yearly intervals from 2010 to 2016), the season of AI (summer-March to June, monsoon- July to October, winter- November to February), the year of AI (yearly intervals from 2010 to 2016), the time of semen collection (hourly intervals between 5 AM to 12 PM), collection interval ($\leq$2 days, 3 days, 4 days, $\geq$5days), agro-climatic zone (Central plain of Uttar Pradesh, Mid-western plain of Uttar Pradesh, Western plain zone of Uttar Pradesh, North-west alluvial plain of Bihar, Central plateau with assured rainfall regions of Maharashtra), the body condition of the cow (No ribs exposed, 1 rib exposed, 2 ribs exposed, 3 ribs exposed, all ribs exposed), the heat stage in which AI was done (early, mid, late), parity (heifers, first, second, third, fourth, fifth, beyond fifth), and AI sequence (first, second). The age of the bull was taken as a covariate. The effects of the semen collector, bull, and AI technician were included as random effects.

Statistical analysis

The Bayesian approach was used for obtaining the posterior distributions of parameter estimates using MCMC (Markov Chain Monte Carlo) and the Gibbs sampling algorithm (Magnabosco et al., 2000) to generate Gibbs samples. The average of the samples (posterior mean) as a point estimate of variance components was calculated. The standard deviation of samples (posterior SD), which is corresponding to the standard error in a frequentist approach (e.g., REML) was also obtained. In this study, a linear model was used to model a binary trait like the conception rate instead of a threshold model as the number of observations was higher in which case the normality assumption of the linear models can be met. Guerra *et al.* (2006) have reported that linear and threshold models rank sires similarly. In general, logistic regression is used for modeling probability of binary outcomes but linear models have been a suitable alternative for use in mixed models, which enable estimation of variance components and further predict breeding value, corrected for various factors affecting the trait. (Gomila (2021).

Records beyond mean ± 4 SD were excluded before analysis as outliers to reduce the effect of sampling error. Collectors with less than 20 records, bulls with less than 30 records, and AI technicians with less than 100 records were eliminated from the analysis. The second

insemination recorded which were within 10 days of the first insemination were discarded. Records of cows that were sold or which died after the service were also eliminated. Exploratory and descriptive analysis of the traits was done using the "psych" package in R software. Eight models were formed with different interactions of the fixed factors. The best model with the lowest Deviance Information Criterion (DIC) was selected for the identification of fixed factors. The fixed factors that were significant at a 5% level of significance and were included in the further analysis were the breed of the bull, the breed of the cow, year of AI, location of semen station, body condition of the cow, parity of the cow, AI sequence, heat stage of the cow, and time of semen collection. The factors related to the cow which affect the bull fertility like the breed, body condition, parity, and heat stage of the cow are known as nuisance variables that were included to predict bulls' true capability of impregnating cows (Norman *et al.*, 2008; McWhorter *et al.,* 2020). The model can be represented as given below

$$Y_{ijklmnopqrstuv} = \mu + L_i + B_j + C_k + CT_l + +S_m + Y_n + R_o + H_p + P_q + A_r + W_s + U_t + T_u + e_{ijklmnopqrstuv}$$

$Y_{ijklmnopqrstuv}$	= Conception record
μ	= Overall mean
L_i	= Fixed effect of ith location
B_j	= Fixed effect of jth bull breed
C_k	= Fixed effect of kth cow breed
CT_l	= Fixed effect of lth collection time
S_m	= Fixed effect of mth AI sequence
Y_n	= Fixed effect of nth year of AI
R_o	= Fixed effect of oth body condition of the cow
H_p	= Fixed effect of pth heat stage of the cow
P_q	= Fixed effect of qth parity of the cow
A_r	= Age of the bull in days taken as a covariate
W_s	= Random effect of sth semen collector, NID $(0, \sigma_s^2)$
U_t	= Random effect of tth bull, NID $(0, \sigma_a^2)$
T_u	= Random effect of uth AI technician, NID $(0, \sigma_t^2)$
$e_{ijklmnopqrstuv}$	= Random error associated with each record, NID $(0, \sigma_e^2)$

The significant fixed factors identified from the best model were then used for obtaining the variance component estimates using univariate and random regression models. For both analyses, 200,000 Gibbs samples were generated with a burn-in of 50,000 and thinning interval of 50. The stability of the model was ascertained using trace plots, which were obtained from post-Gibbs samples, of the parameters plotted along with the number of iterations.

For univariate analysis, a repeatability animal model was used for obtaining the (co) variance components and estimating the genetic parameters. For individual conception records,

$$y = Xb + Za + Wpe + e$$

Where $y = n \times 1$ vector of observations with $n =$ number of records; $b = p \times 1$ vector of fixed effects with p as the number of levels for all fixed effects; $a = q \times 1$ vector of random animal effect with q as the number of animals including pedigree; $pe = r \times 1$ vector of random permanent environmental effects and non-additive genetic effects with r as the number of animals with records; $e = n \times 1$ vector of random residual effects; $X =$ design matrix of order $n \times p$ which relates records to fixed effects; $Z =$ design matrix of order $n \times q$ which relates records to animal's direct genetic random effects and $W =$ design matrix of order $n \times r$ which relates records to permanent environmental effects. The assumed variance-covariance structure will be

$$V \begin{bmatrix} a \\ pe \\ e \end{bmatrix} = \begin{bmatrix} A\sigma_a^2 & 0 & 0 \\ 0 & I\sigma_{pe}^2 & 0 \\ 0 & 0 & I\sigma_e^2 \end{bmatrix}$$

Animal genetic effect 'a' was assumed to be normally distributed with mean 0 and variance $A\sigma_a^2$ where A is the numerator relationship matrix and σ_a^2 is the additive genetic variance. Permanent environmental and residual effects were assumed to be normally distributed with mean 0 and variances $I\sigma_{pe}^2$ and $I\sigma_e^2$ respectively where I is the identity matrix of the order of the number of records and σ_{pe}^2 and σ_e^2, the variances for permanent environmental and residual effects, respectively. In addition to the above effects, semen collector and AI technician were included as random effects for production and fertility traits with mean 0 and variances σ_s^2 and σ_t^2 respectively.

For random regression models, the age of the bulls in days was taken as the control variable to obtain the trajectories of genetic parameters for conception rate over the age of the bulls. The animal and permanent environmental effects were modeled using Legendre

polynomials up to the order of fit of four with error variance modeled as a homogenous class of random effects. Seven models with different combinations of animal and permanent environmental effects were formed for purebreds and crossbreds. The best model with the lowest DIC value was selected which was then used for obtaining the trajectories o genetic parameters over the age of the bulls.

$$Y_{ij} = Xb + \sum_{k=0}^{k_a-1} Z_a a_k + \sum_{k=0}^{k_p-1} Z_p p_k + C_m + e$$

Where Y_{ij} is the conception rate of ith animal at j^{th} age, b is the vector of significant fixed effects or incidence matrix relating fixed effects with Y, a_k and p_k: set of n values (n = number of bulls) of k random regression coefficients corresponding to animal and permanent environment effects, with the order of fit k_a and k_p respectively, Z_a and Z_p are incidence matrices with dimensions $n \times k_a$ and $n \times k_p$ respectively, C_m: random effect of semen collector with mean zero and variance σ_m^2 and 'e' is the random residual heteroscedastic error variance. The model also included fixed regression for age with the order of that of the animal effect.

The elements of the different Z matrices are

$$Z = \phi_i = \Lambda_i(t_{ij})$$

Where, where ϕ_i is the ith (i=0,..,k-1) Legendre polynomial for a k-order of fit, Λ_i are the coefficients of Legendre polynomial for order i, and t_{ij}, the elements for i^{th} order and j^{th} age of Legendre polynomial are the ages standardized between -1 and +1, derived as

$$t_{ij} = \left(\frac{2(T - T_{min})}{T_{max} - T_{min}}\right) - 1$$

The Legendre polynomials for the respective ages were obtained using the '*Orthopolynom*' package in R.

Mixed model equations for the effects included in these models are

$$\begin{bmatrix} X'X & X'Z_a & X'Z_p \\ Z_a'X & Z_a'Z_a + A^{-1} \otimes k_a^{-1} & Z_a'Z_p \\ Z_p'X & Z_p'Z_a & Z_p'Z_p + I_p \otimes k_p^{-1} \end{bmatrix} \begin{bmatrix} b \\ a \\ p \end{bmatrix} = \begin{bmatrix} X'y \\ Z'_a y \\ Z'_p y \end{bmatrix}$$

Where A is the numerator relationship matrix, I is the identity matrix, $\otimes$ is the Kronecker's product, and K_i is the (co)variance matrix of the random regression coefficients of the effects indicated in subscript.

The genetic (co)variance between ages was estimated from the matrix of random regression coefficients using the general expression

$$G_{xj} = \Phi_{xj} K_{xj} \Phi'_{xj}$$

Where G_x is the (co)variance matrix for x = animal or individual permanent environment and Φ_{xj} is the vector of Legendre polynomials for the random effect of x and j^{th} age group.

All analyses were done in a Bayesian framework using the BLUPF90 family of software (Misztal *et al.* 2018). THRGIBBS1F90 was used for generating Gibbs samples and Post-Gibbs analyses were done with POSTGIBBSF90.

Heritability estimates were calculated as the ratio of additive genetic variance (σ_a^2) to total phenotypic variance (σ_p^2).

$$h^2 = \frac{\sigma_a^2}{\sigma_p^2}$$

Repeatability (r) was estimated as a ratio of the sum of additive genetic variance (σ_a^2) and permanent environmental variance (σ_{pe}^2) to total phenotypic variance (σ_p^2).

$$r = \frac{\sigma_a^2 + \sigma_{pe}^2}{\sigma_p^2}$$

RESULTS AND DISCUSSION

The numbers of AI records available over the age of the bulls in months have been plotted in Figure 1. The numbers of records for both breeds were lower at the extreme ages. A higher number of records were available for HF crossbreds than purebreds which could be attributed to earlier semen collection in the case of crossbred bulls.
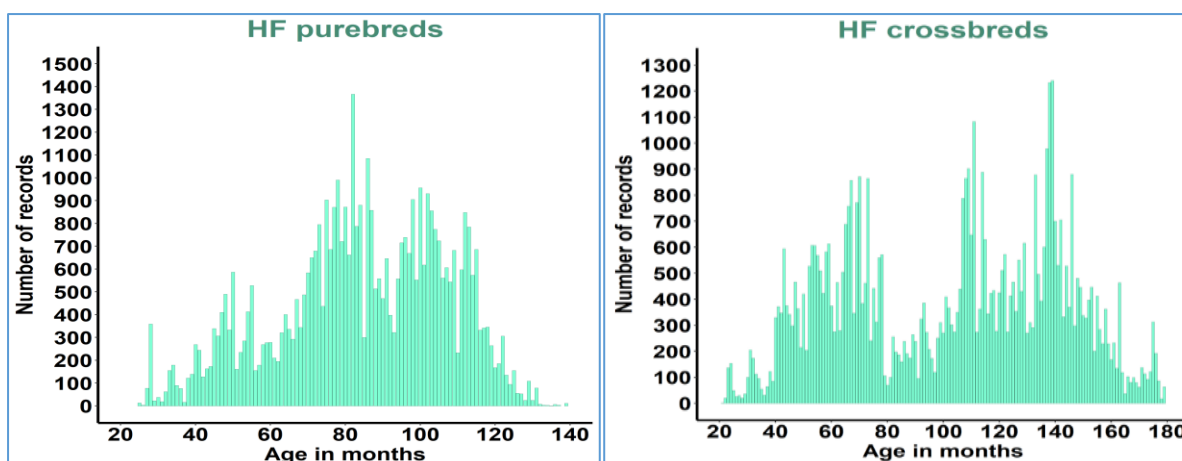
Figure 1: Number of records for conception rate over the age at collection in months

The results of the descriptive statistics and the genetic parameter estimates obtained through the univariate analysis have been represented in Table 1.

Table 1: Descriptive statistics, heritability and repeatability estimates with their posterior standard deviations

Breed	N	n	Mean	SD	CV	h^2	PSD	r	PSD
HF purebreds	87	45,497	53	50	94.34	0.0023	0.0021	0.0053	0.0033
HF crossbreds	78	58,497	49	50	102.04	0.0006	0.0005	0.0013	0.0008

N: number of bulls, n: number of records, SD: standard deviation, CV: coefficient of variation, h^2: heritability, r: repeatability, PSD: posterior standard deviation

The mean conception rate was higher in purebreds than in crossbreds though the standard deviation remained constant for both the genetic groups. The conception rate in HF purebred bulls was in accordance with Ortega *et al.* (2018) and Bhave (2021) while it was very high compared to McWhorter *et al.* (2020). In the case of binary data, the standard deviation approaches 0.5 as the number of records increases (Schumm *et al.,* 2019). This could be the reason why the standard deviation was larger than the mean in the case of HF crossbred bulls which lead to a larger coefficient of variation. A lower mean for conception rate in the case of crossbreds could be due to a higher number of morphologically abnormal spermatozoa (Sarder, 2003; Rabidas *et al.*, 2012). Kumaresan *et al.* (2021) also reviewed male sub-fertility in the case of crossbred bulls and attributed it to spermatozoal abnormalities which are greater in the case of crossbred bulls compared to purebreds.

The heritability and the repeatability estimates obtained from the univariate analysis were very low in both the genetic groups. These estimates though low, were precise as the PSD obtained for the estimates was also lower. The heritability estimates from other studies were also low and were below 0.1 (Averill *et al.,* 2004; Aguilar *et al.,* 2011; Hagiya *et al.,* 2018; Berry *et al.,* 2014) for HF purebred and crossbred bulls. Fertility is a fitness trait and thus as observed in the present study heritability is expected to be low. As this is a binary trait, even a small difference in the genetic ability of the bulls could determine the outcome (conceived or not conceived) of some inseminations. This trait is influenced more by the environment and thus improvement in this trait requires more sources of information from relatives to improve the accuracy of selection. Indirect selection where the correlation of fertility (conception rate) is high with some semen production traits is also another possibility. Berry *et al.* (2011) studied the correlation between male and female fertility and concluded that selection in one will improve fertility in the other. This shows that even though the estimates of genetic parameters are lower for bull conception rate, improvement in bull fertility will improve the cow fertility which is desirable in any breeding program.

Berry *et al.* (2011) and McWhorter *et al.* (2020) studied the variation in the sire conception rate along with the age of the bulls and suggested that the age of the bull at semen collection had a large impact on the conception rate. Averill *et al.* (2004) implied that the relationship between the conception rate and the age of the bull cannot be studied using simple regression techniques as they are non-linearly related. This phenotypic variability with age could have underlying genetic variability which was understood in this study using random regression models to model the variance components and the genetic parameter estimates for the conception rate in bulls.

Models with Legendre polynomials of different orders of fit up to 4 for the additive effect and the permanent environmental effect were needed to accommodate for the variance in the fertility trait. The DIC values for each combination are given in Table 2. HF purebreds showed best fit of 4th order for additive effects and 3rd for permanent environmental effects whereas the reverse was true in the case of crossbreds. This shows that there was higher additive genetic variability in HF purebreds and higher environmental variability in HF crossbreds.

Table 2: Order of fit of Legendre polynomials for additive and permanent environmental effects along with the DIC values

Order of fit		Breeds	
σ_a^2	σ_{pe}^2	HF purebred	HF crossbred
2	2	64683.85	83840.58
2	3	64682.63	83831.80
3	2	64685.70	83839.07
3	3	64687.12	83835.93
3	4	64682.26	**83831.78**
4	3	**64678.98**	83835.96
4	4	64693.76	83832.73

DIC: Deviance information criteria, σ_a^2: additive genetic variance, σ_{pe}^2: permanent environmental variance

Figure 2 depicts the trajectories of heritability and repeatability over the age in months and Table 3 summarizes the estimates for additive genetic effect, permanent environmental effect, heritability and repeatability for conception rate in HF purebred and HF crossbred bulls.
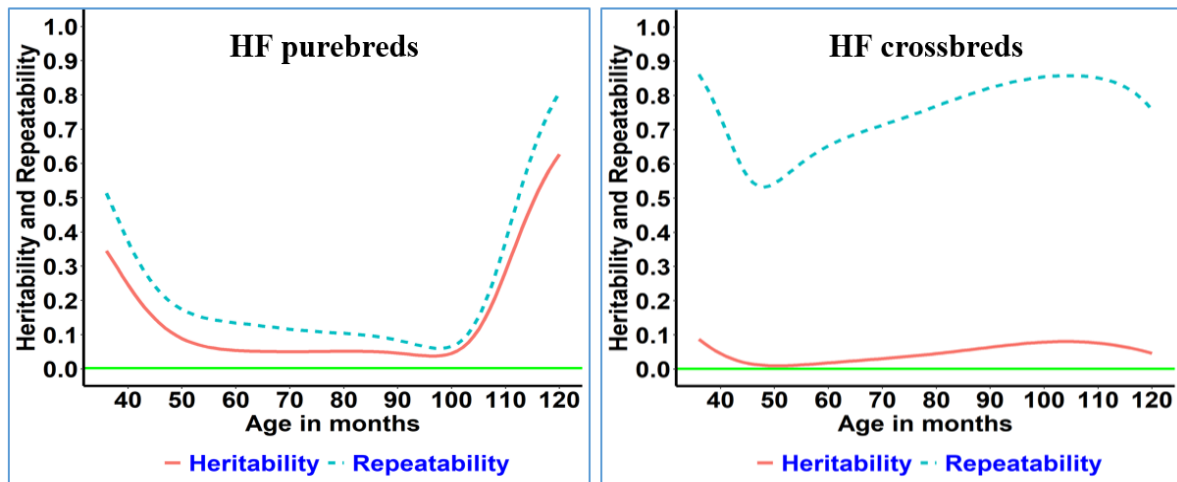

Figure 2: Heritability and repeatability estimates over the age of the bulls (Horizontal green line is the heritability for post-thaw motility obtained through univariate analysis)

In purebreds, the trend for additive genetic and permanent environmental variance was almost horizontal except at the endpoints where the variances were higher. The heritability and repeatability also followed a similar trend and the two estimates did not differ much. The estimates of heritability were very low in the middle and overall it ranged from 0.038 (8 years) to 0.627 (10 years) while repeatability ranged from 0.060 to 0.809. However, the higher

estimates were found at the extreme ages with less no of records. The values were uniform and low for the ages between 4 and 8 years and were under 0.15 for heritability and 0.2 for repeatability.

In the case of HF-crossbreds, the trends for all the estimates declined initially up to 4 years of age and then gradually increased up to 9 years followed by a short declining phase again. Heritability was again very low with a narrow range of 0.011 (4 years) to 0.087 (3 years). Estimates obtained were uniform and closely mimicked the values obtained through univariate analyses. Repeatability ranged from 0.532 (4 years) to 0.862 (3 years) and was considerably higher than heritability for all the ages.

The conception rate had a low heritability in both breeds excluding extreme ages. This overestimation could be attributed to the less number of records (Carabaño *et al.*, 2007; Strathe *et al.*, 2013; Al-Kanaan *et al.*, 2015) as seen in Figure 1 as well as the 'end-of-range' problem or 'Runge's phenomenon' (Meyer, 2005; Venkataramanan, 2021). These higher estimates were imprecise as seen from the higher PSD for these ages (Table 3).

Lower heritability estimates obtained from univariate, as well as random regression models, is expected for a trait like fertility which is related to fitness. A part could be attributed to stringent protocols followed during lab screenings to eliminate spermatozoa that do not meet the required criteria and sperm concentration modifications by dilution which could reduce the genetic variability (Kuhn *et al.,* 2008). Further estimates obtained using threshold models are usually on the higher side (Kadarmideen *et al.,* 2000; Kuhn *et al.,* 2008). Effect of the permanent environment was also low in HF purebred bulls which is evident from less gap present between the heritability and repeatability values. Estimates of heritability were very close to the univariate values and were mostly consistent without any major fluctuations and so selection on the basis of univariate analyses could be practiced for these traits.

Table 3: Additive genetic effect, permanent environmental effect, heritability and repeatability of conception rate in HF purebred and HF crossbreds

	σ_a^2	σ_{pe}^2	h^2	PSD	r	PSD	σ_a^2	σ_{pe}^2	h^2	PSD	r	PSD
Breed **Age**	HF purebreds						HF crossbreds					
3 years	0.176	0.086	0.345	0.158	0.513	0.004	0.026	0.026	0.087	0.130	0.862	0.070

4 years	0.033	0.027	0.107	0.159	0.194	0.006	0.003	0.007	0.011	0.127	0.532	0.104
5 years	0.016	0.023	0.054	0.148	0.134	0.007	0.005	0.011	0.018	0.109	0.653	0.117
6 years	0.014	0.018	0.051	0.141	0.113	0.007	0.009	0.013	0.033	0.099	0.724	0.113
7 years	0.014	0.013	0.051	0.143	0.099	0.006	0.015	0.018	0.052	0.098	0.792	0.107
8 years	0.010	0.007	0.038	0.150	0.063	0.006	0.022	0.024	0.074	0.101	0.845	0.102
9 years	0.071	0.022	0.208	0.159	0.272	0.005	0.024	0.027	0.079	0.111	0.856	0.098
10 years	0.817	0.236	0.627	0.166	0.809	0.005	0.013	0.014	0.046	0.127	0.757	0.094

σ_a^2: additive genetic variance, σ_{pe}^2: permanent environmental variance, h^2: heritability, r: repeatability, PSD: Posterior standard deviation

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