

Short communication

Bayesian random regression threshold models for genetic evaluation of pregnancy probability in Red Sindhi heifers



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ABSTRACT

We proposed a Bayesian random regression threshold model for genetic evaluation of pregnancy probability (PP) in Red Sindhi heifers over different months. Since this breed was recently introduced in Brazil, the age of 14 months usually preconized for Nellore cattle may not reflect the reality of the fertility indicator. In this context, the pregnancy success was evaluated at other ages aiming to understand its genetic variability pattern over time. A total of 4828 phenotyped heifers belong to 657 contemporary groups were used for the analysis. The estimated connectedness was equal to 99.75% considering 6189 individuals in the final pedigree. The random regression threshold models were implemented by combining second, third and fourth order Legendre polynomials to describe the average, the additive genetic and the permanent environmental curves. Additionally, the heterogeneity of the residual variance was also tested here. Based on DIC (deviance information criterion) and posterior model probabilities, the fourth order Legendre polynomials (LEG_4441) for the average, the additive genetic and the permanent environmental effects, assuming homogeneity of the residual variance, outperformed the simplest models. Thus, the fitting quality compensated the increased in the model complexity. The negative genetic correlations between PP at 15 months with PP at latter months indicates that rankings of animals for selection would be few similar in advanced ages. The high values for heritability (varying from 0.32 to 0.45) suggest that PP, mainly until 19 months, can be used as selection criterion for reproductive female performance in breeding programs for Red Sindhi cattle in Brazil. These practical results were only obtained due to the advantages of the proposed random regression threshold models to describe PP over different months.

1. Introduction

Red Sindhi is a zebu breed originated from Pakistan that has been mainly exploited for milk production in several countries of Asia, such as India, Bangladesh and Sri Lanka (Tiwari et al., 2012). However, it is also used for beef purposes in tropical countries in reason of its heat tolerance, tick and disease resistances and high fertility rates. Currently, in Brazil, the breed goes through significant population growth, mainly in the Northeast region, since this breed is more adapted to dry conditions.

Independently of the production approach (dairy, beef or dual-

purpose), low reproductive efficiency is still the major reason for high culling rates of cows. One of the most used reproductive trait for female fertility in breeding programs is the age at first calving, since it is easily measured and expressed in almost all cows of the herd. However, according to Eler et al. (2002), more reliable indicators of fertility can be reached under a sexual precocity viewpoint based on the pregnancy probability (PP). According to Davis et al. (1993), the selection of sires for PP leads to improved fertility in heifers and four-year-old lactating cows without adverse effects on progeny growth. However, as Red Sindhi cattle sometimes can be exploited as dual purpose animals in Brazil, possible impacts of early pregnancy on milk production should

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be expected. According to Pietersma et al. (2006), in general, delayed calving showed a tendency for increased milk production in the first lactation.

In summary, PP is defined as the probability that a heifer be pregnant after the end of the breeding season. When measured under this viewpoint, it is a binary trait assuming the value “one” for pregnant and “zero” for non-pregnant heifers. In dairy cattle, binary responses such as the outcome of an insemination event seems to be the trait of choice, because it is conveniently measured and taken in early to mid-stages of lactation (Buaban et al., 2016). In some situations, when the cows contain more than one binary outcome over time (several insemination events across time), the use of the random regression models (RRM) allows to infer on the PP over the lactation. In an extensive review on RRM, Schaeffer (2004) reported that when reproductive performance are repeatedly observed on the same animal, RRM are useful to estimate genetic changes over time. As preconized by Averill et al. (2004), given the discrete nature of PP and its variation over time, it becomes necessary to accommodate threshold theory into random regression models, thereby allowing the use of all available information and accounting properly for all factors affecting female fertility.

According to Eler et al. (2002) and Santana et al. (2013), the results obtained for the pregnancy probability at 14 month are encouraging for the genetic evaluation of Nelore breed, since besides being highly heritable, it is inexpensive and practical to record. However, for breeds recently introduced in breeding programs, such as Red Sindhi in Brazil, the age of 14 months may not reflect the reality of the fertility indicator. Thus, the pregnancy success can be evaluated at other ages aiming to understand its genetic variability pattern over time, which requires the use of random regression threshold models.

Given the lack of information on genetic analysis of reproductive traits for Red Sindhi cattle in Brazil, we aimed to estimate genetic parameters for pregnancy probability at different ages through Bayesian random regression threshold models.

2. Material and methods

Animal Care and Use Committee approval was not necessary for this study because the data were obtained from an existing database. The data set was provided by Brazilian Association of Zebu Breeders (ABCZ, Uberaba, Minas Gerais, Brazil). The data included phenotypic information from 4828 Red Sindhi heifers born between 1964 and 2013 in the Northeast, Midwest and Southeast Brazilian regions.

The data consistency was checked considering only heifers maintained exclusively on pasture, which had pregnancy either originated from artificial insemination or natural service. The effect of insemination method was tested and was not significant, thus, this effect was not included in the model. The contemporary groups (CG) were composed from farm, birth season (December to February, March to May, June to August, and September to November) and year of birth. However, CGs containing less than 5 animals as well as CG for in which all animals presented same response (0 or 1) were not included in the analysis. The average number of animals by GC was equal to 9.79 with standard deviation of 3.33 and maximum equal to 51. Genetic connectedness among CGs was evaluated through AMC software (Roso and Schenkel, 2006). The CGs with less than 10 genetic connections were removed. The estimated genetic connectedness was equal to 99.75% considering 6189 individuals in the final pedigree (713 sires and 1673 cows from eleven generations). A total of 4828 heifers with phenotypic records belong to 657 CGs were considered for analysis.

Under a longitudinal binary data approach used here, if the heifer is pregnant at a given age, its phenotypic value is equal to one, otherwise it is equal to zero. Thus, the phenotypic dataset was composed by individual information of binary trait (pregnant or not pregnant) in each considered month. The number of animals with phenotype equal to zero and one in each month of measurement was 4786 and 42, 4441 and 387, 4279 and 549, 3967 and 861, 3909 and 919, 4272 and 556, 4406

and 422, and 4465 and 363, respectively to 15, 19, 23, 27, 31, 35, 39 and 43 months. These values correspond, respectively, to pregnancy percentages equal to 0.88, 8.71, 12.83, 21.70, 23.50, 13.01, 9.57 and 8.12.

The random regression threshold models were implemented by combining second, third and fourth order Legendre polynomials to describe the average, the additive genetic and the permanent environmental curves. We assumed the same polynomial order to describe the additive genetic and permanent environmental effects as suggested by Schaeffer (2016). Legendre polynomials are indicated to model longitudinal trajectories that tends to be smooth (Speidel et al., 2010), as expected for female fertility over time. In this context, the higher tested polynomial order was fourth, since the high order Legendre polynomials usually implies in overfitting when describing smooth trajectories. Additionally, two approaches were considered for the residual variances: homogeneity (the same variance for all ages) and heterogeneity (one variance for each age). A general notation to represent all tested models is given by: $LEG_{\alpha\beta\gamma\delta}$, where α , β and γ correspond to the values of the polynomial order for the average, additive genetic and permanent environmental effects, respectively. The term δ assumes the values one and two, respectively for the conditions of homogeneity and heterogeneity of the residual variance. As mentioned earlier, the phenotypic observations were defined as a binary trait measured over different months, which is represented by the vector \mathbf{Y} given by:

$\mathbf{Y} = [y_{11}, y_{12}, \dots, y_{1n}, y_{21}, y_{22}, \dots, y_{2n}, \dots, y_{N1}, y_{N2}, \dots, y_{Nn}]'$, where y_{ij} represents the binary outcome of animal i ($i = 1, 2, \dots, N$) at age j ($j = 1, 2, \dots, n$). Under a threshold model framework, $y_{ij} = 1$ if $l_{ij} > \tau$, and $y_{ij} = 0$ if $l_{ij} \leq \tau$, where τ is the threshold for the latent variable l_{ij} (so called liability). However, τ must be fixed, so as to center the distribution (Sorensen and Gianola, 2002). Here we opted for the typical assignment $\tau = 0$. Considering the longitudinal nature of the binary data, the liability can be described by the Legendre polynomial model given by:

$$l_{ijk} = CG_k + \sum_{m=0}^M \beta_m \phi_{ijm} + \sum_{m=0}^M a_{im} \phi_{ijm} + \sum_{m=0}^M p_{im} \phi_{ijm} + e_{ijk} \quad (1)$$

where: l_{ijk} is the liability record for animal i made on month j within contemporary group subclass k (CG_k , $k = 1, 2, \dots, 657$); β_m is the average regression coefficient of order m ($m = 0, 1, \dots, M$); a_{im} and p_{im} are the random regression coefficients of order m for additive genetic and permanent environmental effects of animal i , respectively; ϕ_{ijm} is the m^{th} Legendre polynomial for month j from animal i ; and e_{ijk} is the random residual term. Second, third and fourth order Legendre polynomials were defined assuming $M = 2, 3$ and 4 , respectively.

In the matrix notation, the model (1) is described under a Bayesian framework as follow:

$$\mathbf{l} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}\mathbf{a} + \mathbf{W}\mathbf{p} + \mathbf{e},$$

where: \mathbf{l} is the vector of liability (latent variable) records, assumed as $\mathbf{l}|\boldsymbol{\beta}, \mathbf{a}, \mathbf{p}, \mathbf{G}_a, \mathbf{R}_p, \sigma_e^2 \sim \mathbf{N}(\mathbf{X}\boldsymbol{\beta} + \mathbf{Z}\mathbf{a} + \mathbf{W}\mathbf{p}, \mathbf{I}\sigma_e^2)$, where \mathbf{G}_a and \mathbf{R}_p are the additive genetic and permanent environmental (co)variance matrices, respectively; and σ_e^2 is the residual variance. Once assumed the heterogeneity of variances, this value varies over months ($j = 1, 2, \dots, n$), i.e., $\sigma_e^2_j$. The mentioned j index correspond to the following months: 15, 19, 23, 27, 31, 35, 39 and 43. The incidence matrices for $\boldsymbol{\beta}$, \mathbf{a} and \mathbf{p} are given by \mathbf{X} , \mathbf{Z} and \mathbf{W} , respectively; $\boldsymbol{\beta}$ is the vector of systematic effects (average coefficients and contemporary groups), assumed as $\boldsymbol{\beta} \sim \mathbf{N}(\mathbf{0}, \boldsymbol{\Sigma}_\beta \otimes \mathbf{I})$, being $\boldsymbol{\Sigma}_\beta$ a known diagonal matrix with values $1e + 10$ (large variances) to represent vague prior knowledge; \mathbf{a} is the vector of additive genetic coefficients, assumed as $\mathbf{a} | \mathbf{G}_a, \mathbf{A} \sim \mathbf{N}(\mathbf{0}, \mathbf{G}_0 \otimes \mathbf{A})$, being \mathbf{A} the additive relationship matrix among the animals and \mathbf{G}_a the additive genetic variance-covariance matrix. Furthermore, it was assumed that \mathbf{G}_a follows an inverted Wishart distribution, $\text{IW}(\nu_a, \mathbf{V}_a)$, with hyperparameters $\nu_a = 3$ and $\mathbf{V}_a = \hat{\mathbf{G}}_0$. The IW distribution was used because it is a conjugate prior for the (co)variance matrix when assuming multivariate normal distribution for the observed data

(Sorensen and Gianola, 2002); \mathbf{p} is the vector of permanent environmental coefficients, assumed as $\mathbf{p}|\mathbf{R}_p \sim N(0, \mathbf{R}_p \otimes \mathbf{I})$, being \mathbf{I} the identity matrix and \mathbf{R}_p the permanent environmental variance-covariance matrix. Similarly as assumed for $\mathbf{G}_0, \mathbf{R}_p \sim IW(\nu_p, \mathbf{V}_p)$, with hyperparameters $\nu_p = 3$ and $\mathbf{V}_p = \hat{\mathbf{R}}_p$; \mathbf{e} is the vector of residual terms with variance described earlier, for which was assumed a scaled inverted chi-squared distribution given by $\sigma_e^2 | \nu_e, S_e \sim \nu_e S_e \chi_{\nu_e}^{-2}$.

The length of Gibbs sampler chain was 800,000 cycles, considering a burn-in period of 300,000 cycles, and a sampling interval (thin) of 10 cycles was established for all analyses. The convergence criterion was based on graphical analysis and Geweke criterion available in the package Bayesian Output Analysis (Smith, 2007) of the R software (R Core Team, 2016). The (co)variance components were estimated by Bayesian inference using the GIBBS3F90 software (Misztal et al., 2002). The used codes (renf90.par) and the head of dataset (renf90.dat) are available in Supplementary material.

All tested models were compared through DIC (Deviance Information Criterion, Spiegelhalter et al., 2002): $DIC = D(\bar{\theta}) + 2p_D$, where $D(\bar{\theta})$ is a point estimate of the deviance obtained by replacing the parameters by their posterior means estimates in the likelihood function; and $2p_D$ is the effective number of parameters in the model. Models with lower DIC are preferred. Aiming to facilitate the DIC interpretation, the posterior model probability (PMP) were calculated from DIC using the approximation presented by Ventura et al. (2015), which is given by: $p(M_s | \mathbf{Y}) = \exp(-\Delta_s/2) / \sum_{s=1}^S \exp(-\Delta_s/2)$, where $p(M_s | \mathbf{Y})$ is the posterior probability of model s ($s = 1, 2, \dots, S$) be the best one among all candidate models; and Δ_s is the DIC difference between model s and the best model. The model with higher PMP is preferred to describe the observed data.

The posterior marginal distribution samples of the heritability for PP over the months were obtained at each Gibbs sampler iteration q as follows: $\hat{h}_j^{2(q)} = \hat{\sigma}_{aj}^{2(q)} / (\hat{\sigma}_{aj}^{2(q)} + \hat{\sigma}_{pj}^{2(q)} + \hat{\sigma}_{ej}^{2(q)})$, where: $\hat{h}_j^{2(q)}$, $\hat{\sigma}_{aj}^{2(q)}$, $\hat{\sigma}_{pj}^{2(q)}$ and $\hat{\sigma}_{ej}^{2(q)}$ are, respectively, the estimates of heritability, additive genetic, permanent environmental, and residual variances in the iteration q at month j . In the same context, the samples for genetic correlations were generated as follows: $\hat{r}_{jj'}^{(q)} = \hat{\sigma}_{ajj'}^{(q)} / \sqrt{\hat{\sigma}_{aj}^{2(q)} \hat{\sigma}_{aj'}^{2(q)}}$, where: $\hat{r}_{jj'}^{(q)}$ is the genetic correlation between PP at months j and j' ; $\hat{\sigma}_{ajj'}^{(q)}$ is the genetic covariance between j and j' ; $\hat{\sigma}_{aj}^{2(q)}$ and $\hat{\sigma}_{aj'}^{2(q)}$ are the additive genetic variances for PP at months j and j' , respectively.

3. Results and discussion

The DIC and the respective PMP calculated for the models are shown in Table 1. The best model was denoted by LEG_4441, which represents the Legendre polynomial of fourth order for the average, for the additive genetic and for the permanent environmental effects assuming homogeneity of residual variance. According to these results, the more parameterized models for average and random effects, in this case the fourth order polynomial, outperformed the simplest models. Thus, the improvement in the quality of the fit compensated the increased in the models complexity. However, this selected model assumes homogeneity of residual variance, indicating that the variance due to non-explained effects remains constant over the evaluated months.

In Table 2 are presented the variance components (additive genetic, permanent environmental and residual) as well as the heritability estimates (posterior means) for PP at each observed month. In general, all parameters were estimated with considerable precision, since the range of the 95% HPD intervals were narrow in relation to the punctual estimation. Additive genetic variances were in a range of 2.85 (at 15 months) to 14.68 (at 31 months), whereas the permanent environmental variances were in a range of 4.62 (at 15 months) to 25.84 (at 35 months), which is almost twice that of the additive genetic variance. These estimates indicate that environment differences over months has

Table 1

Deviance Information Criterion (DIC) and the Posterior Model Probabilities (PMP) calculated for random regression threshold models based on Legendre polynomials to describe pregnancy probability of Red Sindhi heifers over different months.

Models ^a	DIC	PMP
LEG_4441	-3.447.793,99	≈ 1,0
LEG_3441	-3.380.695,99	≈ 0,0
LEG_2441	-3.374.810,88	≈ 0,0
LEG_4331	-2.600.137,20	≈ 0,0
LEG_2331	-2.598.419,13	≈ 0,0
LEG_3331	-2.568.241,67	≈ 0,0
LEG_4442	-2.205.113,99	≈ 0,0
LEG_2442	-2.044.458,68	≈ 0,0
LEG_3442	-2.036.944,21	≈ 0,0
LEG_3221	-1.912.702,16	≈ 0,0
LEG_4221	-1.905.029,58	≈ 0,0
LEG_3332	-1.825.290,45	≈ 0,0
LEG_4332	-1.805.149,02	≈ 0,0
LEG_2221	-1.768.328,06	≈ 0,0
LEG_4222	-1.662.787,69	≈ 0,0
LEG_3222	-1.605.325,46	≈ 0,0
LEG_2332	-1.506.151,91	≈ 0,0
LEG_2222	-825.568,43	≈ 0,0

^a The model notation LEG_αβγδ indicates that α, β and γ correspond to the values of the polynomial order for the average, additive genetic and permanent environmental effects, respectively. The term δ assumes the values one and two, respectively for the conditions of homogeneity and heterogeneity (one variance for each month) of the residual variance.

Table 2

Additive genetic (σ_a^2), permanent environmental (σ_p^2), residual (σ_e^2) variances and heritability (h^2) parameter (Par.) estimates (Est.) with respective 95% highest probability density (HPD) intervals for pregnancy probability of Red Sindhi heifers over different months.

Month	Par.	Est.	HPD	Month	Par.	Est.	HPD
15	σ_a^2	2.85	2.31–3.47	31	σ_a^2	14.68	12.23–17.33
	σ_p^2	4.62	4.15–5.10		σ_p^2	24.56	22.49–26.64
	σ_e^2	0.92	0.90–0.94		σ_e^2	0.92	0.90–0.94
19	h^2	0.34	0.28–0.39	35	h^2	0.37	0.31–0.41
	σ_a^2	5.73	4.66–6.86		σ_a^2	12.70	10.35–15.27
	σ_p^2	7.41	6.58–8.27		σ_p^2	25.84	23.71–27.95
23	σ_e^2	0.92	0.90–0.94	39	σ_e^2	0.92	0.90–0.94
	h^2	0.41	0.34–0.46		h^2	0.32	0.27–0.37
	σ_a^2	9.76	8.19–11.45		σ_a^2	11.52	9.25–14.07
27	σ_p^2	11.21	10.04–12.42	43	σ_p^2	23.60	21.51–25.71
	σ_e^2	0.92	0.90–0.94		σ_e^2	0.92	0.90–0.94
	h^2	0.45	0.38–0.50		h^2	0.32	0.26–0.37
	σ_a^2	13.96	11.74–16.39		σ_a^2	3.84	3.05–4.69
	σ_p^2	19.02	17.28–20.78		σ_p^2	7.00	6.28–7.69
	σ_e^2	0.92	0.90–0.94		σ_e^2	0.92	0.90–0.94
	h^2	0.41	0.35–0.46		h^2	0.33	0.26–0.38

great influence on ability to impregnate. Furthermore, given the binary nature of the used fertility traits, a small difference in the environment could be the reason for a successful (or failed) pregnancy. However, to the best of our knowledge, no previous longitudinal study of PP has been conducted, thus the estimated variances cannot be compared with literature values.

The heritability estimates varied from 0.32 (at 35 and 39 months) to 0.45 (at 23 months), presenting a trend to increase from 15 to 23 months; however, for additive genetic and permanent environmental variances this increasing trend is extended up until 35 months (Fig. 1). Thus, the explanation for the high heritability values at initial ages is the relative increase of permanent environmental in relation to additive genetic variances after 23 months (Fig. 1). Probably, the acceleration in the genetic individual differences at intermediary ages (from 23 to 35 months of age) can be due to the period of time needed to the

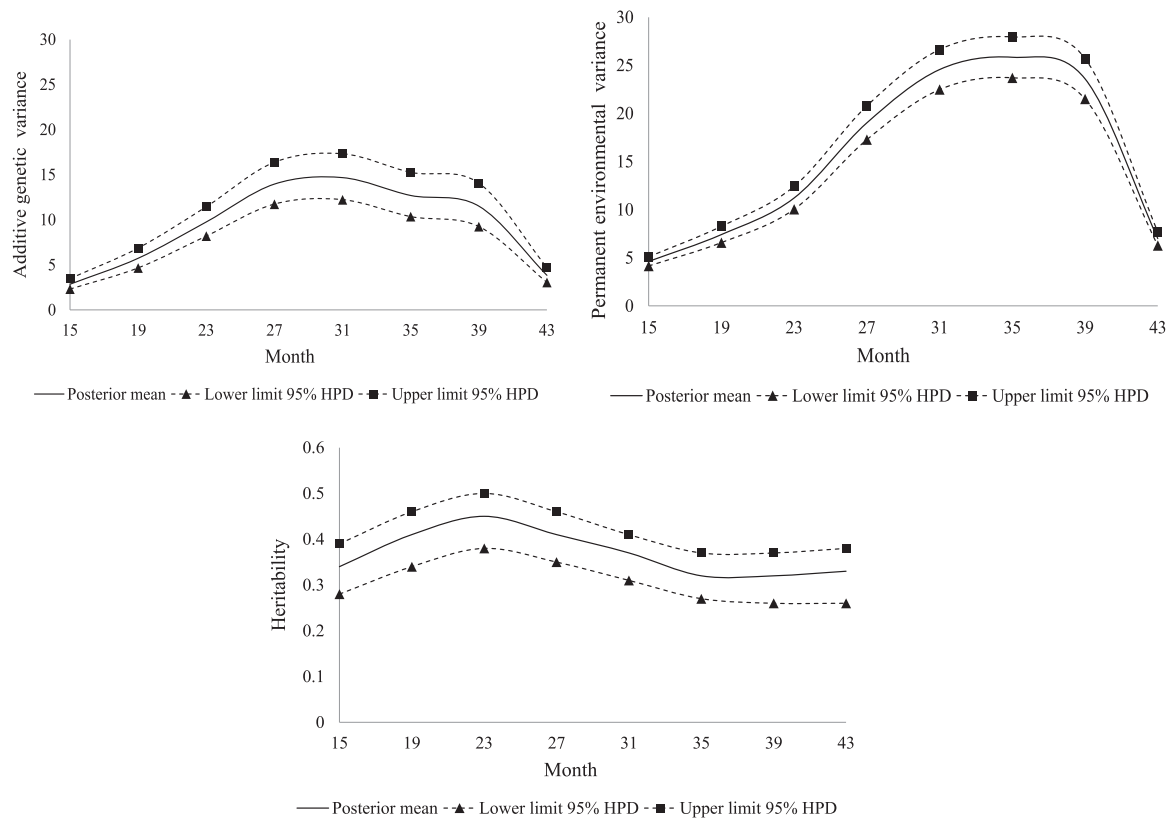


Fig. 1. Additive genetic, permanent environmental and heritability estimates (posterior means) with respective 95% HPD intervals for pregnancy probability over different months in Red Sindhi heifers.

expression of the most relevant genes related to the reproductive efficiency in this breed. Additionally, it can be justified by the higher phenotypic pregnancy percentages observed between these ages as previously mentioned in Section 2.

In general, the heritability estimates obtained here were slightly lower than those reported in the literature for Nelore cattle at 14 months, which represents the closest source of comparison for PP data of Red Sindhi cattle. Under this reference, Eler et al. (2002) and Santana et al. (2013) found estimates equal to 0.57 and 0.50, respectively. Also for Nelore cattle, Shiotsuki et al. (2009) obtained an estimate of 0.49 for PP at 16 months. The mentioned high values for heritability suggest that PP can be used as selection criterion for reproductive female performance in breeding programs for Red Sindhi cattle. The high heritability values at initial months 15–23 suggest that exposing the heifer to sires in earlier ages increase the genetic gain for this trait.

The genetic and phenotypic correlation estimates (posterior means) between PP evaluated in different months are shown in a heatmap type graph (Fig. 2). With an exception for PP at 15 and 19 months, higher

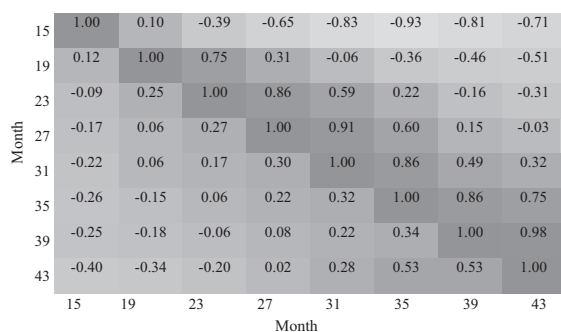


Fig. 2. Genetic (above the diagonal) and phenotypic (below the diagonal) correlations between pregnancy probability evaluated over different months in Red Sindhi heifers.

correlations were estimated for all other pairs of closest ages: 0.75 (19 and 23 months), 0.86 (23 and 27 months), 0.91 (27 and 31 months), 0.86 (31 and 35 months), 0.86 (35 and 39 months), and 0.98 (39 and 43 months). As expected, this correlation decrease as the distance between the ages increase, even resulting in negative genetic correlations between PP at 15 months with PP evaluated at other months, except for 19 months (for which the correlation was positive and equal to 0.10). Under a practical viewpoint, these results indicate that ranking of animals for PP at 15 months would be few similar with ranking obtained from advanced ages (mainly for 31, 35, 39 and 43 months). One reason for this is that early physiological events such as puberty and growth hormones pools might be affecting PP in initial ages, whereas late events such as maintenance energy control might be influencing PP in advanced ages (Pietersma et al., 2006).

The simultaneous action of these events on PP over time are being reflected in the direction of the estimated genetic covariance. The observed differentiated genetic profile related to female fertility highlighted in the present study can not be obtained when using age at first calving, for which this differentiation given in terms of genetic correlation over months is not possible to be exploited.

The phenotypic correlations are also negative between the same ages reported for the genetic correlations, allowing to infer that environment covariance also changes over time. According to Terakado et al. (2015), changes in environmental effects can be due to climate and feeding that influence reproductive traits in general, and to the physiological stress imposed by the nutritional requirements in different growth phases.

4. Conclusions

The more parameterized Legendre polynomials outperformed the simplest models, indicating that the fitting quality compensated the increased in the model complexity. The negative genetic correlations

between PP at 15 months with PP at latter months indicates that rankings of animals for selection would be few similar in advanced ages. The high values for heritability suggest that PP, mainly until 19 months, can be used as selection criterion for reproductive female performance in breeding programs for Red Sindhi cattle. These practical results were only obtained due to the advantages of the proposed random regression threshold models to describe PP over different months.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at <http://dx.doi.org/10.1016/j.livsci.2017.06.005>.

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