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RESEARCH ARTICLE

Genetic parameters of milk yield using random regression in Jersey crossbred cattle

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Abstract: Random regression models (RRM) using Legendre polynomials (LP) of varying orders were used for genetic evaluation of test-day milk yield (TDMY) in Jersey crossbred cows. A total of 5,794 first lactation test-day records from 571 cows of ICAR-National Dairy Research Institute, Eastern Regional Station, West Bengal, India was used to estimate the genetic parameters and evaluate the performance of random regression models (RRM) employing LP functions for first-lactation test-day milk yields. Among the evaluated models, LP of order 3 for additive genetic and order 4 for permanent environmental effects (A3P4) provided the best overall fit according to Akaike Information Criterion (AIC) and Bayesian Information Criterion (BIC) values. The pattern of additive genetic variance was relatively stable during early to mid-lactation and declined thereafter whereas permanent environmental variance peaked at the first test day, decreased sharply until mid-lactation then increased slightly towards the end, highlighting the influence of environmental factors during the initial and terminal stages of lactation. Heritability estimates were lowest at the onset and end of lactation and peaked during mid-lactation (0.10 to 0.36), reflecting the stronger influence of genetic factors during this stage. Genetic correlations between adjacent test days were high and gradually declined as intervals increased. Correlations were close to unity during mid-lactation, suggesting stable genetic expression and supporting selection based on early test-day records to improve overall lactation performance. The findings of this study suggested the use of differential orders of Legendre polynomials for additive genetic and permanent environmental effects as it provides a flexible and robust framework for modelling genetic variation in milk yield across lactations in Jersey crossbred cattle.

Keywords: Random regression models, Legendre polynomials, Test days, crossbred cattle

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Introduction

The genetic evaluation methods for milk production traits have largely transitioned to test-day random regression models and have been adopted as per the official genetic evaluation methods for dairy cattle across multiple countries (https:// interbull.org/ib/geforms). The basic concept of RRM is to model an average lactation trajectory for the population while incorporating animal-specific curves to represent deviations from this average (Mrode, 2005; Schaeffer, 2004). Moreover, it utilizes individual daily records instead of the traditional cumulative 305-days yield, thereby enabling a finer resolution of genetic and environmental effects across test days and lactation stages (Schaeffer, 2004; Jamrozik & Schaeffer, 1997).

To implement this method, a critical component is the selection of an appropriate covariance function to model additive genetic and permanent environmental effects. Legendre Polynomials (LP) are widely used for this purpose, commonly in milk production traits (Li et al. 2020; Bohmanova et al. 2008), as they can efficiently describe the daily additive genetic and permanent environmental (co)variances as well as reducing correlations among regression coefficients, thereby, minimizing dependence between variables and improving model convergence (López-Romero & Carabaño, 2003; Kettunen et al. 2000).

A number of studies have shown that higher-order LP yield lower AIC and BIC values, indicating better fit, but at the cost of more parameters and greater computational demands (Soumri et al. 2023; Li et al. 2020; López-Romero et al. 2004). Meyer (2005) also further emphasized that although high-order Legendre polynomials are effective in modelling variance changes along a continuous scale, they often yield unrealistic estimates at the beginning and end of the trajectory due to overemphasis on

extreme observations. Thus, choosing a suitable parametric function that can adequately describe the lactation curve while avoiding overparameterization is especially important in relatively small populations when applying random regression test-day models to estimate genetic parameters and breeding values (Li et al. 2020).

Several studies have been conducted on Jersey crossbreds in India with the objective of improving their genetic composition and milk production through different methodologies (Kasiviswanathan et al. 2024; Rahman et al. 2023; Mandal et al. 2022; Al Kalaldeh et al. 2021). However, research on the application of RRM for genetic evaluation remains limited. Given that precise genetic evaluation forms the cornerstone of breeding programs aimed at improving animal selection, achieving accurate parameter estimation is of paramount importance. Accordingly, this study sought to estimate genetic parameters and evaluate the performance of random regression models (RRM) employing LP functions for first-lactation test-day milk yields in Jersey crossbred cows of organized farm.

Materials and Methods

Data

Records on first lactation test day milk yield (TDMY) of Jersey × *Bos indicus* (Tharparkar or Red Sindhi) cattle from ICAR-National Dairy Research Institute, Eastern Regional Station, Kalyani, West Bengal, India, spanning a period of 40 years (1984-2023) were collected for the current study. The history, establishment, and management practices of this experimental herd, which provide essential context for interpreting the present findings, have been comprehensively documented by Koloi and Mandal (2020). For the analysis, lactation yield from 5 days after calving up to 305 days was included and animals having abortion, stillbirth, culled during lactation and outliers (>mean ± 3SD) were removed to ensure normal distribution before analysis. Furthermore, animals with fewer than four test-day records were not considered. Ultimately, 5794 first lactation test days of 30 days intervals (5, 35, 65, 95, 125, 155, 185, 215, 245, 275, 305), designated as TD1 to TD11 corresponding to each respective DIM were analysed. Year of calving was divided into 8 periods with 5 years intervals (1984-88, 1989-93, 1994-98, 1999-03, 2004-08, 2009-13, 2014-18, 2019-23) to ensure substantial number of observations due to limited calving records annually. Three calving seasons, summer (March-June), rainy (July-October) and winter (November-February) were also created, reflecting the climatic conditions of the area.

Statistical analysis

To identify significant impact of fixed effects, least squares analysis was performed (Harvey,1990) and were subsequently incorporated in the genetic evaluation. The fixed effects included year of calving and season of calving. A single trait linear mixed random regression test day model was used for genetic evaluation of test day records of Jersey crossbred for the current study. LP of third order was used to model the fixed regression while different order combinations were used for modelling the additive genetic and permanent environmental effects. The model used for analysis was as follows

$$\mathbf{Y_{ij}} = \boldsymbol{X_{ij}} + \sum_{k=0}^{nf} \Phi_{ijk}\boldsymbol{\beta_k} + \sum_{k=0}^{nr} \Phi_{ijk}\boldsymbol{u_{ik}} + \sum_{k=0}^{nr} \Phi_{ijk}\boldsymbol{pe_{ik}} + \boldsymbol{e_{ijk}}$$

Where, Y_{ij} denotes the j^{th} test day record of i^{th} animal; X_{ij} represents the fixed effects and β_k, the coefficients of fixed regression; u_{ik} and pe_{ik} are the kth random regression for animal and permanent environmental effects for i^{th} animal; Φ_{ijk} is kth LP for test day record of cow i^{th} on day j; nf and nr are order of LP fitted as fixed and random effects, respectively. e_{ijk} is the random residuals.

The postulates related to the components of the random regression animal model are outlined as follows

$$E\begin{bmatrix} y \\ u \\ pe \\ e \end{bmatrix} = \begin{bmatrix} Xb \\ 0 \\ 0 \\ 0 \end{bmatrix}; V(u) = K_A \otimes A; V(pe) = K_P \otimes I; Ve = R$$

Where, K_A and K_P are the (co)variance matrices of additive genetic and permanent environmental regression coefficients respectively, A represents the additive genetic relationship matrix, I is the Identity matrix, R signifies a matrix of residual covariance and *, the Kronecker product function.

Legendre polynomials (LP) of third and fourth order, as well as their combinations were applied to model additive genetic and permanent environmental (co)variances. Residual variance was considered as heterogeneous (11-class) across test days and the goodness of fit of the models were assessed using the Akaike's information criterion (AIC) and Bayesian information criterion (BIC). Each model was assigned as A_yP_y where A and P signify additive genetic and permanent environmental effects while y denotes the order of the polynomial utilised to model these effects. For instance, A3P3 represents a RRM where the additive genetic and permanent environmental effects are modelled using 3rd order. The analysis was performed using an AIREML algorithm implemented in WOMBAT (Meyer, 2007). The estimates of genetic parameters i.e., heritability (h^2) and correlations were calculated from the (co)variances as follows: $h^2_{(i)} = \sigma^2_{a(i)}/\sigma^2_{a(i)} + \sigma^2_{pe(i)} + \sigma^2_{e(i)}$, $r_{g(ij)} = \sigma_{a(ij)}/\sqrt{\sigma^2_{a(i)}\sigma^2_{pe(j)}}$, $r_{pe(ij)} = \sigma_{pe(ij)}/\sqrt{\sigma^2_{a(i)}\sigma^2_{pe(j)}}$, where, $\sigma^2_{a(i)}$, $\sigma^2_{pe(i)}$ are additive genetic and permanent environmental variances respectively, $\sigma^2_{a(ij)}$ and $\sigma^2_{pe(ij)}$ are additive genetic and permanent environmental

covariances between i^{th} and j^{th} test days while $r_{g(ij)}$ and $r_{pe(ij)}$ are the genetic and permanent environmental correlation between i^{th} and j^{th} test days respectively.

Results and Discussion

Table 1 presents the descriptive statistics and pedigree information pertaining to the TDMY data utilized in this study. The average test day milk yield of Jersey crossbred cattle was 7.12 kg, with a standard deviation of 2.7 kg. The goodness of fit of RRM using different orders of LP was evaluated through the calculated AIC and BIC values (Table 2), where lower values indicate a superior fit. Based on the observations, A3P4 model is the most suitable model which is consistent with the conclusions reported by Laureano et al. (2014) where the better fit of the model can be attributed to the recalibration of the polynomial order for additive genetic and permanent environmental effects. Pool et al. (2000) and López-Romero & Carabaño (2003) also reported that models employing a higher polynomial order for permanent environmental effects than for additive genetic effects resulted in an improved model fit.

Variance components estimation

The estimates of variances of TD milk yield differed slightly among the models, indicating that different LP order influences the variance partitioning. The pattern of additive genetic variance (Va) across test days for the evaluated models (A3P3, A3P4, A4P3, and A4P4) is presented in Figure 1. Across the models, the estimates of Va remained relatively stable during the early and mid-lactation period, followed by a gradual decline towards the end of lactation. A4P4 and A4P3 model showed the greatest fluctuation, characterized by a notably high estimate at TD1, followed by a sharp decrease in A4P4 model and a resurgence at TD3 and TD4 in the A4P3 model which is possibly suggestive of overestimation by high order polynomials in a small sample size. Strabel et al. (2005) further emphasized that increasing the number of parameters in a model can reduce the precision of the estimates, as fewer records support each parameter. In such cases, excessively high estimates of genetic variance in certain stages of lactation may inflate the average genetic variance across the entire lactation, ultimately leading to an overestimation of the accuracy of genetic evaluations. Meanwhile, A3P3 and A3P4 models exhibited smoother trajectories with smaller deviations across test days which was also supported by the AIC and BIC values. The highest additive genetic variance was observed during the initial month of lactation followed by a gradual decline with values ranging from 1.04 to 2.12 in both the models. Analogous trends were observed by Al-Kalaldeh et al. (2021), and Muasya et al. (2014) utilizing RRM with LP of varying orders across different cattle breeds. Further, the reduction in variance observed towards the end of lactation in this study may be attributed to the smaller number of records available during this period, which limits the capacity of the mathematical functions to adequately capture and explain the additive genetic effects (Gonzalez-Herrera et al. 2015).

Evaluating the trend of permanent environmental variance (Vpe) across test days, it was revealed that all models had the highest estimates at the first test day (TD1), followed by a sharp decline until approximately TD4, after which the values gradually stabilized and showed a slight increase towards the end of lactation. This trend demonstrates that environmental factors have profound effect on TDMY during the initial and end of first lactation in Jersey crossbred cows. In line with these observations, several authors have reported a concave trajectory of permanent environmental variance, with higher values consistently occurring during the early and late stages of lactation (Kasiviswanathan et al. 2024; Aerts et al. 2021; Li et al. 2020). Furthermore, consistent with previous findings (Strabel et al. 2005; Albuquerque & Meyer, 2001), the present results indicate that increasing the polynomial order used to model the permanent environmental effect altered the variance pattern at the extremes and resulted in an additional reduction of Vpe.

In this study, residual variance (Ve) followed similar trends with negligible differences in magnitude in all the four models, indicating that model order had minimal impact on the estimation of residual variance. The highest Ve estimates occurred on TD1, ranging from 0.72 to 13.51, indicating substantial unexplained variability in early lactation when cows experienced the greatest physiological stress and management fluctuations. However, from TD2 onward, Ve continued to decrease and stabilized during mid-lactation, suggesting that measurement error and short-term environmental fluctuations were minimal during this period. Various workers (Soumri et al. 2023, Li et al. 2020, Bignardi et al. 2011, Strabel et al. 2005) also reported heterogenous residual

Table 1: Summary of descriptive statistics

Particulars	
No. of test day records	5794 Units
Average (SD) of test-day milk yield(kg)	7.12 (± 2.7)
Minimum test-day milk yield (kg)	0.5
Maximum test-day milk yield (kg)	16
Number of animals with records	571
Number of sires with progeny in data	59
Average number of daughters per sire	9.47

SD, standard deviation

Table 2: Goodness of fit of RRM with different orders of Legendre polynomials (LP)

Models	No. of parameters	AIC	BIC
A3P3	23	10565.842	10719.076
A4P4	31	10524.394	10730.926
A3P4	27	10517.946	10697.828
A4P3	27	10540.608	10720.492

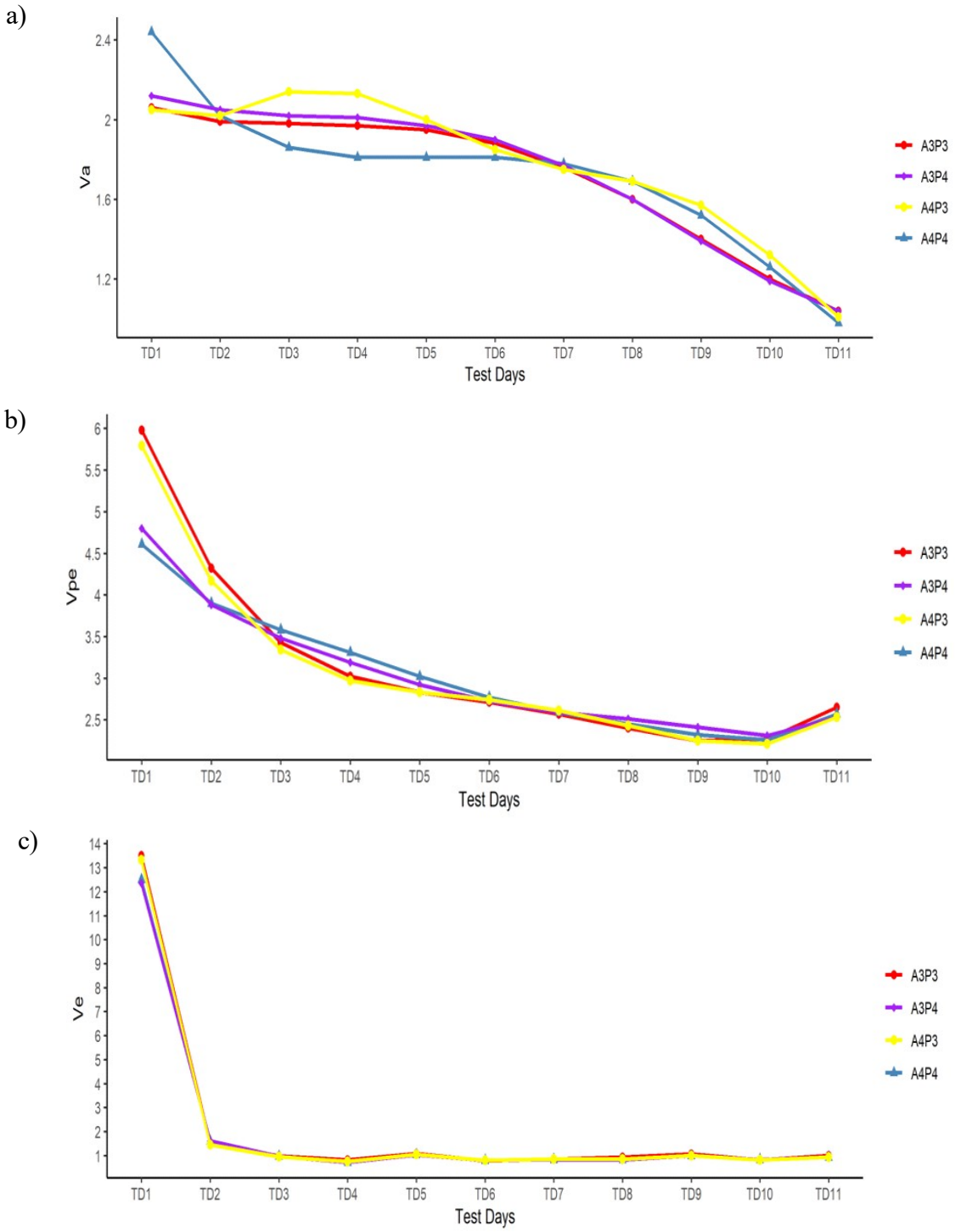


Fig. 1 Estimates of a) additive genetic variances (Va), b) permanent environmental variances (Vpe), and c) residual variances (Ve) across the test days from models with different orders of LP

variances with similar pattern as observed in this study across the lactations, confirming the greater residual variability in the early lactation. Thus, these findings further emphasize the importance of accounting for heterogeneous residual variances in random regression models to improve the accuracy of genetic evaluations based on test-day records.

Estimates of genetic parameters

The trajectories of heritability of TDMY initially exhibited a low estimate for all the models and progressively escalated, reaching its peak during mid lactation then gradually decline towards the end (Figure 2). Notably, A4P3 showed a peak estimate at TD7 while the overall trend remained consistent for other models and

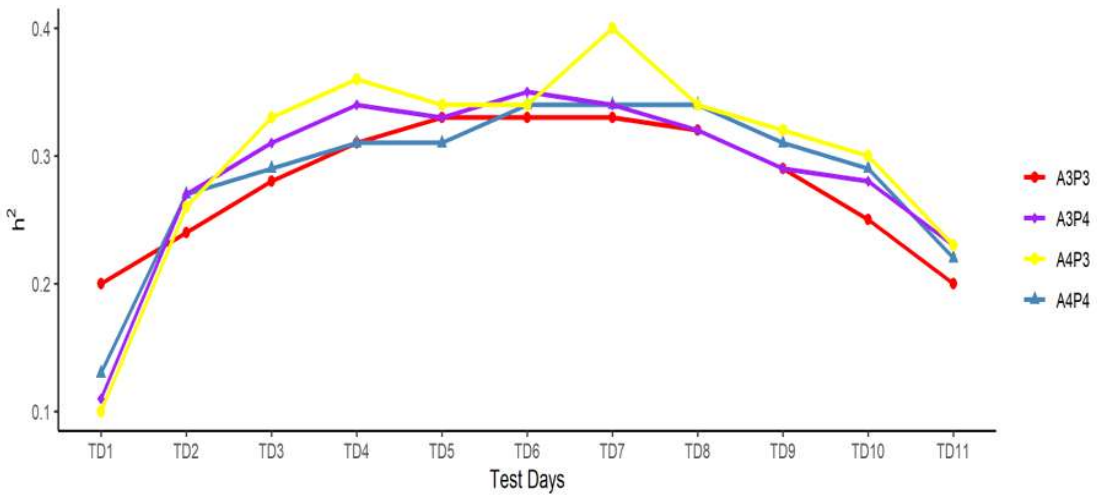


Fig. 2 Estimates of heritability across the test days from models with different orders of LP

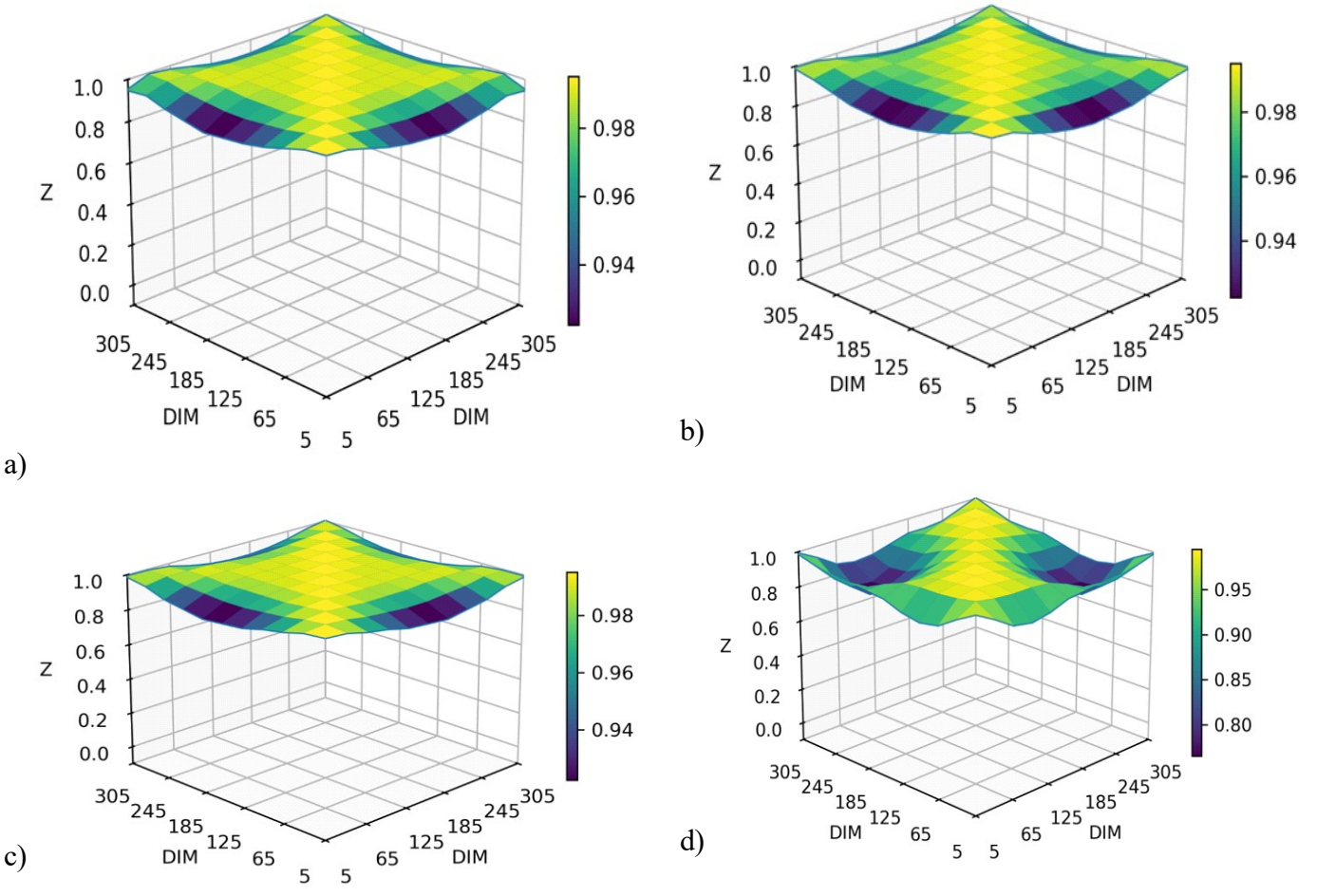


Fig. 3 Additive genetic correlations estimate between test days from models with different orders of LP a) A3P3 b) A4P4 c) A3P4 d) A4P3

the overall estimates ranged from 0.1 to 0.36. A heritability curve characterized by lower values both at the onset and end of lactation is generally considered desirable because these periods are significantly shaped by non-genetic factors ahead of calving as well as management practices such as time of drying (Stabel et al. 2005; Druet et al. 2003). Similar h^2 pattern as noticed in the present study have also been observed for milk yield using RRM of different orders in various cattle breeds (Paiva et al. 2022;

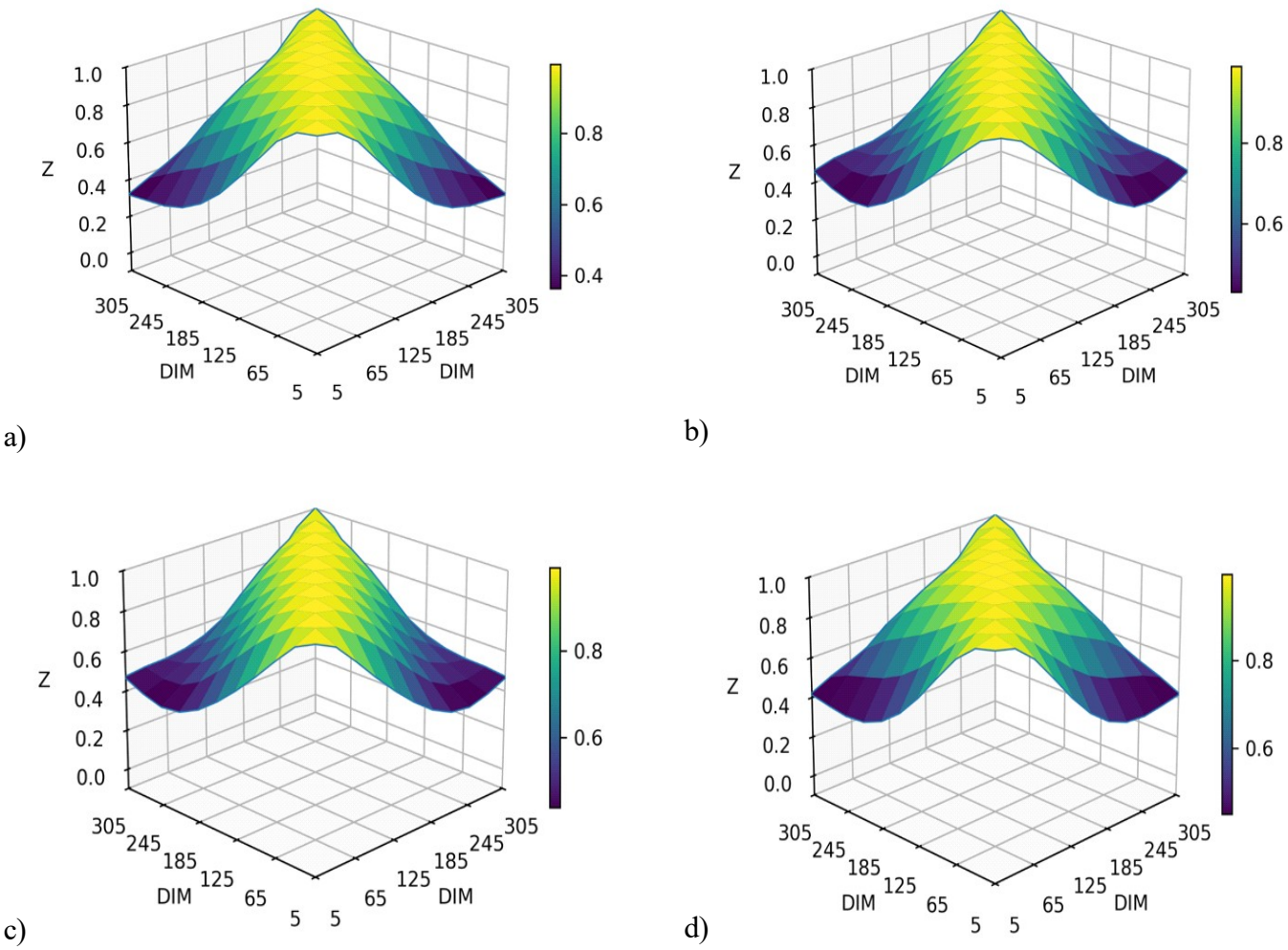


Fig.4 Permanent environmental correlations estimate between test days from models with different orders of LP a) A3P3 b) A4P4 c) A3P4 d) A4P3

Aerts et al. 2021; Singh et al. 2015; Çankaya et al. 2014). In contrast, highest heritability estimates at the peripheries of lactation and lowest during mid-lactation have also been documented (Otwinowska-Mindur et al. 2025; Kasiviswasnathan et al. 2024; Li et al. 2020; Samaraweera et al. 2020) in other cattle breeds.

The genetic and permanent environmental correlations between test-day milk yields (TDMY) in Jersey crossbred cattle are presented in Figures 3 and 4. In this study, all the correlations were highest between adjacent test days milk yields and gradually declined as the interval between records increased. Genetic correlations were particularly close to unity during mid-lactation, indicating a high degree of stability in genetic expression across this period of the lactation, with estimates ranging from 0.66 to 0.99. These findings were consistent with the reports of Gebreyohannes et al. (2016), Çankaya et al. (2014) and Laureano et al.(2014) in different cattle breeds and Breda et al. (2010) in Murrah buffaloes. The consistently high genetic correlations for TDMY observed in the present study suggest that selection based on early test day could be an efficient strategy for improving overall lactation performance. Furthermore, the results of permanent environmental correlation between test days illustrates the variability of permanent environment along the lactation period. Similar findings were also reported by Paiva et al. (2022) and Bignardy et al. (2011) in Holstein cows where the permanent environmental correlation decreased as the test days interval increased.

Conclusion

The fitted random regression models for genetic evaluation of Jersey crossbred exhibited substantial genetic variability for test-day milk yields and able to describe the genetic variability for TDMY along the lactation. TDMY heritability estimates were moderate in the course of the lactation, suggesting the possibility for further improvement through selection. Among the evaluated

models, A3P4 provided the best overall fit based on AIC and BIC, depicting that using a higher polynomial order for permanent environmental effects than for additive genetic effects offered better fit to model the changes in genetic variation along the lactation period in this herd.

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