ESTIMATES OF HERITABILITY OF MILK YIELD IN IRISH DAIRY COWS USING RANDOM REGRESSION TEST-DAY MODELS

BY

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DECLARATION

I declare that this thesis is my original work and has not been presented before in this university or any other university for the award of this or any other degree.

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DEDICATION

This thesis is dedicated to His Excellency Arefaine Berhe and my beloved parents, Kiflay Ghebrewoldi and Haddas Zerai, for their unwavering love and support throughout my academic journey

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ABSTRACT

As exists globally, an accurate genetic evaluation for individual dairy cows in Ireland is a prerequisite for genetic gain in milk yield. This entails using more sophisticated mixed models to model the variances and covariances across the lactation trajectory. The study aimed to model the genetic, permanent environmental and residual variance components for milk yield of Irish research dairy cows using a random regression test-day model. Therefore, routinely recorded milk test-day records of dairy cows milking in the 2019 calendar year were obtained from *Teagasc Animal & Grassland Research & Innovation Centre, Moorepark*. The records totaled 209,047 test day records. Information on 901 crossbred and purebred cows with varying proportions of Holstein, Friesian, and Jersey genotypes were available; the pedigree of each animal was traced back to founders which were subsequently assigned to genetic groups. The pedigree included 25,725 individuals. Herd-test-date (the interaction between experimental treatments and test dates), heterosis, recombination loss, the fixed effect of lactation curve nested within parity as well as the effect of age at calving relative to parity were associated with milk yield ($p < 0.05$). Random regression model involving fourth order Legendre polynomial was used to model the fixed lactation curve. The models were developed in stages. This was based on the analysis of the eigenvalues of the additive genetic and permanent environment covariance matrices to determine the usefulness of additional orders to the fitted polynomials. Therefore, various orders of Legendre polynomials were tested to optimize the order of Legendre polynomial for both additive genetic and permanent environmental effects. Ten residual error classes associated with 10 different lactation stages were modelled . Additive genetic variances, permanent environmental variances, residual variances, heritability, repeatability, genetic and permanent environmental correlations across days in milk were estimated. Based on the goodness of fit statistics evaluated (i.e., log likelihood, Akaike's (AIC), Schwarz's Bayesian (BIC) information criteria, residual variance, eigenvalues) and also the genetic parameter estimates, random regression model with second order Legendre polynomial (RRM2) can sufficiently model the genetic and permanent environmental effects for milk yield across lactation trajectory. The genetic and permanent environmental variances of milk yield from random regression second order Legendre polynomial (RRM2) ranged from 2.37 to 5.37 kg and from 1.48 to 6.86 kg, respectively. Daily heritability and repeatability estimate of milk yield from RRM2 varied from 0.22 to 0.39 and from 0.49 to 0.82, respectively. The phenotypic and genetic correlations from RRM2 weakened consistently as the interval between days in milk increased varying from -0.03 to 0.97 and from 0.46 to 0.99, respectively. The heritability estimates reflect exploitable genetic variations across the lactation profiles in Irish dairy cows allowing farmers to select genetically superior cows with more confidence.

LIST OF ABBREVIATIONS

AIC	Akaike Information Criterion
BIC	Bayesian Information Criterion
BCS	Body Condition Score
BLUP	Best Linear Unbiased Prediction
DIM	Days in Milk
EBV	Estimated Breeding Value
FCR	Feed Conversion Ratio
HTD	Herd Test Day
Het	Heterosis
Rec	Recombination Loss
REML	Restricted Maximum Likelihood
RRM	Random Regression Model
SCC	Somatic Cell Count
SD	Standard Deviation
SE	Standard Error
SNF	Solid Non- Fat
TD	Test Day
TDM	Test Day Model
TDY	Test Day Yield
TS	Total Solids
VCE	Variance Component Estimates
VFA	Volatile Fatty Acids

CHAPTER ONE

INTRODUCTION

1.1 Background of the study

Animal breeding aims to maximize profitability via the selection of high-producing animals, particularly in the context of dairy cows, where criteria such as milk yield, reproductive performance, and longevity play a significant role (Ambhore et al., 2016; Singh et al., 2016; Dev & Dahiya, 2018). These factors are influenced by the genotype and the animal management system in use (Kiplagat et al., 2012) . There is, therefore, a requirement for a proper genetic evaluation system coupled with the appropriate selection of genetically elite animals in the pursuit of genetic improvement (Dev & Dahiya, 2018) .

Traditionally, selection for improving milk yield in dairy cows involved using 305-day lactation records (Bilal & Khan, 2009). Olori and De Jong (1999) stated that the full lactation models have now been replaced by test-day models (TDM) to improve the genetic evaluation of milk yield (Schaeffer & Dekkers, 1994) . In the traditional lactation model, 7 to 10 test day (TD) yields are utilized to predict a 305-day lactation yield. This is not representative of the conditions across the lactation curve as the factors change across lactation and test days (Jamrozik & Schaeffer, 1997) . The accuracy of genetic evaluations is improved by introducing correction factors that are highly accurate and optimally defined for contemporary groups, thereby removing as much of the environmental influence as possible (Bilal & Khan, 2009) . Failure to accurately define CGs has the more persistent cows have breeding values underestimated, while the less persistent cows have breeding values overestimated because the projection factors assume that a cow from a certain breed and lactation number has a lactation curve of a standard shape (Jamrozik & Schaeffer, 1997).

Individual test day records are advantageous over lactation aggregates because they increase the accuracy of EBVs and provide more comprehensive management information for use by farmers (Kettunen et al., 2000). A TDM is defined as the analysis that makes use of several test days per individual lactation through statistical adjustments for the environmental effects on each test day. Test-day models have the following advantages:

They can handle variations observed in milk production over time during lactation account by defining herd test-date (HTD) as a contemporary group (CG) (Swalve, 2000). Solutions obtained from HTD effects can provide details on the prevailing herd management (Dzomba et al., 2010). Information from all test days (TDs) is optimally used (Wiggans and Goddard, 1996). They avoid the utilization of records that are extended for culled cows and records that are still in progress (Jensen, 2001). A genetic evaluation of persistency within and across lactations is possible (Jensen, 2001). When more persistent milkers are selected, especially in grass-based systems like those in Ireland, there is an increase in milk production from grazed grass. Grazed grass serves as a cost-effective feed option, resulting in higher milk yield (Berry, 2008).

Genetic evaluations for milk production using test-day observations utilize various statistical models (Savegnago et al., 2013). The widely utilized models in dairy production traits are repeatability models and random regression models (RRMs) (Oliveira et al., 2016). The RRMs are more flexible, accurate, and precise compared to the other statistical methods used (Henderson, 1982).

1.2 Objectives

1.2.1 Broad objective

To estimate the genetic, permanent environmental and residual variance components for milk yield of Irish research dairy cows using a random regression test-day model.

1.2.2 Specific objectives

i. To develop a parsimonious statistical model that accurately fits the data
ii. To estimate the variance components using the newly developed models and

then utilize these estimates to estimate the heritability of milk yield across lactation

1.3 Hypothesis

Null Hypothesis

i. No significant difference exists among the random regression models involving Legendre polynomials in modelling the covariance matrix of the lactation trajectory in Irish dairy cows
ii. No genetic variation exists in the shape of the lactation profile of milk yield across lactation in Irish dairy cows

1.4 Problem statement

In any breeding program, accurate genetic evaluation for individual dairy cows is a requisite for genetic gain. This necessitates the use of RRTDMs, which have been scientifically proven to be more accurate than lactation models and have been recommended by Irish Cattle Breeding Federation for genetic evaluation of milk yield in Irish dairy cows. Given the seasonal nature of milk production in Ireland, a genetic evaluation for persistency is desirable, a task facilitated by RRTDMs. Persistency refers to a cow's capacity to sustain its milk production rate over the entire lactation period following peak yield, characterized by a slower decline compared to non-persistent cows. There is a genetic basis behind persistency. Random regression test-day models utilize various orders of Legendre polynomials, enabling the optimization of the order of these polynomials for additive genetic and permanent environmental effects in test day models, thereby further enhancing the accuracy of genetic evaluation for milk yield. This thesis utilizes routinely recorded TD milk yields from Teagasc Moorepark experimental farms, with the expectation that the use of RRTDMs will yield valuable insights for future breeding programs.

1.5 Justification

A genetic evaluation model is said to be accurate when all known genetic and environmental factors are accounted for. The partitioning of variance can be achieved using mixed models. In the simplest of model s, a phenotype is regressed on both fixed and random effects. In a situation where the phenotype may vary across a trajectory, the approach until recently was to average the phenotype across the trajectory and consider that as the dependent variable. A more sophisticated approach is to model the variance and covariances across the trajectory using RRMs. The RRMs also allow for shape of the lactation profile of each cow to differ across lactation trajectory. Therefore, using random regression models, parameter estimates can be generated for each point along the trajectory. This thesis intends to employ RRMs to produce daily estimates of variance components (VCE) in milk, which will be utilized to estimate daily heritability for the milk yield of dairy cattle across days in milk. Alternative orders of fixed and random polynomials will be tested. The fit of the models will be evaluated using a combination of criteria namely the likelihood ratio test, Akaike Information Criterion (AIC), Bayesian Information Criterion (BIC), residual variances, eigenvalues and estimates of the genetic parameters. The most appropriate and parsimonious model will be recommended for use.

CHAPTER TWO

LITERATURE REVIEW

2.1 Milk Production in Ireland

In Ireland, milk production predominantly relies on seasonal calving pasture-based systems (Dillon et al., 2008). In these systems, milk production is maximized from low-cost grazed grass to achieve efficiency (McCarthy et al., 2007). Therefore, a compact calving pattern is sought to align with the initiation of grass, contributing to the profitability of the dairy industry (Dillion et al., 2003).

In Ireland, cattle breeding involve a range of breeds and crosses, with the primary dairy breeds being North American Holstein-Friesian, Friesian, Jersey, and Montbéliarde. Cross-breeding is also common in the dairy industry (Penasa et a., 2010).

The Economic Breeding Index (EBI) and the Cow's Own Worth index (C.O.W.) are used in Ireland as decision support tools for breeding and culling of dairy animals, respectively (Dunne et al., 2020) . Sub-indexes representing pertinent traits with respective economic weights on individual animals are converted into a single value profit index called the EBI. Therefore, the EBI informs decisions for a selection of genetically superior animals to ensure sustainable increases in profitability while maintaining genetic diversity among Irish dairy herds (McParland et al., 2008).

2.2 Sources of variation in milk production

Milk comprises water, proteins, vitamins, lipids, fatty acids and minerals. Humans, including neonates, require these nutrients in order to grow and develop (Agata et al., 2012). Milk yield plays a crucial role in determining the profitability of a dairy farm. It is governed by a combination of genetic and environmental factors (Alpan and Aksoy, 2015).

2.2.1 Non- genetic factors

The non-genetic factors include season, year, number of parity, age at calving, milking frequency, feedstuff and feeding strategies, management conditions and permanent environmental effects, among others. The ability to control the non-genetic factors is critical for livestock to survive and to achieve their genetic potential (Santosa et al., 2019).

2.2.1.1 Effect of season

Many studies have demonstrated variability in milk yield across seasons. For instance, a study conducted in Afghanistan found that Holstein-Friesian cows produced the peak milk yield during spring, followed by summer, while the least yield occurred in winter (Habibi et al., 2021). Another study on Danish Red and Jersey dairy cows in South Africa found that the month of calving significantly influenced both milk yield and composition. The Danish Red produced highest in June and July, while the Jersey produced highest in September and December (Nyamushamba, 2014).

2.2.1.2 Effect of parity number

Several researchers have reported that parity significantly influences milk yield in dairy cows (Mohsen et al., 1999; Bajwa et al., 2004; M'handi et al., 2012; Nyamushamba et al., 2014; Petrovic et al., 2015). Studies conducted on different breeds of cows in different countries showed that cows in their first parity tend to yield less compared to those in their subsequent parity and beyond (Stanton et al., 1992; Hansen et al., 2006; Dematawewa et al., 2007, Mayakrishnan et al., 2017). Higher milk production in older parities was associated with a more mature and larger udder with greater tissue development as revealed in a study conducted on Danish Red cows in South Africa (Nyamushamba, 2014).

2.2.1.3 Effect of stage of lactation

A study in Korean Holstein dairy cows demonstrated that milk yield peaks in early lactation with an exponential increase generally up to 90 days (Vijayakumar, 2017; Tamami et al.,

2018) and an almost linear decline thereafter as demonstrated in Holstein-Friesian cows in Ireland using a Wilmink model (Horan et al., 2005; Roche et al., 2005).

2.2.1.4 Effect of age at calving

Studies conducted on Ayrshire and Jersey breeds in South Africa reported an association between age at calving and milk yield (Du toit et al., 1998). Italian Holstein-Friesian cows exhibited higher milk yields when the age at calving was delayed, indicating an association between delayed calving age and increased milk production. The lower milk yield observed in cows with earlier calving ages is likely attributed to the relatively lower body weight of younger heifers at the onset of their first lactation (Pirlo et al., 2011). However, Polish Holstein-Friesian cattle showed a negative association between age at first calving, yield per milking day, and lifetime milk yield (Sawa et al., 2019). Conversely, Holstein-Friesian cows calving between the ages of 22 and 32 months do not experience a significant influence on their lifetime milk yield (Curran et al., 2013). Cows that calve earlier tend to have more lactations and more lactation days throughout their lifetime.

2.2.1.5 Effect of milking frequency

Milk production also changes based on frequency of milking (Vijayakumar et al, 2017). Research involving sixty-six spring-calving, multiparous Holstein-Friesian cows in Ireland concluded that milking once daily decreases milk yield during early lactation (Patton, 2006). Another study conducted on Moroccan Holstein-Friesian cows demonstrated that significantly more milk yield was associated with thrice-daily milking compared to twice-daily milking (Boujenane , 2019).

2.2.1.6 Effect of feedstuffs, feeding strategies and herd

Daily supplementing with concentrates was suggested for Irish dairy cows very early in lactation, especially where grass was scarce, to help cows meet their milk production requirements (Dillon, 1997). Milk production and fat content decline when there are imbalances in nutrition or poor feeding practices as a result of low microbial protein content and low volatile fatty acids in the rumen (Garamu , 2019). In a study by Kgole (2013), it was found that herd test day has a significant impact on TD milk yield in Holstein cattle in South Africa. Furthermore, Kgole et al. (2012) concluded that variations in HTD could stem from differences in nutritional management, particularly when studying the environmental factors influencing milk urea nitrogen levels in South African cattle.

2.2.1.7 Permanent Environmental Effects

In routinely recorded measurements, the assumption is that similarities between an individual's records are due to environmental factors that influence the individual's lifetime performance (Mrode, 2014). There is thus a non-genetic effect between-individual variance, referred to as permanent environmental effect (Kruuk & Hadfield, 2007).

Phenotypic performance is permanently affected later in life as a result of the foetal development which may be impacted by intrauterine environment stimuli (Berry et al., 2008). This phenomenon may be attributed to epigenetic regulation, which is suggested to account for a significant portion of the unexplained phenotypic variation in dairy cows (Singh et al., 2010) . Epigenetic regulation is a non-sequence inheritable change in chromatin, such as DNA methylation and histone modifications, which alters the expression of gene and therefore contributes to how the mammary should function (Singh et al., 2010; Berry et al., 2011; Lesta et al., 2023) . Mammary gland cells undergo significant epigenetic modifications during lactation, which aid in the activation of the genes necessary for milk synthesis and secretion (Lesta et al., 2023). Overfeeding of replacement heifers during the prepubertal stage to induce fast growth rates also affects mammary development causing low milk production later in life (Sejrsen & Purup, 1997). To improve the precision of genetic evaluation model's permanent environment effects should be fitted in the RRMs to capture management, chance, but also possible epigenetic effects (Singh et al., 2010; Berry et al., 2014).

2.2.2 Genetic effects

Genetic gain is thought to contribute to half the improvements in animal phenotypic performance in carefully designed breeding programs (Berry, 2015). A portion of the observable performance of a trait can be attributed to both additive and non-additive genetic components (Kiplagat et al., 2012). Heterosis, also known as hybrid vigor, arises from non-additive genetic components and is evident in crossbred offspring that exhibit performance advantages exceeding the mid-parent average for a specific trait (Simm, 1998). Sophisticated mixed models such as RRMs have provisions for predicting the effects of heterosis and recombination loss coefficients. The failure to account for these non-additive genetic effects contributes to an overestimation of genetic variances and heritability (Fadili & Leroy, 2001).

2.2.2.1 Effect of breed

Breeds are vital in enhancing the genetic improvement and preserving diversity within species (Shrestha, 2005). As is the case in any biological system, breeds are subject to constant changes. Therefore, the breed of cattle significantly influences both the quantity and quality of milk produced (Palii, 2021). A study conducted in Ireland revealed that Norwegian Red cattle produced slightly less milk than Holstein-Friesians (Walsh et al., 2008). In a separate study, it was found that Irish Holstein-Friesian cows yield significantly more milk than Jersey cows. Additionally, variations in milk component concentrations have been observed across different breeds (Franzoi et al., 2019)

2.3 Genetic Evaluation Models

Enhancing the efficiency of breeding programs requires more precise model definitions in genetic evaluations. Therefore, the statistical model to be used in the TD data should encapsulate precisely the effects and the structure of (co)variance among observations as well as estimation of genetic parameters (Rekaya et al., 1999) . Selection index methods have been replaced by the mixed models with the new method being more advantageous in having best linear unbiased prediction (BLUP) properties (Powell, 2006) . Predictions based on BLUP provide the basis for ranking animals for selection in most developing countries (INTERBULL, 1992). When estimating genetic merit using BLUP, the analysis simultaneously estimates and adjusts for systematic environmental factors (such as herd) and genetic effects (Berry, 2008). The genetic relationships between all animals must be considered so that the breeding values could be accurately predicted (Thompson et al., 2005). Animal models have the wherewithal in this regard; therefore, it is possible to provide genetic merit indicators for all animals by considering selection within the population and assortative mating (Berry, 2008). The BLUP using an animal model has been demonstrated to contribute to accelerated genetic gain (Jeyaruban et al., 1995).

2.3.2.1 Test day models used for genetic evaluations

Repeatability Model (REP)

Most of the methods used to analyze longitudinal data consider a patterned covariance matrix but they differ from each other by their assumptions regarding the covariance matrix structure (White et al., 1999). The repeatability model assumes a consistent genetic variance across days in milk (DIM) and a genetic correlation of one between TD records taken at different intervals (Ptak & Schaeffer, 1993). This model accounts for the curvilinear pattern of production using fixed regressions on DIM (Reents, et al., 1995) While the random components of the model are defined according to the traditional repeatability model (Vargas et al., 1998; Jensen, 2001). As a result, individual measurements are modeled appropriately. There is a higher accuracy of breeding value resulting from large number of records per animal and better adjustments (Komprej, 2009). However, when dealing with repeated measurements that typically follow specific curves like growth or lactation curves, the correlations between closely spaced measurements tend to be stronger than those taken at greater intervals. Therefore, a more sophisticated model that takes into account the diverse correlation structure among all observations becomes imperative.

A complete Multi-trait Model

Multi-trait model has been utilized for genetic evaluations (Pander et al., 1992; Meyer et al., 1989; Pander et al., 1992). This approach considers every TD as an independent trait and also allows heterogenous correlations among time-points (i.e., traits). This kind of analysis is limited by multitude of traits to be analyzed and parameters to be estimated (Jakobsen et al., 2002). This model is prone to unnecessary computational demands and estimation issues near the parameter bounds (Meyer, 1998). Fitting a random regression model presents a more suitable approach for dealing with repeated measurements over time.

Random Regression Model (RRM)

Random regression models make better use of data at their disposal (Berry, 2008), so they are widely used in dairy genetic evaluation systems (Mrode, 2014). In RRMs, the correlations between DIM are assumed to be less than unity allowing for the TDM to adjust for the stage of lactation. In RRMs, the lactation curve is divided into a fixed component and a random component (distinct to each animal). The fixed part models the lactation curves for distinct groups of animals, considering factors such as age, lactation stage, parity, and season of birth (Bormann et al., 2003). The VCs of the RR coefficients determine the covariance function for each DIM as explained by Pool and Meuwissen (2000). Therefore, these models provide genetic merit estimates at each point along the lactation trajectory (Berry, 2008). Therefore, selection of animals with differing lactation profiles is facilitated when such estimates at each point along the lactation trajectory are combined with economic analysis (Berry, 2008). The RRMs can produce persistency estimates of lactation as a by-product, which provides an additional tool to select cows that are easier to manage, have fewer fertility problems and less production stress (Muir et al., 2007).

The matrix form of the RRM has been described by Mrode (2005) as follows:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Qu} + \mathbf{Zpe} + \mathbf{e}$$

where **y** is a vector of routinely recorded TD yields for each cow, **X** is an incidence matrix that connects observations in **y** to fixed effects and fixed regression coefficients, **b** is a vector that contains solutions corresponding to fixed effects and fixed regressions, **Q** is an incidence matrix of covariates that connects observations in **y** to random additive genetic regression coefficients, **u** corresponds to a vector representing random additive direct genetic effects, **Z** represents an incidence matrix of covariates connecting observations in **y** to permanent environmental RR coefficients, **pe** is a vector of random permanent environmental regression coefficients for each animal, **e** is a vector of random residuals which includes the temporary environmental effects for each observation.

Variances assumed for this model are:

$$var\begin{bmatrix} u \\ pe \\ e \end{bmatrix} = \begin{bmatrix} \mathbf{A} \otimes \mathbf{G} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{I} \otimes \mathbf{P} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & I\sigma_e^2 \end{bmatrix}$$

here **A** is Wright's numerator relationship matrix, **G** is the (co)variance matrix of the additive genetic RR coefficients, **I** is an identity matrix whose order is equal to the total number of observations, **P** is the (co)variance matrix of the permanent environmental RR coefficients, and σ_e^2 is the variance of random residuals.

Heterogeneity of Residual Variance

Several studies have discovered heterogeneous residual variance across lactation. (Jamrozik et al., 1997; Olori et al., 1999; Rekaya et al., 2000). The residual variance can be due to many environmental factors such as herd management, weather conditions, region, month of calving, DIM, medical treatments, pregnancy status and milking times (Perochon etal., 1996; Swalve, 2000). Residual variance is greater at the extremes of the lactation and it is related to lactation stage (López-Romero et al., 2003). Changes in the residual variance can affect heritability estimates (Olori et al., 1996; Fujii & Suzuki, 2006). Models that assumes a heterogenous residual variance achieve a better goodness of fit in RRM studies (Gao et al., 2020). So, the lactation should be partitioned into classes assuming homogeneity within, but heterogeneity across stages to achieve more accurate estimates of variance components (Olori et al., 1999; Rekaya et al., 1999).

2.3.2.2 Modelling the lactation curve

There exists a curvilinear relationship between TD yields and DIM which needs to be modelled with the use of appropriate function (Abdullahpour et al., 2013). There also exist mathematical functions for modelling the lactation curve and predicting 305-day milk production in dairy (Wood, 1967; Ali & Schaeffer, 1987). The two basic approaches are RR based on a functional lactation curve like the Wilmink’s (1987) function and RR based on Legendre polynomials (Jamrozik & Schaeffer, 2002). Orthogonal legendre polynomials have the following advantages.

1. They are flexible in terms of parameter counts that can be used to describe the pattern of milk production (Jamrozik & Schaeffer, 2002).
2. The derived coefficients in Legendre polynomials are highly valuable for examining genetic variation patterns by computing eigenfunctions and eigenvalues derived from the covariance function (Kirkpatrick et al., 1990).
3. The Legendre polynomials demonstrate less oscillatory patterns rendering them appropriate from biological perspective (Kirkpatrick et al., 1990).
4. Legendre polynomials are less expensive to calculate and produce more accurate lactation curves than Wood's and Wilmink's functions. (Fujii et al, 2006) .
5. Legendre polynomials can function by changing orders and have the ability to combine with other lactation curves (Kirkpatrick et al., 1994).

Legendre polynomials have been applied in various TDMs (Pool and Meuwissen, 1999). Nonetheless, for lack of “gold standard” in literature concerning the optimal order of fit, data structure and populations are considered in choosing the order of fit (Muir et al., 2007).

2.4 Variance Components and Genetic Parameter Estimation

The variance partitioning framework sheds light into a particular trait’s response to selection which materlises as the ability to predict change in the mean phenotype for each generation after selection (Wolak & Keller, 2014). The total variance of a TD record is the sum of genetic, permanent environmental, and residual variance (Jensen, 2001). Genetic parameter estimates are essential inputs for selection indices, and also for prediction of breeding values of animals (Gadini, 1997). To predict the expected response to selection and estimate breeding values using the BLUP approach, accurate estimates of VCs and correlations are essential (Montaldo et al., 2010). Genetic and residual (co)variance components vary across populations, so accurate estimation should occur within the specific population where they will be applied. Additionally, genetic parameters can evolve over time due to selection and management choices (Imbayarwo, 2010).

2.4.1 Heritability

The heritability of a trait reflects how strongly an individual's true genetic merit for the trait is related to its phenotypic expression (Berry et al., 2019). It is estimated after adjustments for systematic environmental effects are made (Berry et al., 2019) and therefore, represents the level of confidence that should be put in animals’ performance while selecting parents for the next generation (Bennet, 2009). The heritability estimated in this thesis refers specifically to narrow-sense heritability, which quantifies the proportion of phenotypic variation attributed to additive genetic variation (Berry et al., 2011). Heritability ranges from 0 interpreted as not heritable to 1 interpreted as fully heritable (Berry et al., 2011). When a trait has high heritability, it indicates that the observed phenotypes closely align with the animal’s breeding value for that specific trait. Conversely, in cases of low heritability, phenotypic values are a poor reflection of the breeding value and consequently selection based on the phenotypic performance of the observed trait becomes ineffective in the prediction of the performance of the offspring (Bourdon, 2000). In dairy cattle, heritability estimates may differ from breed to breed and may also change slowly over time (Bennet, 2009). The analysis of single TD milk records of Friesian cows showed that the heritability thereof was low in the early stage of lactation which then increased in mid lactation period (Swalve, 1995).

2.4.2 Genetic and phenotypic correlation

Multiple measurements on a given time can be considered as multiple traits (Van der Werf & Schaeffer, 1997) and the correlation structure among them can be modelled (Diggle et al., 1994). Knowing the genetic correlations among traits is important for the careful construction of breeding programs (Bennet, 2009; Van Vleck & Henderson, 2009). Many studies have confirmed genetic correlations for TD milk yield at various lactation stages to be lower than unity (Lidauer et al., 2003; Negussie et al., 2008; Bignardi et al., 2011; Torshiz et al., 2013; Gebreyohannes, 2013). Genetic correlations between adjacent test-day records have been demonstrated to be strong, weakening as the interval between TD increases (Swalve, 1995; Jamrozik and Schaeffer, 1997). Therefore, it can be suggested that distinct sets of genes control test-day yields, suggesting they should be regarded as separate traits (Meseret et al., 2015).

2.4.3 Methods for parameter estimation

In animal breeding restricted maximum likelihood (REML) as well as Bayesian via Gibbs sampling are two methodologies used in estimating variance components (Thompson et al., 2005). In Bayesian inference, the Gibbs sampler achieves its target of obtaining a random sample from the marginal posterior distribution by sampling iteratively from the conditional distributions of all parameters in the model. This method allows for a thorough investigation of the parameter space as well as significant insights into the posterior distribution (Waldmann & Ericsson, 2006). The REML, modified version of the maximum likelihood procedure (ML), is preferred to ML, particularly for its ability to reduce bias in selection (Meyer, 1991). The REML technique considers the loss of degrees of freedom caused by fixed effects (Patterson and Thompson, 1971). The REML procedure of necessity derive covariance functions for both additive genetic and permanent environmental covariance components in estimating of VC for TD milk records (Meyer and Hill, 1997). To produce REML estimations, parameter values that maximize the logarithm of the probability function based on the assumed distribution of the data should be located (Boldman & Van Vleck, 1991). The log-likelihood is a complex nonlinear function requiring iteration for the maximization thereof (Hofer, 1998). Depending on the order of derivatives available, maximization can be performed in a variety of ways (Thompson and Mäntysaari, 1999). In REML, the algorithms currently in use are either dependent on the derivative-free (Graser et al., 1987), the EM, or the AI algorithm (Johnson and Thompson, 1995, Jensen et al., 1997).

2.5 Model assessment and selection

Responsible data analysis must address the issue of model assessment and model selection (Gelfand, 1996). This can be simplified by using a selection criterion, which assigns a score to each model in a candidate, set to help identify the best model (Neath & Cavanaugh, 2012). A selection criterion will, in general, eliminate candidate models that are either too simplistic to fully fit the data or overly complex (Neath & Cavanaugh, 2012). In the TDM technique, the most often used metrics for comparing the goodness of fit of different functions are LogL, AIC, BIC, and mean square error of predictions (MSEP) (Ødegard, et al., 2003; Aspilcueta-Borquis et al., 2012).

The AIC is formulated as the sum of negative log-likelihood (-2logL) with a penalty term (+2p) that increases with the number of parameters in a given model (Lin et al., 2017).

Selecting the model with the lowest predicted information loss is asymptotically identical to selecting the model with the lowest AIC score (Wagenmakers & Farrell, 2004). Akaike information criterion has been challenged because of its proclivity to favor the model with the highest order when sample sizes are very big (McQuarrie et al. 1997).

The BIC is a common alternative model selection criterion (Burnham & Anderson, 2002). Schwarz (1978) developed it in a Bayesian setting as an asymptotic approximation to a transformation of a candidate model's posterior probability (Neath & Cavanaugh, 2012). The BIC has the same goodness-of-fit term (-2logL), but when it comes to the penalty term, it uses a complexity penalization of k log n rather than 2k. As a result, BIC prefers fitted models that are more parsimonious than those preferred by AIC (Cavanaugh & Neath, 2019). The BIC behaves poorly in the absence of genuine model among the candidates (Burnham et al., 2011). The -2logL can be used together with chi square where the difference in number of parameters between any 2 successive models is the degree of freedom and the difference between the -2logL of the models is the calculated chi square value.

CHAPTER THREE

MATERIALS AND METHODS

3.1 Data

Milk test-day records of dairy cows milking in the 2019 calendar year were obtained from *Teagasc Animal & Grassland Research & Innovation Centre, Moorepark.* Only data between 5 and 305 days in milk (DIM) from animals with known parents were retained. The records totaled 209,047 test day records. The parity number was recoded as 1, 2, 3, 4 or 5+. All cows calved between 22 and 78 months of age. The age of the cows was categorized into three age groups relative to parity median. Cows calving more than 6 months from the parity median were discarded. Lactations <120 days in duration were discarded. Test-days where the milk yield was either < 2 kg or > 40 kg were removed. These data edits were undertaken in R program to extract more informative records, following the data editing rules employed in test-day model analysis.

Data on a total of 901 cows was available, with the pedigree of each individual animal traced back to its respective founder. These founders were then assigned to certain genetic groups. The pedigree included a total of 25,725 individuals. The cows were purebred and also crossbred with different proportions of Holstein, Friesian, and Jersey genotypes. General heterosis and recombination loss coefficients were computed for each cow as $1-\sum_{i=1}^{n} sire_i * dam_i$ and $1-\sum_{i=1}^{n}\frac{sire^2{}_i+dam^2{}_i}{2}$, respectively, where sire $_i$ and dam $_i$ are the proportion of breed i in the sire and dam, respectively (Van Raden & Sanders, 2003) . Heterosis values were categorized into 10 levels as (0%, ≤20%, ≤30%, ≤40%, ≤50%, ≤60%, ≤70%, ≤80%, <100%, or 100%, and recombination loss into 7 levels as 0, ≤0.10, ≤0.20, ≤0.30, ≤0.40, ≤0.50, or >0.50 (Judge et al., 2019).

There were 2078 herd test dates (HTD) formed by concatenating experimental treatment, and date of test. The treatments were specific to the seven herds available. So, the number of treatments was the same as the number of herds.

The mean and standard deviation of milk yield was calculated for each parity by stage of lactation (5 to 35, 36-65, ….. 276-305 DIM) and test-day records where the milk yield deviated more than 3 standard deviations from the respective mean were discarded, as they are considered outliers.

3.1.1 Data Analyses

A preliminary analysis was undertaken to identify factors associated with milk yield (Gilmour et al., 2013). The model tested included

$$Y_{ij\,klmnopq} = trt*dates_j + p_l * age_m + leg(dim,4).parity_n + het_p + rec_q + \varepsilon_{j\,klmnopq}$$

where $Y_{ij\,klmnopq}$ = Test date milk yield;

$trt*dates_j$ =the interaction effect between test dates and experimental treatment;

$p_l * age_m$ = the effect of age at calving class relative to parity;

dim_l = the fixed effect of lactation curve (Legendre polynomial order 4) nested within parity;

het_o = the fixed effect of heterosis class; and

rec_q = the fixed effect of recombination loss

$\varepsilon_{j\,klmonpq}$ are the residual effects for Test dates milk yield.

Random regression using Legendre polynomials were used to model the additive genetic and within-animal permanent environmental effects (Strabel and Misztal, 1999; Olori et al., 1999; Araújo et al., 2006).

The model equation fitted in ASReml (Gilmour et al., 2013) was:

$$Y_{tijk} = rec_q + het_i + trt * dates_j + P_l * \ age_m + \sum_{k=o}^{4} \Phi_{jtk}\ \beta_k + \sum_{k=o}^{nr} \Phi_{jtk}\ U_{jk} + \sum_{k=o}^{np} \Phi_{jtk}\ pe_{jk} + e_{tijk}$$

where, Y_{tijk} = Test dates milk yield;

rec_q is the fixed effect of recombination loss

het_i is the fixed effect of heterosis class

$trt * dates_j$ is the interaction effect between test date and experimental treatment

$p_l * age_m$ = the effect of age at calving class relative to parity;

β_k are fixed regression coefficients, u_{jk} and pe_{jk} are the k-th random regression coefficients for the j-th animal for additive genetic and permanent environmental effects respectively, Φ_{jtk} is the k-th Legendre polynomial for the standardized test day record of cow j made on day t.

nr and np represent the orders of Legendre polynomial for the additive genetic effect and permanent environmental effect, respectively.

$\mathbf{e}_{tijk}$ is the random residual effect

Different residual error classes associated with different lactation stages were modelled. This was done by dividing DIM into 10 residual classes across lactation stages as (5–35, 36–65, 66–95, 96–125, 126–155, 156–185, 186–215, 216–245, 246–275, and 276–305 DIM) (Pereira et al., 2013).

Variance estimation for the permanent environmental effects was based on $\hat{\mathbf{P}} = \boldsymbol{\phi}\hat{\mathbf{K}}\boldsymbol{\phi}$ while for that of additive genetic effects was based on $\hat{\mathbf{G}} = \boldsymbol{\phi}\hat{\mathbf{K}}\boldsymbol{\phi}$; where $\hat{\mathbf{G}}$ represents the additive genetic (co)variance matrix for DIM with dimension t×t (t is the number of days in milk), $\boldsymbol{\phi}$ represents the matrix of Legendre polynomials for standardized DIM with dimension of t×k (k is the order of Legendre polynomials for this random effect) and $\hat{\mathbf{K}}$ is the estimated (co)variance matrix for random regression coefficients which is a k×k matrix (Mrode, 2014).

Heritability, repeatability, genetic and permanent environmental correlations were also estimated using the formula given by Mrode (2014):

The variances were estimated for each day and they were used to estimate the daily heritability of and repeatability of milk yield as:

$$\hat{h}^2 = \frac{\sigma_a^2}{\sigma_{pe}^2 + \sigma_a^2 + \sigma_e^2}$$

$$t = \frac{\sigma_a^2 + \sigma_{pe}^2}{\sigma_{pe}^2 + \sigma_a^2 + \sigma_e^2}$$

where, σ_a^2 is the additive genetic effect;

σ_{pe}^2 is permanent environmental effect and

σ_e^2 is residual variance.

The additive genetic covariance between days $\boldsymbol{d_i}$ and $\boldsymbol{d_j}$ and genetic variances of $\boldsymbol{d_i}$ and $\boldsymbol{d_j}$ were used to calculate the genetic correlation between two days in lactation.

$$\mathbf{r}_{a(di,dj)} = \frac{\boldsymbol{\Phi}'_{(di)}\mathbf{G}\boldsymbol{\Phi}_{(dj)}}{\sqrt{\boldsymbol{\Phi}'_{(di)}\mathbf{G}\,\boldsymbol{\Phi}'_{di}\cdot\boldsymbol{\Phi}'_{(dj)}\mathbf{G}\,\boldsymbol{\Phi}'_{(dj)}}}$$

The calculation of the permanent environmental correlation followed a similar approach to the genetic correlation described earlier with **G** (the covariance matrix of the genotypic regression coefficient) replaced by **P** (the permanent environmental counterpart of **G**),

$$\mathbf{r}_{a(di,dj)} = \frac{\boldsymbol{\Phi}'_{(di)}\mathbf{P}\boldsymbol{\Phi}_{(dj)}}{\sqrt{\boldsymbol{\Phi}'_{(di)}\mathbf{P}\ \boldsymbol{\Phi}'_{di}\cdot\boldsymbol{\Phi}'_{(dj)}\mathbf{P}\ \boldsymbol{\Phi}'_{(dj)}}}$$

3.2 Model selection criteria

A combination of the LogL, AIC, BIC (Wolfinger, 1993) and residual variances was employed to assess the fit of the RR models. The -2logL can be used together with chi square where the difference in number of parameters between any 2 successive models is the degree of freedom and the difference between the -2logL of the models is the calculated chi square value. Moreover, the variance components and genetic parameters estimated for each random regression model were used as criteria to select the model that most accurately represents the covariance structure of the data These combinations were necessary to enhance a robust decision. The analysis of eigenvalues from the covariance matrices of the additive genetic and permanent environmental effects was used to determine the usefulness of additional orders to the fitted polynomials. Therefore , model development was undertaken in stages initially employing the first order Legendre polynomials to model both the additive genetic and permanent environmental effects and then advancing to the next higher orders of Legendre polynomials provided the corresponding eigenvalues of both the additive genetic and permanent environment covariance matrices could contribute to model improvement. Higher orders of the Legendre polynomials were omitted due to the inability to achieve convergence of the log likelihood. Therefore, model development stopped when the second order Legendre polynomials were fitted for both additive genetic and permanent environmental effects.

CHAPTER FOUR

RESULTS

4.1 Descriptive Statistics

The mean milk yield and standard deviation of the entire population was 19.50 kg and 6.48 kg, respectively. Table 4.1 shows the cows mean milk yield and the respective standard deviations by parity and days in milk (DIM). The data shows that the mean milk yield generally increased as parity advanced. Cows in parity one had the lowest mean milk yield of 15.91 kg, while cows in parity two produced a mean milk yield of 19.71 kg. Parity five cows produced the highest mean milk yield of 22.11 kg. The mean milk yield showed a percentage increase of 23.89% between parity one and parity two, whereas the percentage increase in mean milk yield between parity one and parity five was 38.97%. The lowest percentage increase of 1.52% was observed between parity four and parity five. The data also showed an upward trend in mean milk yield from 5-35 DIM to a peak at 36-65 DIM declining consistently thereafter until it bottomed out at 276-305 DIM.

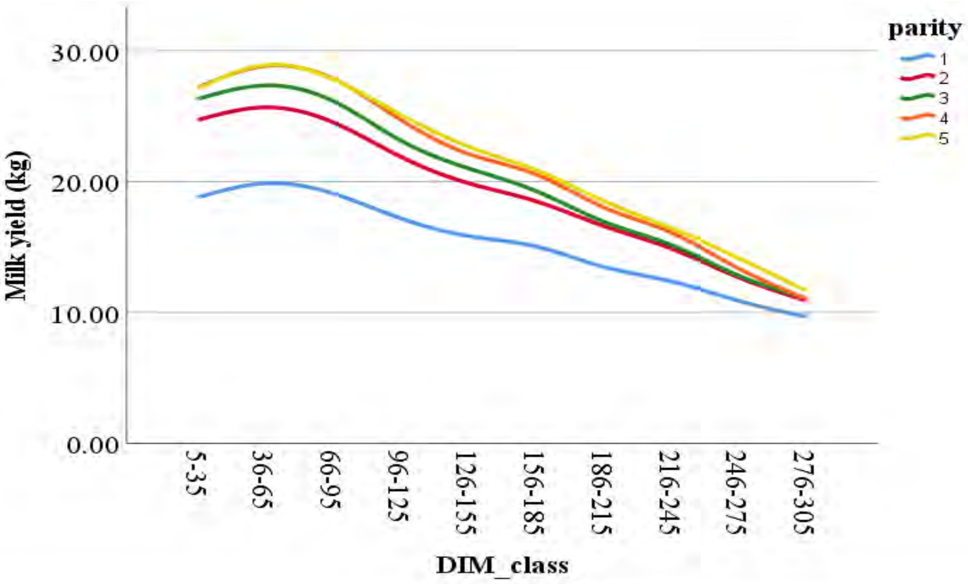

Figure 4. 1: Mean milk yield (kg) by days in milk (DIM) class and Parity.

Table 4.1: Mean milk yield (kg) by days in milk class and Parity

	Parity [*]						
DIM	1	2	3	4	5	Total	No of Records
5-35	18.96 (4.25)	24.71 (4.41)	26.31 (4.84)	27.19 (4.82)	27.06 (4.95)	24.11 (5.71)	22054
36-65	19.86 (4.02)	25.66 (4.47)	27.34 (4.57)	28.82 (4.63)	28.91 (4.83)	25.28 (5.75)	22330
66-95	19.16 (3.87)	24.52 (4.22)	26.14 (4.53)	27.85 (4.40)	27.79 (4.58)	24.28 (5.52)	22262
96-125	17.59 (3.65)	21.89 (4.21)	23.13 (4.41)	24.71 (4.32)	25.11 (4.37)	21.83 (5.06)	21312
126-155	16.13 (3.27)	19.88 (4.21)	21.01 (4.17)	22.11 (3.88)	22.66 (4.10)	19.83 (4.62)	22919
156-185	15.29 (3.17)	18.63 (4.17)	19.35(4.10)	20.55 (4.22)	20.89 (4.10)	18.47 (4.45)	23285
186-215	13.69 (3.14)	16.82 (3.96)	17.12 (3.90)	18.18 (4.19)	18.59 (3.85)	16.49 (4.18)	23141
216-245	12.71 (3.01)	15.11 (3.94)	15.39 (3.82)	16.35 (3.97)	16.6 (3.93)	14.89 (3.96)	22409
246-275	11.28 (2.76)	13.03 (3.55)	13.15(3.30)	13.69 (3.55)	14.31 (3.45)	12.82 (3.44)	18999
276-305	10.26 (2.47)	11.4 (2.89)	11.65 (2.85)	11.62 (3.08)	12.06 (2.95)	11.29 (2.89)	10336
Total	15.91 (4.6)	19.71 (6.08)	20.69 (6.52)	21.78 (6.81)	22.11 (6.67)	19.5 (6.48)	209047

[*] Standard deviations in parenthesis

4.2 Genetic and Non-Genetic Factors

The least square means and standard errors for the fixed effects of heterosis, recombination loss, parity as well as age at calving relative to parity are presented in Tables 4.2, respectively. All factors were associated with milk yield ($p < 0.05$). Overall, the least square means for the heterosis effect on milk yield ranged from 18.10 kg (observed in 0%) to 21.47 kg (observed in >0% and $\leq$ 20%). Mean yields were lowest for the purebred animals that demonstrated no heterosis.

Overall, the least square means for recombination loss on milk yield ranged from 18.87 kg (observed in 0%) to 20.58 kg (observed in >40% and $\leq$ 50%). Mean yields were lowest for animals that demonstrated no recombination loss.

Table 4.2: Least square means (kg) and standard errors of the effects of heterosis, recombination loss, parity and age at calving relative to parity on milk yield

Heterosis value	LSM (kg)	Recombination loss	LSMs (kg)	Age at calving class	Parity	LSMs (kg)	Parity	LSM ((kg)
0%	18.10 ±0.05 ^{a}	0%	18.87 ±0.06 ^{a}	1	1	15.72 (0.03) ^{a}	1	15.44 ±0.04 ^{a}
>0% and ≤ 20%	21.47 ±0.07 ^{b}	>0% and ≤ 10%	19.90 ±0.090 ^{a}	2	1	15.65 (0.04) ^{a}	2	19.85 ±0.04 ^{b}
>20% and ≤30%	20.75 ±0.05 ^{b}	>10% and ≤20%	20.34 ±0.06 ^{a}	3	1	14.94 (0.09) ^{a}	3	21.05 ±0.04 ^{c}
>30% and ≤40%	20.32 ±0.04 ^{b}	>20% and ≤30%	20.19 ±0.06 ^{a}	1	2	19.20 (0.04) ^{b}	4	22.12 ±0.08 ^{c}
>40% and ≤50%	20.23 ±0.04 ^{b}	>30% and ≤40%	20.13 ±0.05 ^{a}	2	2	19.83(0.04) ^{b}	5	22.21 ±0.05 ^{d}
>50% and ≤60%	20.14 ±0.04 ^{b}	>40% and ≤50%	20.58 ±0.04 ^{a}	3	2	20.52 (0.08) ^{bc}		
>60% and ≤70%	20.00 ±0.05 ^{b}	>50%	20.40 ±0.04 ^{a}	1	3	20.72 (0.04) ^{bc}		
>70% &≤80%	20.04 ±0.05 ^{b}			2	3	20.82 (0.04) ^{bc}		
> 80% &≤100%	20.47 ±0.05 ^{b}			3	3	21.59 (0.08) ^{bc}		
100%	19.80 ±0.04 ^{b}			1	4	22.08 (0.04) ^{bc}		
				2	4	21.89 (0.04) ^{bc}		
				3	4	22.38 (0.21) ^{bc}		
				1	5	22.38 (0.04) ^{bc}		
				2	5	21.69 (0.04) ^{bc}		
				3	5	22.56 (0.13) ^{c}		

^{ab}Means with a different superscript in a column are significantly different ($P<0.05$)

^{abcd} Means with a different superscript in a column are significantly different ($P<0.05$)

^{abc}Means with a different superscript in a column are significantly different ($P<0.05$)

Overall, the least square means for parity effect on milk yield increased from 15.44 kg (observed in parity 1) to 22.21 kg^2 (observed in parity 5). Mean yields were lowest in animals that were in their first parity.

Overall, the least square means for the effect of age at calving relative to parity ranged from 15.72 kg (observed in age at calving class 1 relative to parity 1) to 22.56 kg (observed in age at calving class 3 relative to parity 5. The lowest yields were observed in the youngest animals in parity 1.

4.3 Variance Ranges

First (RRM1) and second order (RRM2) Legendre polynomials were fitted for both additive genetic and permanent environmental effects. Higher orders of the Legendre polynomials were omitted due to convergence issues with the log likelihood. Additionally, first order Legendre polynomial for additive genetic and second order Legendre polynomial for permanent environmental effect did not converge and vice versa. Therefore, the results presented are for RRM1 and RRM2, which were fitted for both additive genetic and permanent environmental effects. The solutions from linear polynomial regression (RRM1) and quadratic polynomial regressions (RRM2) are presented in Table 4.3. The analysis of RRM1 and RRM2 each estimated 18 and 24 parameters, respectively. The respective values of LogL, AIC and BIC ranged from -268191.61 to -262849.29, from 525746.59 to 536419.22, and from 525990.80 to 536602.38, respectively. The LogL increased as the order of the polynomial function used to model the additive genetic and environmental covariance increased from 1 to 2. The AIC, BIC and residual variances were lower with the RRM2. Therefore, RRM2 was used to estimate the variance components.

Table 4.3: Log likelihood (LogL), Akaike information criterion (AIC) and Bayesian information criterion (BIC) estimates by different models

Model	LogL	AIC	BIC
RRM1	-268191.61	536419.22	536602.38
RRM2	-262849.29	525746.59	525990.80

RRM1= Random regression with first order Legendre polynomial; RRM2 = Random regression with second order Legendre polynomial

The residual variances across lactation stages for both models are presented in Figure 4.2. The residual variance estimates from RRM1 and RMM2 ranged from 2.61 kg to 8.41 kg and from 2.07 kg to 6.84 kg, respectively. The highest residual variance was observed at DIM (5-35) after which it decreased until it bottomed out at DIM (276-305) for both models.

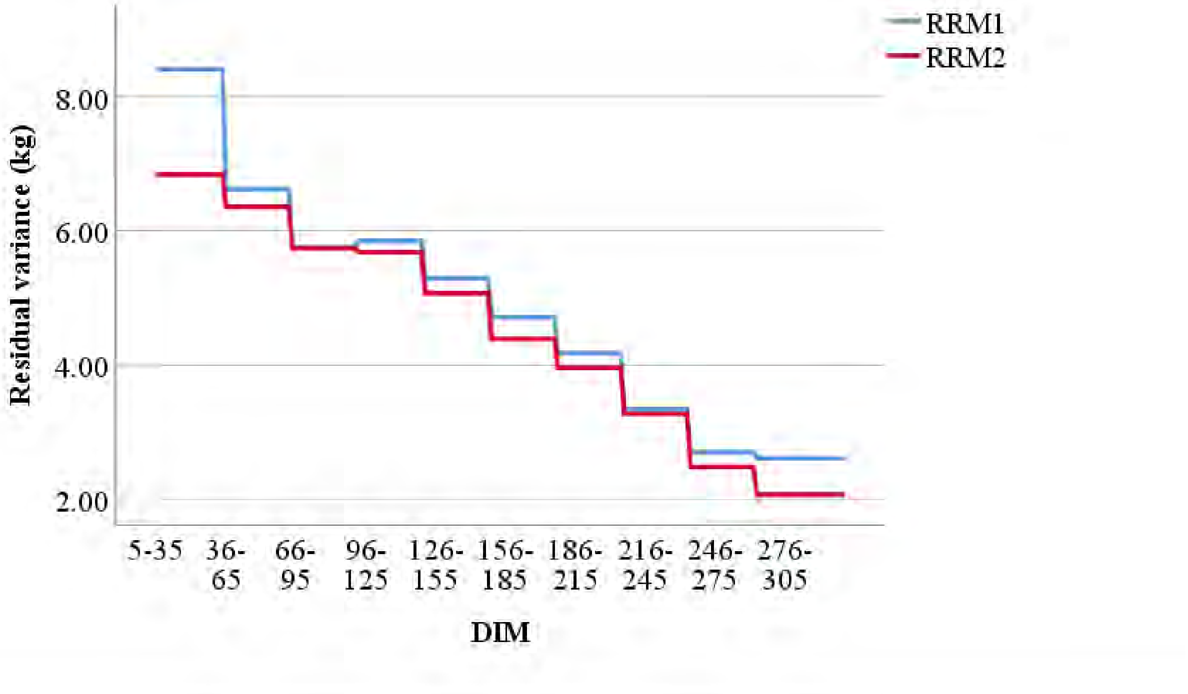

Figure 4. 2: Residual Variance estimates from random regression model with first order Legendre polynomial (RRM1) and second order Legendre polynomial (RRM2) across days in milk (DIM)

Table 4.4 provides a summary of the eigenvalues of the additive genetic and permanent environmental covariance matrices. The eigenvalues quantify the amount of variation explained by the linear and quadratic terms. The sum of the eigenvalues or the amount of variation explained increased as the order of the Legendre polynomial fitted increased. The first and second eigenvalues of the RRM1 model were 6.50 and 0.66 which translates to 90.80 % and 9.20% of the total, respectively. Similarly, the first, second and third eigenvalues of the RRM2 model were 6.25, 0.61 and 0.3 which translates to 87.32%, 8.55% and 4.12% of the total variation explained, respectively. This means that the ability to explain the additive genetic covariance matrix increased by 4.12% due to the additional order of the fitted polynomial. Similarly, the first and second eigenvalues of the permanent environmental covariance matrix was 2.61 and 1.36 which translates to 65.73% and 34.28% of the total variation of RRM1, respectively. The first, second and third eigenvalues of RRM2 was 2.6, 1.52 and 0.66 which translate to 54.35%, 31.79% and 13.85%, respectively. Therefore, the addition of second order of Legendre polynomial increased the ability to explain variation by 13.85%.

Table 4.4: Eigenvalues and their proportions for the covariance function of the additive genetic and permanent environment.

Eigenvalues							
Additive Genetic				Proportion of total (100%)			
Polynomial regression	First	Second	Third	Total	First	Second	Third
RRM1	6.50	0.66		7.16	90.80	9.20	
RRM2	6.25	0.61	0.30	7.16	87.32	8.55	4.12
Permanent Environment							
RRM1	2.61	1.36		3.97	65.73	34.28	
RRM2	2.60	1.52	0.66	4.78	54.35	31.79	13.85

RRM1 = random regression with first order Legendre polynomial; RRM2= random regression with second order Legendre polynomial

The estimates of variances of the additive genetic and permanent environmental effects from RRM1 and RRM2 are plotted in Figure 4.3. The estimates of variances of the additive genetic effect from RRM1 and RRM2 ranged from 2.79 kg to 5.70 kg and 2.27 kg to 5.37 kg, respectively. Genetic variance estimates from both RRM1 and RRM2 showed a decreasing trend with the greatest variability observed in early lactation. These variances declined over time until they bottomed out during the mid of the late lactation stage with a slight upturn after 276 DIM. Overall, estimates of the additive genetic variances from the RRM2 were lower than that from the RRM1 during early and late lactation stages but higher between 76 and 222 DIM.

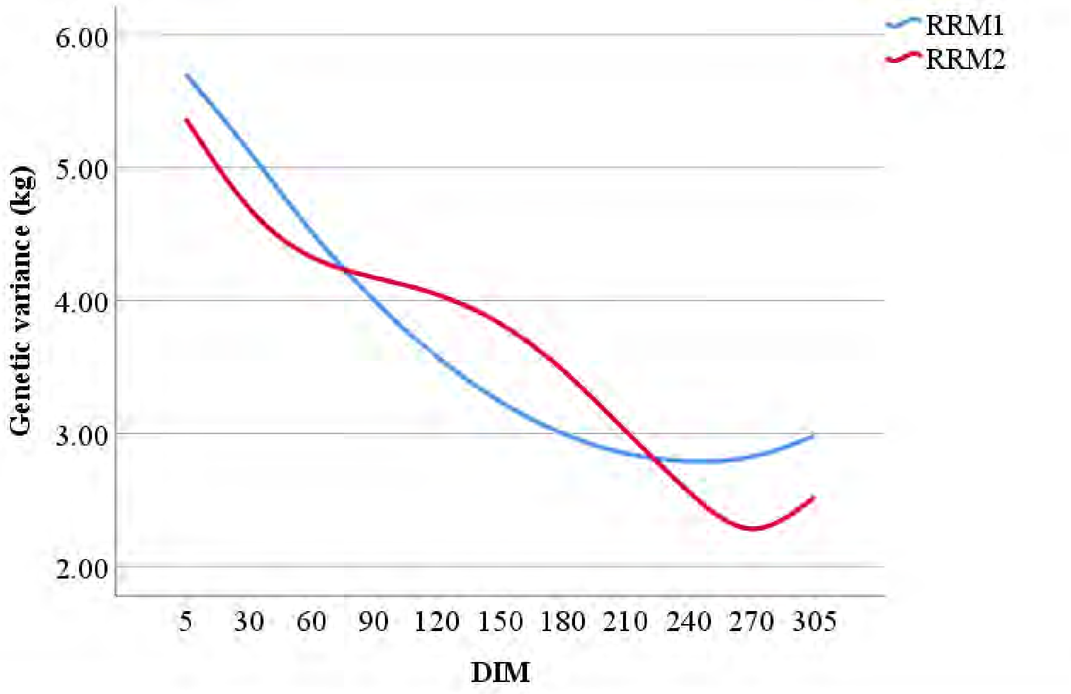

Figure 4. 3: Estimates of the additive genetic variance of milk yield across days in milk (DIM)

DIM = Days in milk; RRM1 = random regression with first order Legendre polynomial; RRM2 = random regression with second order Legendre polynomial

Estimates of permanent environmental variance from RRM1 and RRM2 were greatest in late lactation stage followed by early lactation demonstrating a concave shape. The estimates of the permanent environment from RRM2 were higher than their RRM1 counterparts in almost all cases. The differences were greater in early and late lactation stages. The estimates of the permanent environment ranged from 1.24 kg to 3.97 kg for RRM1 and 1.48 kg to 6.86 kg for RRM2.

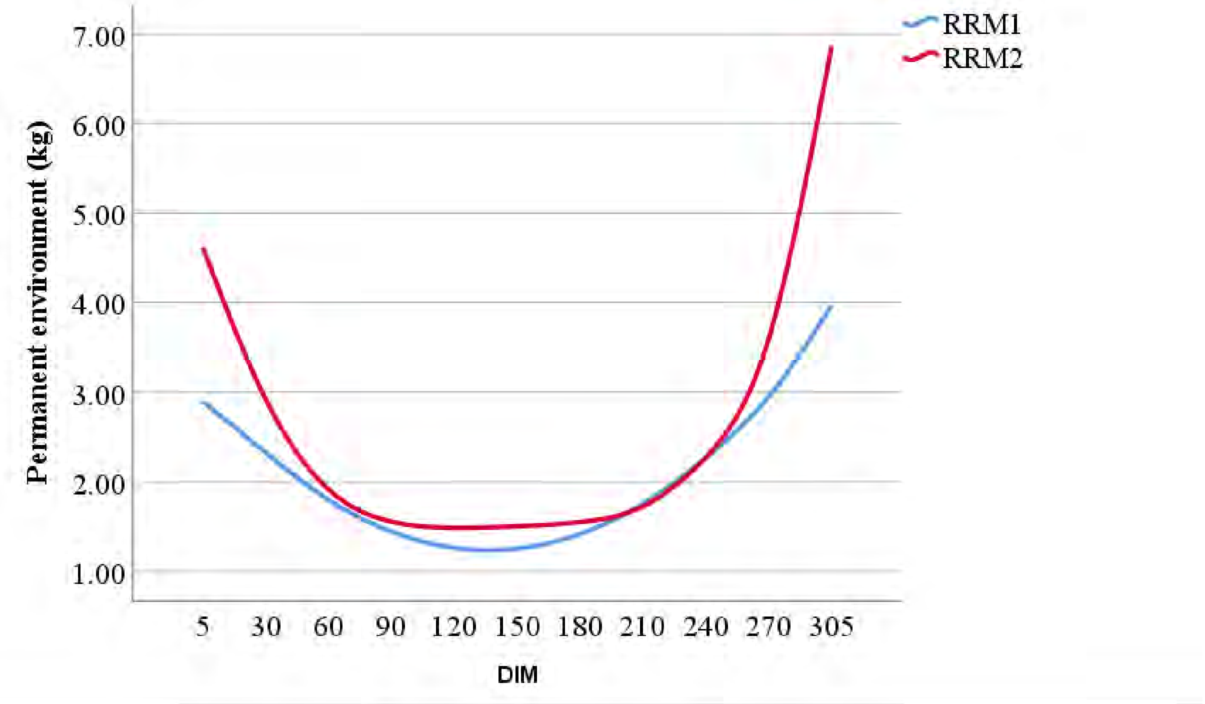

Figure 4. 4: Estimates of the permanent environment variance across days in milk (DIM)

DIM = Days in milk; RRM1 = random regression with first order Legendre polynomial; RRM2 = random regression with second order Legendre polynomial

4.5 Heritability and repeatability estimates

Heritability estimates from RRM1 and RRM2 across DIM are plotted in Figure 4.5. Daily heritability estimates from RRM1 varied from 0.31 to 0.37. The daily estimates of heritability from the RRM1 increased in early lactation stage until the highest estimate of 0.37 at DIM 66 declining thereafter and remaining constant at 0.35 from 96 DIM until 246 DIM. The heritability estimates then declined until they bottomed out at 0.31. Mean heritability estimate from RRM1 was 0.34. Heritability estimates from RRM2 ranged from 0.22 to 0.39. These estimates followed an increasing trend in early lactation until a peak at 156 DIM after which it declined until 305 DIM.

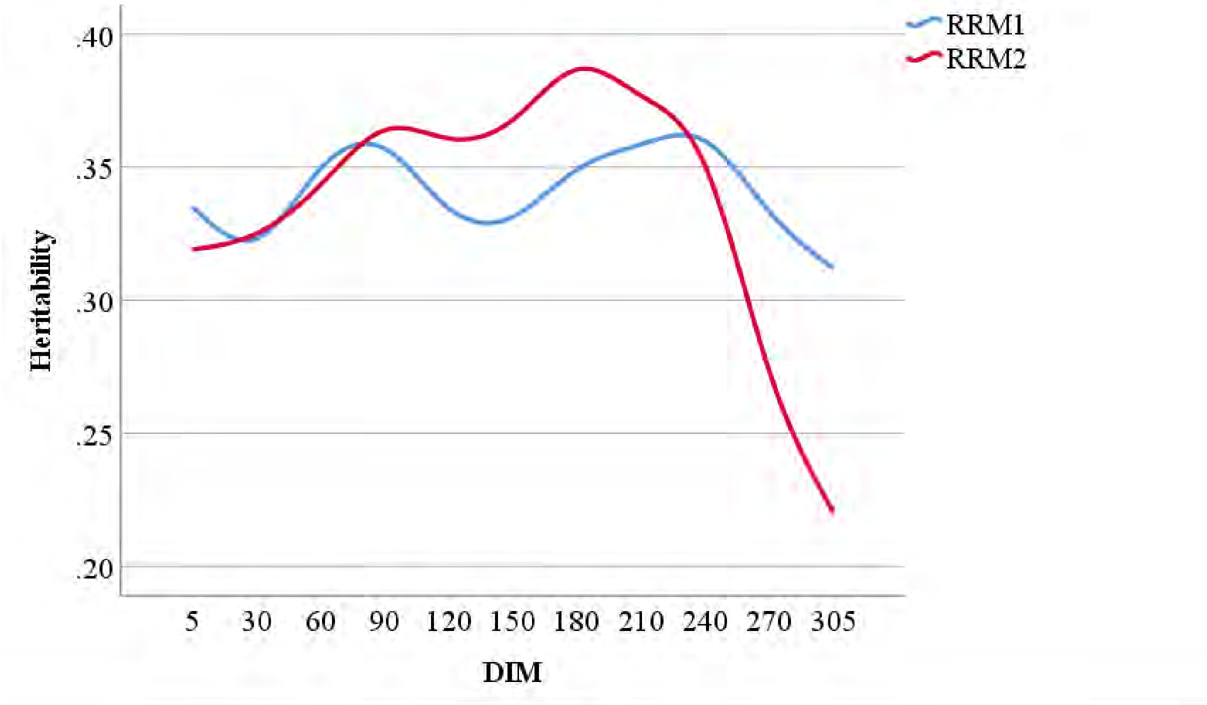

Figure 4.5: Estimates of heritability across days in milk (DIM)

DIM = Days in milk; RRM1 = random regression with first order Legendre polynomial; RRM2 = random regression with second order Legendre polynomial

Estimates of repeatability from RRM1 and RRM2 across DIM are plotted in Figure 4.6. The two models exhibited a decreasing trend during the early lactation followed by a consistent upturn till 305 DIM. The trend was opposite to that of heritability estimates. Repeatability estimates from RRM2 were slightly larger than the estimates from RRM1 ranging from 0.49 to 0.82 and from 0.47 to 0.73, respectively.

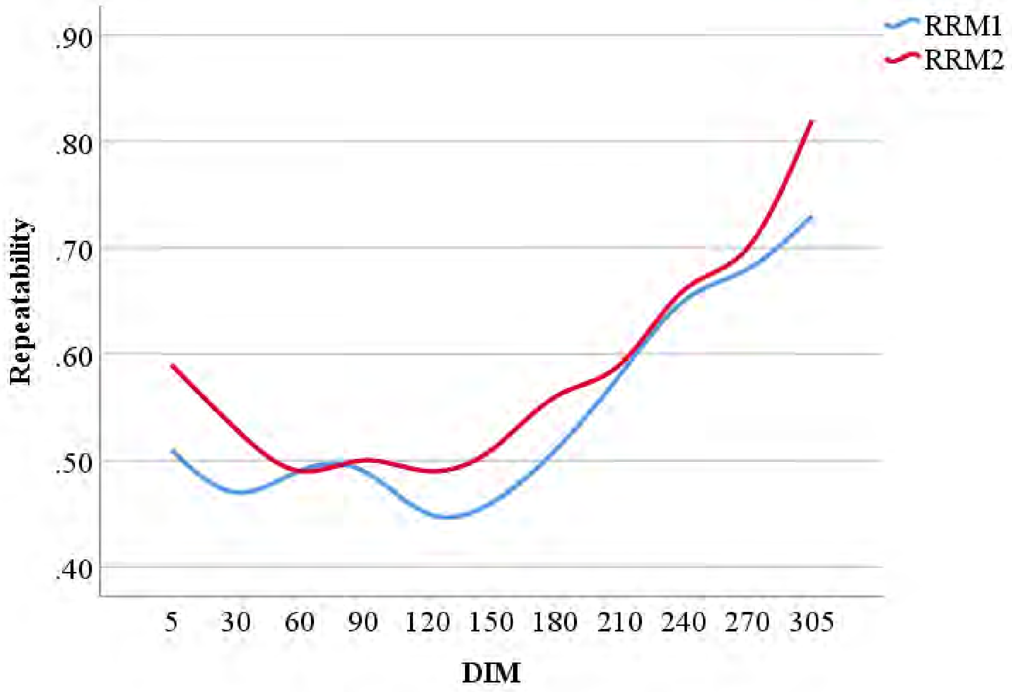

Figure 4.6: Repeatability estimates across days in milk (DIM)

4.6 Genetic and phenotypic correlations associated to test day yields

Genetic and phenotypic correlations for RRM2 are presented in Table 4.5. The phenotypic and genetic correlations weakened consistently as the interval between DIM increased. The genetic correlations varied from 0.46 to 0.99 whereas the phenotypic correlations varied from from -0.03 to 0.97. The genetic correlations exhibited a pattern of a slower weakening in the correlations as the DIM got farther apart compared to the phenotypic correlations which exhibited an abrupt weakening with the increase in the interval between DIM. The genetic correlations were consistently stronger than the corresponding phenotypic correlations.

Table 4. 5: Genetic correlation (below the diagonal) and phenotypic correlation (above the diagonal) between milk yields at specific days in milk (DIM) from random regression model with second order Legendre polynomials (RRM2).

Random regression with second order Legendre polynomial RRM2											
5		0.96	0.81	0.56	0.32	0.15	0.04	0.02	0.05	0.11	0.18
30	0.97		0.94	0.77	0.56	0.39	0.25	0.16	0.10	0.08	0.08
60	0.91	0.98		0.94	0.8	0.65	0.51	0.35	0.20	0.08	0.00
90	0.83	0.93	0.99		0.96	0.86	0.73	0.54	0.32	0.12	-0.03
120	0.75	0.88	0.96	0.99		0.97	0.88	0.70	0.46	0.22	0.03
150	0.69	0.83	0.92	0.97	0.99		0.96	0.84	0.62	0.37	0.17
180	0.65	0.79	0.89	0.95	0.98	0.99		0.95	0.79	0.58	0.39
210	0.62	0.76	0.85	0.91	0.95	0.97	0.99		0.94	0.80	0.65
240	0.59	0.71	0.79	0.84	0.88	0.91	0.95	0.98		0.96	0.86
270	0.55	0.62	0.67	0.70	0.73	0.77	0.82	0.88	0.96		0.97
305	0.47	0.47	0.47	0.46	0.48	0.51	0.57	0.67	0.80	0.94	

4.8 DISCUSSION

4.8.1 Descriptive Statistics

The mean daily milk yield obtained in the current study was consistent with McParland et al. (2015) who reported a mean milk yield of 19.5 kg per cow in commercial dairy herds in Ireland. The increase in mean milk yield with each advancement in parity was consistent with O'Brien et al. (2009), who reported mean milk yield ranging from 20.42 to 25.33 kg for parities 1 to 5 in Irish dairy cows. The disparity in mean milk yield between the two studies could be attributed to differences in genetic make-up, herd management and year. Consistent with this study, Horan et al. (2005) documented an increase in peak milk yield with each advancement in parity when investigting lactation curve characteristics in Irish cows. The timing of peak milk yield shown in the current study was also consistent with O'Sullivan et al. (2019), whose reported timing of peak milk yield for Holstein-Friesian cows was between week 7 and week 8 of lactation. The differentiation of secretory cells in the mammary gland and increased secretory activity per cell contribute to the rise in milk yield during early lactation (Pollott, 2000). After peak yield, the mammary gland experiences a gradual regression through a process of apoptotic cell death, resulting in a decline in milk yield (Pollott, 2000; Capuco et al., 2001) . Furthermore, multiparous cows were associated with a more metabolically active mammary gland than primiparous cows, especially at the start and peak of lactation (Miller et al., 2006).

4.8.2 Non-genetic and non-additive genetic effects

The inclusion of the effects of herd test date (HTD), heterosis, recombination loss as well as the interaction between lactation stage and parity in the random regression model (RRM) was consistent with Berry et al. (2021) who predicted the genetic merit of dairy cows for live weight and body condition score using routinely available linear type and carcass data. Significant heterosis effects on milk yield were detected in agreement with the analysis of

Penasa et al. (2010) who studied the effects of crossbreeding on milk yield traits in spring-calving Irish dairy cows. Comparing with the effects of herd-year-season, Meyer et al. (1989) found that HTD effects significantly reduce overall residual variances, resulting in slightly higher heritability for test-day yields in Australian dairy cows. The effect of herd test date informs short term environmental changes that affect performances of a particular herd at a particular day.

4.8.3 Selection of a parsimonious statistical model

The RRMs are advantageous as they enable a reduction in parameter numbers to be estimated which as well as having computation benefits, also renders the model simpler and more understandable (Meyer & Hill, 1997; Pool & Meuwissen, 2000). Therefore, one objective was to identify the most parsimonious model where a minimum order of fit was sought without compromising the goodness of fit for the covariance matrix of the lactation trajectory. Model development proceeded in stages: initially using first-order Legendre polynomials to model both additive genetic and permanent environmental effects, then advancing to higher orders as long as the corresponding eigenvalues contributed to model improvement. However, higher orders were omitted due to convergence issues with the log likelihood. Model development ceased when second-order Legendre polynomials were fitted for both additive genetic and permanent environmental effects. A comparison was then made between the random regression model using first-order (RRM1) and second-order Legendre polynomials (RRM2). The estimates of log likelihood increased with increasing order of the Legendre polynomial for the additive genetic and permanent environment effects, consistent with Olori et al. (1999), Kettunen et al. (2000), Berry et al. (2003) and Costa et al. (2008). However, the log likelihood does not account for any increased complexity of nested models but the AIC, and BIC do. However, the estimates for AIC, BIC, and residual variance decreased as the order of fit increased. Consistent with Takma and Akbas (2009) and Meseret et al. (2018), who used RRMs to evaluate TD milk yields in dairy cows. The ability to fit the data well significantly improved ($p < 0.05$) as the order of Legendre polynomial increased. This aligns with findings reported for Turkish (Takma and Akbas, 2009) and Ethiopian (Meseret et al., 2018) Holsteins.

The computation of the eigenvalues associated with the additive genetic and permanent environment covariance matrix was also helpful in determining the most parsimonious model since they reveal the proportion of variation that each additional order of the fitted polynomial explains (Berry et al., 2003). As is always the case, the total eigenvalue increased with the order of the polynomial consistent with Berry et al. (2003) and Meseret et al. (2018) who used RRMs to evaluate milk yield in dairy cows. The ability of the first two eigenvalues to explain > 90% of the total variation of the additive genetic effect was consistent with the reports by El Faro et al. (2008) and Meseret et al. (2018) who studied TD milk yields in dairy cows using RRMs. The ability to explain the variation of the additive genetic covariance matrix increased by 4.12% due to the addition of second order Legendre polynomial. The amount of variation explained by the quadratic term was small and therefore indicates that using a cubic term would contribute much improvement in model fit Williams et al. (2022) found the fourth eigenvalue of a cubic animal random regression explaining less than 1.4% of the additive genetic variance in milk yields in Irish dairy cows. Furthermore, Bignardi et al. (2009) observed that the improvement made in the model fit with an increase in the order of the polynomial after the fourth eigenvalue for the additive genetic effect was small. Moreover, where the last term of a polynomial explained only a small proportion of the genetic variation, then not considering this higher order would have little impact on the estimated breeding values of the animals (Berry et al., 2003). In the case of permanent environment effect, more than 85% of the variation was explained by the first and second eigenvalues agreeing with the results of both El Faro et al. (2008) and Druet et al. (2003) who studied TD milk yields in dairy cows using RRMs.

The choice of a more parsimonious statistical model should also consider the genetic parameter estimates and the models with plausible estimates should be preferred irrespective of the estimates of the log-likelihood, the AIC or the BIC (Berry et al., 2003). In the present study, RRM1 and RRM2 demonstrated plausible genetic parameter estimates although negative phenotypic correlations between distant DIM was evident from the RRM1. Therefore, the quadratic term may suffice to model the covariance matrix across the lactation trajectory in Irish dairy cows. The choice of the quadratic term as most parsimonious statistical model is consistent with Peixoto et al. (2014), Meseret et al. (2018) and Williams et al. (2022) who concluded that the second order Legendre polynomial would be more adequate for explaining the additive genetic and permanent environment variances of milk yields across lactation stages in dairy cows. Furthermore, over-parameterized models can be associated with posing problems of estimation of the genetic parameters in RRMs using legendre polynomials (Rekaya et al., 1999; Meyer, 2005 and Bignardi et al., 2009).

4.8.4 Variance components

4.8.4.1 Additive Genetic Variance

The additive genetic variances estimated from RRM2 (2.37 to 5.37 kg) were in close range with the estimates from a cubic model (2.8 to 6.7kg^2) reported by Berry et al. (2003) who estimated genetic parameters for milk yield, BCS, body weight and fertility using RRMs in spring calving Irish dairy cows. Greater genetic variances at the onset of lactation followed by a decline thereafter towards the late lactation stage tends to be the norm internationally for milk yield in dairy cows (Jamrozik et al., 1997; Berry et al., 2003; Silvestre et al., 2005; Zavadilová, et al., 2005; Cobuci et al., 2005; Hammami et al., 2008 and Bignardi et al., 2009). Similarly, employing multi-trait RRMs for TD milk yields in dairy cows, Van der Werf et al.

(1998) and Rekaya et al. (1999) reported higher genetic variations at the peripheries of lactation.

Nonetheless, De Roos et al. (2004) and Abdullahpour et al. (2013) have reported an opposite trend when employing RRMs for TD milk yields in dairy cows where higher and lower genetic variances were observed in the second half of lactation and around peak days, respectively. Pool et al. (2000) and Druet et al. (2003) reported greatest estimates of the genetic variance of milk yield during the mid-lactation with lower estimates at the peripheries of lactation in dairy cows using RRMs.

The estimates of the additive genetic variance being larger than that of permanent environment variance was in line with De Roos and De Jong (2006) who concluded that this is a function of the genetic differences exerting greater influences on the differences between cows within herd in the long run (De Roos & De Jong, 2006). Genetic variances for milk yield are higher in higher input systems (Berry et al., 2003), in high herd production levels (Veerkamp & Goddard, 1998) and also in mixed populations and crossbreds than single-breed populations (Gebreyohannes et al., 2016).

Therefore, the considerable variation in literature pertaining to the trend of the variance components across lactation stages could be attributed to differences in climatic conditions, genotypes, production systems and herd management levels among countries (Zaabza et al., 2018). The different sub models fitted in the RRMs for the estimation of the additive genetic and permanent environment could be partially responsible for the variations observed (Olori et al., 1999).

4.8.4.2 Permanent Environmental Variance

The pattern for the estimates of permanent environment did not change with the change in the order of Legendre polynomial agreeing with Costa et al. (2008) who evaluated TD milk yields in dairy cows using RRMs. Nonetheless, permanent environmental variance estimates of the RRM2 were larger than that of RRM1 especially at the extremes of lactation. Similarly, Meseret et al. (2015) reported differences in the estimates of the permanent environment due to change in the order of fit in their evaluations of TD milk yields for Holestein Fresian cows in Ethiopia.

The greatest variance estimates observed at peripheries of lactation, assuming a concave shape, substantiates the previous hypothesis that yield at the peripheries of lactation is more susceptible to temporary environmental fluctuations than yield in the middle of lactation, which is more influenced by genetic and permanent environmental differences across animals (Kheirabadi et al., 2014; VanVleck & Henderson 1961). It could also be due to herd-specific changes in the shape of the lactation curve (Bohmanova et al. 2008). This could also be due to problems associated with fewer records at the end of lactation (Meyer, 1999). Unrealistic estimates observed at the borders of lactation were also said to be computing artifacts of the RRMs using Legendre polynomials (Van der Werf et al., 1998 ; Misztal et al., 2000 ; López-Romero et al., 2003); the use of B- splines has been reported to lessen the implausible estimates at the boundaries of the parameter space (Meyer, 2005, Kheirabadi et al., 2014). Of note is that incomplete lactations were allowed in the present study which may have had an effect on the implausible estimates at the extremes of lactation. Extreme increases of variances at the borders of lactations can be handled by the use of only complete lactations in parameter estimation (Pool and Meuwissen, 2000); appropriate mathematical functions for the random regression (Jamrozik and Schaeffer, 2002); a separate modelling of herd curves (Gengler et al., 2001; Jamrozik et al., 2001; De Roos et al., 2004) and accounting for heterogenous residual variances across lactation (Olori et al., 1999). However, Costa et al. (2005) reported that excluding incomplete or lactation in progress may bias variance component estimation particularly in situations where low yielding cows are dried off early.

This could be due to the availability of fewer records due to the closeness to the dry period (Bignardi et al., 2011).

4.8.4.3 Residual variance

Residual variances declined with the increasing order of Legendre polynomial agreeing with Berry et al. (2003), Olori et al. (1999), Kettunen et al. (2000) who employed RRMs assuming heterogeneous residual variances for evaluating milk yields in dairy cows. Similarly, Negussie et al. (2008) and Meseret et al. (2018), in their studies on test-day milk yields in dairy cows, observed a decrease in residual variances as the order of the random regressions increased, assuming a homogeneous residual variance structure.

A change in the estimates of the residual variances across the 10 residual classes defined was observed agreeing with Li et al. (2020) who employed RRMs using Legendre polynomials in evaluating milk yield in Chinese dairy cows. Highest residual variance estimates were reported in the beginning of lactation declining thereafter untill they bottomed as the lactation ends in agreement with the reports of Kettunen et al. (2000), Tonhati et al. (2008), El Faro et al. (2008), Abdullahpour et al. (2013) and Kheirabadi et al. (2014) who estimated genetic parameters of milk yields in dairy cows and buffalo using RRMs. A similar trend, but with a slight increase at the end of lactation, was also reported by Rekaya et al. (1999) and Pool et al. (2000) in multi-trait approach where the lactation was divided into two traits in dairy cows. Similarly, Jakobsen et al. (2002), when evaluating milk yield in Danish Holstein cows, reported a decreasing trend of residual variances throughout lactation which rose again at the end beyond the estimates at the beginning. The greater residual variance in early lactation is attributed to many environmental factors, including feeding before calving (Shadparvar & Yazdanshenas, 2005). The more unstable condition of the cows due to parturition also contributes to the greater variances in early lactation (Abdullahpour et al., 2013).

The estimates of the residual variances across lactation stages were greater than that of additive genetic and permanent environment agreeing with Abdullahpour et al. (2013) who observed greater residual variance estimates for protein and fat yields across lactation stages in Holstien dairy cows in Iran. Pregnancy stage, BCS of the cows, lactation interval and others which could affect milk yield across lactation stages were not accounted for in the current study. Abdullahpour et al. (2013) suggested that the higher residual variances could be attributed to the fact that high yielding cows are preferentially treated in an attempt to meet their requirement for high milk yield in their studies estimating genetic parameter of milk yield and milk composition traits using RRMs in Holstien cows in Iran. Berry et al. (2014) also suggested, in their studies on reproductive performance of dairy and beef cattle in Ireland, that a residual noise is likely to be introduced due to preferential treatment of high yielding cows including, among others, delay in inseminating high yielding cows.

4.8.4.4 Heritability

The trend of heritability estimates found in the current study was consistent with Rekaya et al. (1998), Kettunen et al. (1998) , Strabel and Misztal (1999) , Druet, et al. (2003) , Takma and Akbas, 2007 , Costa et al. (2008), Negussie et al. (2008) and Salimiyekta et al. (2021) who employed RRMs in evaluating milk yields of dairy cows in different countries . An opposite trend was reported by Cobuci et al. (2005), Brotherstone et al. (2000) and El Faro et al. (2008) who also employed RRMs when evaluating milk yields of dairy cows in different countries with the former assuming a constant variance for permanent environment and residual variance across trajectory. Olori et al. (1999) report ed an increasing heritability trend of milk yield in dairy cows from week 8 until it peaked in week 35 using quadratic, cubic and quartic RRMs that assumed heterogeneous residual variance while Meseret et al. (2017) reported heritability estimates of milk yield in Ethiopian Holstien Friesian cows that peaked during 230 to 260 DIM under multi-lactation RRMs that assumed homogenous residual variance. Consistenly low heritability estimates demonstrating an unchanging pattern during the mid-lactation period were reported by Bignardi et al. (2011) who evaluated milk yields in dairy cows using multi-trait models. Besides, the two models used in the present study exhibited biologically unexplainable oscillatory patterns across trajectory reflecting the artifacts of using higher Legendre polynomials (López-Romero & Carabaño, 2003; Strabel & Jamrozik, 2006; El Faro et al., 2008).

The moderately high estimates of heritability shown in the current study were in close range to previous reports for dairy cows, where heritability estimates ranged from 0.16 to 0.44 (Berry et al., 2003; Druet et al., 2003; Costa et al., 2008; and Gebreyohannes et al., 2016). Cobuci et al. (2005) reported higher heritability estimates of milk yield ranging from 0.34 to 0.56 when permanent environment and residual variances were assumed constant across lactation in Holstein cows . Similarly, De Melo et al. (2007) reported higher heritability estimates of milk yield in Holstein cows, ranging from 0.27 to 0.65, using the Wilmink function. In contrast, Salimiyekta et al. (2021) reported lower heritability estimates of milk yield varying from 0.14 to 0.18, using RRMs in Iranian Holestein cows. Estimates of heritability under RRMs were higher than that of multi-trait models (Kettunen et al., 1998).

The considerable variations in the estimates of heritability observed across studies could be due to differences in populations, in the RRMs fitted, the structure of covariance of the random effects as well as differences in feeding plan (Machado et al., 1999; Shadparvar & Yazdanshenas, 2005; Bignardi et al., 2011 ; Gebreyohannes et al., 2016) . Variations in the estimates of heritability due to parity were also reported by Meseret et al. (2017) and Strabel and Misztal (1999) when evaluating milk yield in Ethiopian Holstein and Polish dairy cattle using RRMs, respectively. Variations in the estimates of heritability could also be due to the differences in definition of the lactation stage into either daily milk yields as used in this study or weekly milk yields as used by Olori et al. (1999) or monthly milk yields as used by Meseret et al. (2017).

The daily heritability estimates exhibited standard errors larger than 30%, indicating substantial uncertainty. Consequently, it is prudent to interpret these results with caution.

4.8.4.5 Repeatability

The estimates of repeatability of milk yield increased with the increasing order of the Legendre polynomials fitted agreeing with the results of Li et al. (2020) who evaluated milk yield in Chinese Holstein cattle using RRMs. In line with the trend of repeatability observed in this study, Li et al. (2020) observed a reduction in repeatability in early lactation followed by an increase thereafter till the lactation ends assuming a homogenous residual variance structure when evaluating milk yield in Chinese Holstein cows using RRMs. Assuming heterogeneous residual variances across lactation, Li et al. (2020) observed a reduction in repeatability in the early lactation followed by an increase till about 200 DIM with a slight downturn towards the end of lactation when evaluating milk yield in Chinese Holstein cows using RRMs. A similar trend using RRMs for evaluating milk yield in dairy cows in different countries was reported by others (Santellano-Estrada et al., 2008; Gebreyohannes et al., 2016 and Uribe & Lembeye, 2020)

The moderately high repeatability estimates observed in the current study were in close range to previous reports for Chinese Holstein cows, where repeatability estimates ranged 0.52 to 0.821 and from 0.566 to 0.786 assuming heterogeneous and homogenous residual variances, respectively (Li et al., 2020). Visetin et al. (2017) also reported an estimate of 0.52 for Irish dairy cows using a simple repeatability model. The repeatability estimates for milk yield for first parity Chilean dairy cows ranged from 0.58 to 0.78 under a pasture-based system (Uribe & Lembeye, 2020). Higher repeatability estimates ranging from 0.62 to 0.86 for Holstein dairy cows and from 0.84 to 0.94 for Ethiopian dairy cattle population were reported by

Naderi, (2016) and Gebreyohannes et al. (2016), respectively. Conversely, Worku et al. (2021) found a lower repeatability estimate of 0.37 for milk yield in Indian Karen-Fries cattle using multi-trait Bayesian approach.

The moderately high repeatability estimates obtained in the present study largely reflects the impact of additive genetic variances as the corresponding permanent environmental variances were lower through most of the lactation stages.

4.8.4.6 Genetic correlations for test-day milk yield

There was no change in trend for the estimates of the genetic correlations due to changes in the order of Legendre polynomial fitted consistent with Costa et al. (2008). The moderate to close to unity genetic correlations observed between DIM suggests that selecting for higher milk yield in early lactation will result in a correlated increase in late lactation. The fact that moderately high repeatability estimates were observed in this study also substantiates this. The moderate to strong genetic correlations across lactation stages also indicate that milk yield across lactation trajectory is governed by a similar set of genes with more/less similar expressions in the adjoining and nearby DIM but a lower similarity of expression between distant DIM. The estimates of the genetic correlations were similar in magnitude to Takma and Akbas (2007) whose estimates ranged from 0.51 between most distant DIM to 0.99 between adjoining DIM when evaluating milk yield in Turkish Holstein-Fresian cows using RRMs. Similarly, Olori et al. (1999) reported strong genetic correlations between adjacent weeks but moderate genetic correlations between distant weeks when estimating variance components of milk yields using RRMs Holstein-Fresian cattle. In contrast, Rekaya et al. (1998) found genetic correlations among DIM measures for Holstein-Friesian cows to be larger than 0.8 such that they recommended a repeatability model rather than a RRM for modelling the genetic covariance matrix across lactation. Weaker genetic correlations as weak as 0.18 between distant DIM were reported by Meseret et al. (2015) who evaluated milk yield in Ethiopian Holstein-Fresian cows using RRMs. Others (Meyer et al., 1989; Kettunen et al., 2000; Kettunen et al., 2011; Cobuci et al., 2011; and Bignardi et al., 2011) also demonstrated that genetic correlations weaken as the interval between DIM increases when evaluating milk yield in dairy cows using RRMs.

Genetic correlations found in the present study were all positive across all stages of lactation consistent with Olori et al, (199) who evaluated milk yield in Holstein-Friesian cows using RRMs. In contrast, others (Rekaya et al., 1998; Kettunen et al., 2000; Lopez-Romeo & Carabano, 2003; Bignardi et al., 2011; and Costa et al., 2008 found negative genetic correlations between distant DIM when employing RRMs for test day milk records in dairy cows in different countries.

4.8.4.7 Permanent Environmental correlations

The permanent environmental correlations assumed a pattern where strongest correlations (close to unity) were observed between the adjoining DIM weakening thereafter as the interval between DIM increased consistent with Cobuci et al. (2005), Costa et al. (2008), Bignardi et al. (2011) and Gebreyohannes et al. (2016) who applied TDMs for evaluating milk yield in dairy cows in different countries. The permanent environmental correlation estimates observed in the current study were in close range with Costa et al. (2008) and Padilha et al. (2016) whose permanent environmental estimates for milk yield ranged from 0.07 to near unity in Brazilian Holstein cattle. When evaluating milk yield in Holstein-Fresian and Caracu heifers, respectively, Takma and Akbas (2007) and El Faro et al. (2008) obtained relatively weaker estimates of permanent environmental correlations varying from 0.09 to 0.77. Zavadilová et al. (2005) also reported weaker estimates of permanent environmental correlations with negative correlations varying from -0.29 to 0.33 when evaluating milk yield in Czech Holstein cows using RRMs. In contrast, Bignardi et al. (2009) reported stronger estimates of permanent environmental correlations ranging from 0.24 to 0.99 in their evaluation of milk yield in Brazilian Holstian cows using RRMs and parametric correlation functions.

The permanent environmental correlations were weaker than their genetic counterparts across the lactation consistent with Zavadilová et al. (2005), Takma & Akbas, (2007), El Faro et al. (2008), Bignardi et al. (2011), Gebreyohannes et al. (2016) and Padilha et al. (2016) who estimated variance components of milk yield in Holestian-Friesian cattle in different countries using RRMs

4.9 CONCLUSIONS

The results in this study establish the existence of exploitable genetic variation, as represented in the estimates of heritability of test day yields, in the shape of the lactation profile of milk yield in Irish dairy cows. Therefore, genetic improvement of milk yield is envisaged.

Based on the goodness of fit statistics evaluated (i.e., log likelihood, AIC, BIC, residual variance, eigenvalues) and also the genetic parameter estimates, the quadratic term can sufficiently model the genetic and permanent environmental effects for milk yield across lactation trajectory in Irish dairy cows. That said, pronounced upturns reflecting poor fit rather than real effect were observed at the end of lactation (especially with the permanent environmental effect) presumably caused by fewer records and the mathematical properties of polynomials. Therefore, projection beyond the data was unreasonable, especially in the quadratic context .

The moderate to near unity genetic correlations observed among nearby and distant DIM suggest that measurements taken at any stage of lactation could be assumed as different trait.

4.10 RECOMMENDATION

Considering the exploitable genetic variation observed in the lactation profiles of milk yield in Irish dairy cows, selecting genetically superior cows is recommended to improve milk yield. Additionally, in cases where daily measurement of milk yield is not feasible, it is advisable to utilize monthly test day yields. This approach ensures that two distant Total Daily yields contribute more information compared to those that are closely correlated

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APPENDICES

Appendix 1: Covariance/Variance/Correlation Matrix of additive genetic and permanent environment.

```
  Additive  genetic   RRM1
Covariance/Variance/Correlation      Matrix  US us(leg(dim,1)).nrm(t
   6.387      -0.3556
 -0.7863       0.7657
Permanent   Environment  RRM1
 Covariance/Variance/Correlation      Matrix  US us(leg(dim,1)).ide(t
   2.531       0.1616
  0.3090        1.444
Additive  genetic   RRM2
  Covariance/Variance/Correlation      Matrix  US us(leg(dim,2)).nrm(t

     6.070      -0.4088      -0.3273

   -0.8659       0.7392       0.3928E-01

   -0.4714       0.1974E-01   0.3418

 Permanent   Environment  RRM2
  Covariance/Variance/Correlation      Matrix  US us(leg(dim,2)).ide(t

     2.500       0.1398       0.1235

    0.2782        1.583       0.1575

    0.1634       0.1659       0.700
```

Appendix 2: Eigenvalue analysis for additive genetic and permanent environmental matrix

Additive genetic (RRM1) Eigen Analysis of US matrix for us(leg(dim,1)).nrm(t

```
 Eigen values     6.4946     0.6578
 Percentage        90.8028     9.1972
 Total  %        90.8028   100.0000
     1         -0.9907     0.1360
     2          0.1360     0.9907
```

Permanent environment (RRM1) Eigen Analysis of US matrix for us(leg(dim,1)).ide(t

```
 Eigen values     2.6124     1.3624
 Percentage        65.7245    34.2755
 Total  %        65.7245   100.0000
     1         -0.9668    -0.2557
     2         -0.2557     0.9668
```

Eigen Analysis of US matrix for us(leg(dim,2)).nrm(t

```
Additive genetic  (RRM2)
 Eigen values     6.2446     0.6116     0.2951
 Percentage        87.3211     8.5525     4.1264
 Total  %        87.3211    95.8736   100.0000
     1         -0.9847    -0.1397     0.1040
     2          0.1552    -0.9750     0.1591
     3          0.0792     0.1728     0.9818
Eigen Analysis  of US matrix  for us(leg(dim,2)).ide(t
Permanent   environment   (RRM2)
 Eigen values     2.5999     1.5209     0.6630
 Percentage        54.3474    31.7933    13.8593
 Total  %        54.3474    86.1407   100.0000
     1         -0.9545     0.2913    -0.0636
     2         -0.2786    -0.9473    -0.1584
     3         -0.1064    -0.1335     0.9853
```

Appendix 3: The matrix of Legendre polynomials evaluated at different days in milk

5.00000	0.70711	-1.22474	1.58114
6.00000	0.70711	-1.21658	1.54962
7.00000	0.70711	-1.20841	1.51831
8.00000	0.70711	-1.20025	1.48722
9.00000	0.70711	-1.19209	1.45633
10.00000	0.70711	-1.18392	1.42566
11.00000	0.70711	-1.17576	1.39520
12.00000	0.70711	-1.16759	1.36494
13.00000	0.70711	-1.15943	1.33490
14.00000	0.70711	-1.15126	1.30507
15.00000	0.70711	-1.14310	1.27545
16.00000	0.70711	-1.13493	1.24604
17.00000	0.70711	-1.12677	1.21684
18.00000	0.70711	-1.11860	1.18786
19.00000	0.70711	-1.11044	1.15908
20.00000	0.70711	-1.10227	1.13051
21.00000	0.70711	-1.09411	1.10216
22.00000	0.70711	-1.08594	1.07401
23.00000	0.70711	-1.07778	1.04608
24.00000	0.70711	-1.06961	1.01836
25.00000	0.70711	-1.06145	0.99085
26.00000	0.70711	-1.05328	0.96355
27.00000	0.70711	-1.04512	0.93646
28.00000	0.70711	-1.03695	0.90958

29.00000	0.70711	-1.02879	0.88291
30.00000	0.70711	-1.02062	0.85645
31.00000	0.70711	-1.01246	0.83020
32.00000	0.70711	-1.00429	0.80417
33.00000	0.70711	-0.99613	0.77834
34.00000	0.70711	-0.98796	0.75273
35.00000	0.70711	-0.97980	0.72732
36.00000	0.70711	-0.97163	0.70213
37.00000	0.70711	-0.96347	0.67715
38.00000	0.70711	-0.95530	0.65238
39.00000	0.70711	-0.94714	0.62782
40.00000	0.70711	-0.93897	0.60347
41.00000	0.70711	-0.93081	0.57933
42.00000	0.70711	-0.92264	0.55540
43.00000	0.70711	-0.91448	0.53168
44.00000	0.70711	-0.90631	0.50818
45.00000	0.70711	-0.89815	0.48488
46.00000	0.70711	-0.88998	0.46180
47.00000	0.70711	-0.88182	0.43892
48.00000	0.70711	-0.87365	0.41626
49.00000	0.70711	-0.86549	0.39381
50.00000	0.70711	-0.85732	0.37157
51.00000	0.70711	-0.84916	0.34954
52.00000	0.70711	-0.84099	0.32772
53.00000	0.70711	-0.83283	0.30611

54.00000	0.70711	-0.82466	0.28471
55.00000	0.70711	-0.81650	0.26352
56.00000	0.70711	-0.80833	0.24255
57.00000	0.70711	-0.80017	0.22178
58.00000	0.70711	-0.79200	0.20123
59.00000	0.70711	-0.78384	0.18088
60.00000	0.70711	-0.77567	0.16075
61.00000	0.70711	-0.76751	0.14083
62.00000	0.70711	-0.75934	0.12112
63.00000	0.70711	-0.75118	0.10161
64.00000	0.70711	-0.74301	0.08232
65.00000	0.70711	-0.73485	0.06325
66.00000	0.70711	-0.72668	0.04438
67.00000	0.70711	-0.71852	0.02572
68.00000	0.70711	-0.71035	0.00727
69.00000	0.70711	-0.70219	-0.01096
70.00000	0.70711	-0.69402	-0.02899
71.00000	0.70711	-0.68586	-0.04680
72.00000	0.70711	-0.67769	-0.06441
73.00000	0.70711	-0.66953	-0.08180
74.00000	0.70711	-0.66136	-0.09898
75.00000	0.70711	-0.65320	-0.11595
76.00000	0.70711	-0.64503	-0.13271
77.00000	0.70711	-0.63687	-0.14926
78.00000	0.70711	-0.62870	-0.16560

79.00000	0.70711	-0.62054	-0.18173
80.00000	0.70711	-0.61237	-0.19764
81.00000	0.70711	-0.60421	-0.21335
82.00000	0.70711	-0.59604	-0.22884
83.00000	0.70711	-0.58788	-0.24413
84.00000	0.70711	-0.57971	-0.25920
85.00000	0.70711	-0.57155	-0.27406
86.00000	0.70711	-0.56338	-0.28872
87.00000	0.70711	-0.55522	-0.30316
88.00000	0.70711	-0.54705	-0.31739
89.00000	0.70711	-0.53889	-0.33141
90.00000	0.70711	-0.53072	-0.34522
91.00000	0.70711	-0.52256	-0.35881
92.00000	0.70711	-0.51439	-0.37220
93.00000	0.70711	-0.50623	-0.38538
94.00000	0.70711	-0.49806	-0.39834
95.00000	0.70711	-0.48990	-0.41110
96.00000	0.70711	-0.48173	-0.42364
97.00000	0.70711	-0.47357	-0.43597
98.00000	0.70711	-0.46540	-0.44809
99.00000	0.70711	-0.45724	-0.46001
100.00000	0.70711	-0.44907	-0.47171
101.00000	0.70711	-0.44091	-0.48320
102.00000	0.70711	-0.43274	-0.49447
103.00000	0.70711	-0.42458	-0.50554

104.00000	0.70711	-0.41641	-0.51640
105.00000	0.70711	-0.40825	-0.52705
106.00000	0.70711	-0.40008	-0.53748
107.00000	0.70711	-0.39192	-0.54771
108.00000	0.70711	-0.38375	-0.55772
109.00000	0.70711	-0.37559	-0.56752
110.00000	0.70711	-0.36742	-0.57712
111.00000	0.70711	-0.35926	-0.58650
112.00000	0.70711	-0.35109	-0.59567
113.00000	0.70711	-0.34293	-0.60463
114.00000	0.70711	-0.33476	-0.61338
115.00000	0.70711	-0.32660	-0.62191
116.00000	0.70711	-0.31843	-0.63024
117.00000	0.70711	-0.31027	-0.63836
118.00000	0.70711	-0.30210	-0.64626
119.00000	0.70711	-0.29394	-0.65396
120.00000	0.70711	-0.28577	-0.66144
121.00000	0.70711	-0.27761	-0.66872
122.00000	0.70711	-0.26944	-0.67578
123.00000	0.70711	-0.26128	-0.68263
124.00000	0.70711	-0.25311	-0.68927
125.00000	0.70711	-0.24495	-0.69570
126.00000	0.70711	-0.23678	-0.70192
127.00000	0.70711	-0.22862	-0.70793
128.00000	0.70711	-0.22045	-0.71373

129.00000	0.70711	-0.21229	-0.71931
130.00000	0.70711	-0.20412	-0.72469
131.00000	0.70711	-0.19596	-0.72985
132.00000	0.70711	-0.18779	-0.73481
133.00000	0.70711	-0.17963	-0.73955
134.00000	0.70711	-0.17146	-0.74408
135.00000	0.70711	-0.16330	-0.74841
136.00000	0.70711	-0.15513	-0.75252
137.00000	0.70711	-0.14697	-0.75642
138.00000	0.70711	-0.13880	-0.76011
139.00000	0.70711	-0.13064	-0.76358
140.00000	0.70711	-0.12247	-0.76685
141.00000	0.70711	-0.11431	-0.76991
142.00000	0.70711	-0.10614	-0.77276
143.00000	0.70711	-0.09798	-0.77539
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145.00000	0.70711	-0.08165	-0.78003
146.00000	0.70711	-0.07348	-0.78203
147.00000	0.70711	-0.06532	-0.78382
148.00000	0.70711	-0.05715	-0.78540
149.00000	0.70711	-0.04899	-0.78677
150.00000	0.70711	-0.04082	-0.78793
151.00000	0.70711	-0.03266	-0.78888
152.00000	0.70711	-0.02449	-0.78962
153.00000	0.70711	-0.01633	-0.79015

154.00000	0.70711	-0.00816	-0.79046
155.00000	0.70711	0.00000	-0.79057
156.00000	0.70711	0.00816	-0.79046
157.00000	0.70711	0.01633	-0.79015
158.00000	0.70711	0.02449	-0.78962
159.00000	0.70711	0.03266	-0.78888
160.00000	0.70711	0.04082	-0.78793
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164.00000	0.70711	0.07348	-0.78203
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167.00000	0.70711	0.09798	-0.77539
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169.00000	0.70711	0.11431	-0.76991
170.00000	0.70711	0.12247	-0.76685
171.00000	0.70711	0.13064	-0.76358
172.00000	0.70711	0.13880	-0.76011
173.00000	0.70711	0.14697	-0.75642
174.00000	0.70711	0.15513	-0.75252
175.00000	0.70711	0.16330	-0.74841
176.00000	0.70711	0.17146	-0.74408
177.00000	0.70711	0.17963	-0.73955
178.00000	0.70711	0.18779	-0.73481

179.00000	0.70711	0.19596	-0.72985
180.00000	0.70711	0.20412	-0.72469
181.00000	0.70711	0.21229	-0.71931
182.00000	0.70711	0.22045	-0.71373
183.00000	0.70711	0.22862	-0.70793
184.00000	0.70711	0.23678	-0.70192
185.00000	0.70711	0.24495	-0.69570
186.00000	0.70711	0.25311	-0.68927
187.00000	0.70711	0.26128	-0.68263
188.00000	0.70711	0.26944	-0.67578
189.00000	0.70711	0.27761	-0.66872
190.00000	0.70711	0.28577	-0.66144
191.00000	0.70711	0.29394	-0.65396
192.00000	0.70711	0.30210	-0.64626
193.00000	0.70711	0.31027	-0.63836
194.00000	0.70711	0.31843	-0.63024
195.00000	0.70711	0.32660	-0.62191
196.00000	0.70711	0.33476	-0.61338
197.00000	0.70711	0.34293	-0.60463
198.00000	0.70711	0.35109	-0.59567
199.00000	0.70711	0.35926	-0.58650
200.00000	0.70711	0.36742	-0.57712
201.00000	0.70711	0.37559	-0.56752
202.00000	0.70711	0.38375	-0.55772
203.00000	0.70711	0.39192	-0.54771

204.00000	0.70711	0.40008	-0.53748
205.00000	0.70711	0.40825	-0.52705
206.00000	0.70711	0.41641	-0.51640
207.00000	0.70711	0.42458	-0.50554
208.00000	0.70711	0.43274	-0.49447
209.00000	0.70711	0.44091	-0.48320
210.00000	0.70711	0.44907	-0.47171
211.00000	0.70711	0.45724	-0.46001
212.00000	0.70711	0.46540	-0.44809
213.00000	0.70711	0.47357	-0.43597
214.00000	0.70711	0.48173	-0.42364
215.00000	0.70711	0.48990	-0.41110
216.00000	0.70711	0.49806	-0.39834
217.00000	0.70711	0.50623	-0.38538
218.00000	0.70711	0.51439	-0.37220
219.00000	0.70711	0.52256	-0.35881
220.00000	0.70711	0.53072	-0.34522
221.00000	0.70711	0.53889	-0.33141
222.00000	0.70711	0.54705	-0.31739
223.00000	0.70711	0.55522	-0.30316
224.00000	0.70711	0.56338	-0.28872
225.00000	0.70711	0.57155	-0.27406
226.00000	0.70711	0.57971	-0.25920
227.00000	0.70711	0.58788	-0.24413
228.00000	0.70711	0.59604	-0.22884

229.00000	0.70711	0.60421	-0.21335
230.00000	0.70711	0.61237	-0.19764
231.00000	0.70711	0.62054	-0.18173
232.00000	0.70711	0.62870	-0.16560
233.00000	0.70711	0.63687	-0.14926
234.00000	0.70711	0.64503	-0.13271
235.00000	0.70711	0.65320	-0.11595
236.00000	0.70711	0.66136	-0.09898
237.00000	0.70711	0.66953	-0.08180
238.00000	0.70711	0.67769	-0.06441
239.00000	0.70711	0.68586	-0.04680
240.00000	0.70711	0.69402	-0.02899
241.00000	0.70711	0.70219	-0.01096
242.00000	0.70711	0.71035	0.00727
243.00000	0.70711	0.71852	0.02572
244.00000	0.70711	0.72668	0.04438
245.00000	0.70711	0.73485	0.06325
246.00000	0.70711	0.74301	0.08232
247.00000	0.70711	0.75118	0.10161
248.00000	0.70711	0.75934	0.12112
249.00000	0.70711	0.76751	0.14083
250.00000	0.70711	0.77567	0.16075
251.00000	0.70711	0.78384	0.18088
252.00000	0.70711	0.79200	0.20123
253.00000	0.70711	0.80017	0.22178

254.00000	0.70711	0.80833	0.24255
255.00000	0.70711	0.81650	0.26352
256.00000	0.70711	0.82466	0.28471
257.00000	0.70711	0.83283	0.30611
258.00000	0.70711	0.84099	0.32772
259.00000	0.70711	0.84916	0.34954
260.00000	0.70711	0.85732	0.37157
261.00000	0.70711	0.86549	0.39381
262.00000	0.70711	0.87365	0.41626
263.00000	0.70711	0.88182	0.43892
264.00000	0.70711	0.88998	0.46180
265.00000	0.70711	0.89815	0.48488
266.00000	0.70711	0.90631	0.50818
267.00000	0.70711	0.91448	0.53168
268.00000	0.70711	0.92264	0.55540
269.00000	0.70711	0.93081	0.57933
270.00000	0.70711	0.93897	0.60347
271.00000	0.70711	0.94714	0.62782
272.00000	0.70711	0.95530	0.65238
273.00000	0.70711	0.96347	0.67715
274.00000	0.70711	0.97163	0.70213
275.00000	0.70711	0.97980	0.72732
276.00000	0.70711	0.98796	0.75273
277.00000	0.70711	0.99613	0.77834
278.00000	0.70711	1.00429	0.80417

279.00000	0.70711	1.01246	0.83020
280.00000	0.70711	1.02062	0.85645
281.00000	0.70711	1.02879	0.88291
282.00000	0.70711	1.03695	0.90958
283.00000	0.70711	1.04512	0.93646
284.00000	0.70711	1.05328	0.96355
285.00000	0.70711	1.06145	0.99085
286.00000	0.70711	1.06961	1.01836
287.00000	0.70711	1.07778	1.04608
288.00000	0.70711	1.08594	1.07401
289.00000	0.70711	1.09411	1.10216
290.00000	0.70711	1.10227	1.13051
291.00000	0.70711	1.11044	1.15908
292.00000	0.70711	1.11860	1.18786
293.00000	0.70711	1.12677	1.21684
294.00000	0.70711	1.13493	1.24604
295.00000	0.70711	1.14310	1.27545
296.00000	0.70711	1.15126	1.30507
297.00000	0.70711	1.15943	1.33490
298.00000	0.70711	1.16759	1.36494
299.00000	0.70711	1.17576	1.39520
300.00000	0.70711	1.18392	1.42566
301.00000	0.70711	1.19209	1.45633
302.00000	0.70711	1.20025	1.48722
303.00000	0.70711	1.20841	1.51831

```
    304.00000    0.70711    1.21658    1.54962

    305.00000    0.70711    1.22474    1.58114
```

Appendix 4: Least square means and standard errors of fixed effects on milk yield

Parity

```
Prediction        Stnd_Error      Ecode   parity
   15.43729       0.04057   E       1
   19.84937       0.03969   E       2
   21.04524       0.04066   E       3
   22.11635       0.07716   E       4
   22.21158       0.05079   E       5
 Average  Standard   Error of Difference  .0612

 Predicted   values  and  TDIFF matrix.

  15.437
  19.849      43.02
  21.045      54.68   11.66
  22.116      65.12   22.10   10.44
  22.212      66.05   23.03   11.37    0.93
```

Recombination loss

```
  Prediction      Stnd_Error      Ecode   rec_class
   18.86950       0.05636   E       1
   19.90034       0.08874   E       2
   20.34040       0.06357   E       3
   20.19155       0.06346   E       4
   20.13250       0.04864   E       5
   20.58295       0.04399   E       6
   20.40964       0.04135   E       7
Average  Standard   Error of Difference  .0596

 Predicted   values  and  TDIFF matrix.

 Two sided  Tukey critical  values:  5%  3.53,  1%  4.00  and  0.1%  4.58.
 Two sided  Bonferroni  values:     5%  3.37,  1%  3.79  and  0.1%  4.33.

  18.870
  19.900      12.30
  20.340       7.88  -4.42
  20.192      10.65   -1.65   2.77
  20.133      18.03    5.73  10.15    7.38
  20.583      13.16    0.86   5.28    2.51  -4.87
  20.170      12.68    0.38   4.80    2.03  -5.35  -0.48
```

Heterosis

```
  Prediction      Stnd_Error       Ecode   het_class
   18.10122       0.05124   E        1
   21.47470       0.07084   E        2
   20.74860       0.05174   E        3
   20.32041       0.04254   E        4
   20.22627       0.04108   E        5
   20.14187       0.04313   E        6
   19.99864       0.04501   E        7
   20.04393       0.04602   E        8
   20.46573       0.04646   E        9
   19.79830       0.03778   E       10
 Average  Standard   Error of Difference  .0507

Two sided  Tukey critical  values:  5%  3.43,  1%  3.90  and  0.1%  4.49.
 Two sided  Bonferroni  values:     5%  3.26,  1%  3.69  and  0.1%  4.24.

 18.101
 21.475      32.89
 20.749      25.81   -7.08
 20.320      21.64  -11.25   -4.17
 20.226      20.72  -12.17   -5.09  -0.92
 20.142      19.90  -13.00   -5.92  -1.74  -0.82
 19.999      18.50  -14.39   -7.31  -3.14  -2.22  -1.40
 20.044      18.94  -13.95   -6.87  -2.70  -1.78  -0.95   0.44
 20.466      23.05   -9.84  -2.76   1.42   2.33   3.16   4.55   4.11
 19.798      16.55  -16.35   -9.27  -5.09  -4.17  -3.35  -1.95  -2.40  -6.51
```

Parity*age class

```
  Prediction      Stnd_Error       Ecode   parity   age_class
   15.72463       0.03257   E        1        1
   15.64595       0.04044   E        1        2
   14.94130       0.08626   E        1        3
   19.19916       0.03519   E        2        1
   19.82566       0.04229   E        2        2
   20.52328       0.07909   E        2        3
   20.72441       0.03535   E        3        1
   20.81648       0.04194   E        3        2
   21.59484       0.08337   E        3        3
   22.07560       0.03861   E        4        1
   21.89255       0.04442   E        4        2
   22.38090       0.21145   E        4        3
   22.38298       0.03877   E        5        1
   21.69258       0.03860   E        5        2
   22.55919       0.12519   E        5        3
 Average  Standard   Error of Difference  .1059

 Predicted   values   and  TDIFF matrix.
```

Two sided Tukey critical values: 5% 3.65, 1% 4.11 and 0.1% 4.68.
Two sided Bonferroni values: 5% 3.49, 1% 3.85 and 0.1% 4.43.

15.725														
15.646	-0.77													
14.941	-7.64	-6.87												
19.199	33.88	34.65	41.52											
19.826	39.99	40.75	47.62	6.11										
20.523	46.79	47.56	50.92	12.91	6.80									
20.724	48.75	49.52	56.39	14.87	8.76	1.96								
20.816	49.65	50.41	57.29	15.77	9.66	2.86	0.90							
21.595	57.24	58.00	60.26	23.36	17.25	10.18	8.49	7.59						
22.076	61.92	62.69	69.56	28.05	21.94	15.14	13.17	12.28	4.69					
21.893	60.14	60.91	67.78	26.26	20.15	13.35	11.39	10.49	2.90	-1.78				
22.381	31.68	31.89	33.10	15.13	12.07	8.38	7.89	7.40	3.52	1.45	2.31			
22.383	64.92	65.69	72.56	31.04	24.93	18.13	16.17	15.27	7.68	3.00	4.78	0.01		
21.693	58.19	58.96	65.83	24.31	18.20	11.40	9.44	8.54	0.95	-3.73	-1.95	-3.26	-6.73	
22.559	54.95	54.92	51.87	27.00	21.52	14.41	14.68	13.77	6.63	3.84	5.23	0.73	1.40	6.92

Appendix 5: Genetic parameter estimates from RRM1

DIM	Genetic variance	Permanent environment	Residual variance	Total variance	Heritability	Repeatability
5	5.703982	2.89629	8.413684	17.01396	0.335253	0.505483409
6	5.679655	2.87109	8.413684	16.96443	0.334798	0.504039661
7	5.655399	2.846051	8.413684	16.91513	0.33434	0.502594343
8	5.631276	2.821236	8.413684	16.8662	0.333879	0.50115107
9	5.607254	2.796613	8.413684	16.81755	0.333417	0.499708152
10	5.583306	2.772152	8.413684	16.76914	0.332951	0.498263899
11	5.559488	2.747914	8.413684	16.72109	0.332484	0.496821927
12	5.535744	2.723838	8.413684	16.67327	0.332013	0.495378783
13	5.51213	2.699985	8.413684	16.6258	0.331541	0.493938082
14	5.48859	2.676295	8.413684	16.57857	0.331065	0.492496374
15	5.465181	2.652826	8.413684	16.53169	0.330588	0.491057274
16	5.441845	2.629521	8.413684	16.48505	0.330108	0.489617338
17	5.41864	2.606438	8.413684	16.43876	0.329626	0.488180176
18	5.395508	2.583518	8.413684	16.39271	0.329141	0.486742352
19	5.372507	2.560819	8.413684	16.34701	0.328654	0.485307473
20	5.349579	2.538285	8.413684	16.30155	0.328164	0.483872109
21	5.326782	2.515971	8.413684	16.25644	0.327672	0.482439863
22	5.304059	2.493822	8.413684	16.21156	0.327178	0.481007315
23	5.281466	2.471893	8.413684	16.16704	0.326681	0.479578061
24	5.258948	2.450129	8.413684	16.12276	0.326182	0.478148689
25	5.236559	2.428585	8.413684	16.07883	0.32568	0.476722791
26	5.214244	2.407206	8.413684	16.03513	0.325176	0.475296965
27	5.19205	2.386047	8.41368	15.9917	0.32467	0.47387479

	9		4	9		4
28	5.169949	2.365054	8.413684	15.94869	0.324161	0.472452887
29	5.147968	2.344279	8.413684	15.90593	0.323651	0.471034821
30	5.126063	2.323671	8.413684	15.86342	0.323137	0.469617216
31	5.104286	2.303281	8.413684	15.82125	0.322622	0.468203638
32	5.082585	2.283059	8.413684	15.77933	0.322104	0.466790722
33	5.061012	2.263054	8.413684	15.73775	0.321584	0.465382023
34	5.039515	2.243217	8.413684	15.69642	0.321062	0.46397419
35	5.018146	2.223596	8.413684	15.65543	0.320537	0.462570767
36	4.996853	2.204145	6.618123	13.81912	0.36159	0.521089448
37	4.975689	2.184909	6.618123	13.77872	0.361114	0.51968525
38	4.9546	2.165843	6.618123	13.73857	0.360634	0.518281395
39	4.93364	2.146992	6.618123	13.69875	0.360152	0.516881427
40	4.912755	2.128311	6.618123	13.65919	0.359667	0.515482025
41	4.891999	2.109845	6.618123	13.61997	0.359178	0.514086725
42	4.871319	2.091549	6.618123	13.58099	0.358687	0.51269222
43	4.850767	2.073468	6.618123	13.54236	0.358192	0.511302035
44	4.830291	2.055558	6.618123	13.50397	0.357694	0.509912877
45	4.809943	2.037862	6.618123	13.46593	0.357194	0.508528261
46	4.789672	2.020337	6.618123	13.42813	0.356689	0.507144908
47	4.769527	2.003025	6.618123	13.39068	0.356183	0.505766321
48	4.74946	1.985885	6.618123	13.35347	0.355672	0.504389238
49	4.72952	1.968959	6.618123	13.3166	0.35516	0.50301715
50	4.709658	1.952204	6.618123	13.27998	0.354643	0.50164681
51	4.689921	1.935663	6.618123	13.24371	0.354125	0.500281695
52	4.67026	1.919293	6.618123	13.2076	0.353602	0.49891857

	3		3	8		9
53	4.650731	1.903137	6.618123	13.17199	0.353077	0.497560919
54	4.631277	1.887153	6.618123	13.13655	0.352549	0.496205512
55	4.611949	1.871381	6.618123	13.10145	0.352018	0.494855797
56	4.592699	1.855782	6.618123	13.0666	0.351484	0.493508592
57	4.573575	1.840395	6.618123	13.03209	0.350947	0.492167318
58	4.55453	1.825182	6.618123	12.99783	0.350407	0.490828813
59	4.53561	1.810179	6.618123	12.96391	0.349864	0.48949648
60	4.516769	1.795351	6.618123	12.93024	0.349318	0.488167181
61	4.498053	1.780734	6.618123	12.89691	0.34877	0.486844298
62	4.479417	1.766291	6.618123	12.86383	0.348218	0.485524715
63	4.460905	1.752058	6.618123	12.83109	0.347664	0.484211792
64	4.442472	1.738001	6.618123	12.7986	0.347106	0.482902441
65	4.424165	1.724153	6.618123	12.76644	0.346546	0.481599998
66	4.405937	1.710481	5.764886	11.8813	0.370829	0.514793472
67	4.387833	1.697018	5.764886	11.84974	0.370289	0.513500924
68	4.369809	1.683731	5.764886	11.81843	0.369745	0.512212042
69	4.351909	1.670653	5.764886	11.78745	0.369199	0.51093012
70	4.33409	1.657751	5.764886	11.75673	0.368648	0.509652155
71	4.316395	1.645058	5.764886	11.72634	0.368094	0.508381415
72	4.298779	1.632542	5.764886	11.69621	0.367536	0.507114926
73	4.281288	1.620233	5.764886	11.66641	0.366976	0.50585593
74	4.263877	1.608103	5.764886	11.63687	0.366411	0.504601481
75	4.24659	1.596179	5.764886	11.60765	0.365844	0.503354792
76	4.229383	1.584433	5.764886	11.5787	0.365273	0.502112951
77	4.2123	1.572894	5.76488	11.5500	0.364699	0.50087913

			6	8		9
78	4.195298	1.561534	5.764886	11.52172	0.364121	0.499650478
79	4.178418	1.55038	5.764886	11.49368	0.36354	0.498430116
80	4.16162	1.539405	5.764886	11.46591	0.362956	0.497215209
81	4.144945	1.528636	5.764886	11.43847	0.362369	0.496008874
82	4.128352	1.518046	5.764886	11.41128	0.361778	0.494808299
83	4.11188	1.507662	5.764886	11.38443	0.361185	0.493616568
84	4.095491	1.497458	5.764886	11.35783	0.360587	0.492430905
85	4.079224	1.487458	5.764886	11.33157	0.359988	0.491254359
86	4.063039	1.477639	5.764886	11.30556	0.359384	0.490084191
87	4.046976	1.468025	5.764886	11.27989	0.358778	0.488923411
88	4.030996	1.458591	5.764886	11.25447	0.358168	0.48776932
89	4.015137	1.449361	5.764886	11.22938	0.357556	0.486624888
90	3.99936	1.440312	5.764886	11.20456	0.35694	0.485487458
91	3.983705	1.431468	5.764886	11.18006	0.356322	0.484359958
92	3.968133	1.422804	5.764886	11.15582	0.355701	0.483239772
93	3.952682	1.414344	5.764886	11.13191	0.355077	0.482129787
94	3.937315	1.406066	5.764886	11.10827	0.354449	0.481027427
95	3.922068	1.397991	5.764886	11.08495	0.353819	0.479935537
96	3.906905	1.390099	5.849357	11.14636	0.350509	0.475222691
97	3.891862	1.382408	5.849357	11.12363	0.349873	0.47415021
98	3.876903	1.374901	5.849357	11.10116	0.349234	0.473086007
99	3.862064	1.367595	5.849357	11.07902	0.348593	0.472032831
100	3.847309	1.360473	5.849357	11.05714	0.347948	0.470988244
101	3.832675	1.353552	5.849357	11.03558	0.347301	0.469954943
102	3.81812	1.346816	5.84935	11.0143	0.346652	0.46893054

	4		7			
103	3.803694	1.34028	5.849357	10.99333	0.346	0.467917682
104	3.789348	1.333929	5.849357	10.97263	0.345345	0.466914028
105	3.775121	1.327777	5.849357	10.95226	0.344689	0.465922175
106	3.76098	1.321811	5.849357	10.93215	0.344029	0.464939831
107	3.746957	1.316045	5.849357	10.91236	0.343368	0.46396954
108	3.73302	1.310464	5.849357	10.89284	0.342704	0.463009062
109	3.719201	1.305083	5.849357	10.87364	0.342038	0.462060885
110	3.705468	1.299888	5.849357	10.85471	0.34137	0.461122822
111	3.691854	1.294891	5.849357	10.8361	0.340699	0.460197304
112	3.678325	1.290081	5.849357	10.81776	0.340026	0.459282197
113	3.664915	1.285469	5.849357	10.79974	0.339352	0.458379876
114	3.65159	1.281044	5.849357	10.78199	0.338675	0.457488261
115	3.638384	1.276817	5.849357	10.76456	0.337997	0.456609666
116	3.625264	1.272778	5.849357	10.7474	0.337315	0.455742069
117	3.612262	1.268936	5.849357	10.73055	0.336633	0.454887722
118	3.599346	1.265281	5.849357	10.71398	0.335948	0.45404466
119	3.586548	1.261824	5.849357	10.69773	0.335263	0.453215073
120	3.573836	1.258555	5.849357	10.68175	0.334574	0.452397054
121	3.561242	1.255483	5.849357	10.66608	0.333885	0.451592729
122	3.548735	1.252599	5.849357	10.65069	0.333193	0.450800251
123	3.536345	1.249912	5.849357	10.63561	0.3325	0.450021679
124	3.524042	1.247413	5.849357	10.62081	0.331805	0.449255226
125	3.511856	1.245111	5.849357	10.60632	0.33111	0.448502887
126	3.499758	1.242998	5.287087	10.02984	0.348934	0.472864403
127	3.48777	1.24108	5.28708	10.0159	0.348222	0.47213286

	6		7	4		4
128	3.475881	1.239352	5.287087	10.00232	0.347508	0.471413971
129	3.464104	1.237819	5.287087	9.989009	0.346792	0.470709603
130	3.452414	1.236477	5.287087	9.975977	0.346073	0.470018152
131	3.44084	1.235328	5.287087	9.963255	0.345353	0.469341424
132	3.429354	1.234371	5.287087	9.950812	0.344631	0.468677876
133	3.417985	1.233608	5.287087	9.938679	0.343907	0.468029242
134	3.406703	1.233036	5.287087	9.926826	0.343182	0.467394042
135	3.395538	1.232657	5.287087	9.915282	0.342455	0.466773939
136	3.384461	1.232471	5.287087	9.904018	0.341726	0.466167519
137	3.373499	1.232477	5.287087	9.893063	0.340996	0.46557637
138	3.362626	1.232676	5.287087	9.882389	0.340265	0.464999143
139	3.351869	1.233067	5.287087	9.872023	0.339532	0.464437352
140	3.341201	1.233651	5.287087	9.861938	0.338798	0.463889716
141	3.330647	1.234427	5.287087	9.852161	0.338063	0.463357669
142	3.320183	1.235397	5.287087	9.842666	0.337326	0.462840002
143	3.309834	1.236557	5.287087	9.833478	0.336588	0.46233807
144	3.299574	1.237912	5.287087	9.824573	0.335849	0.461850731
145	3.289429	1.239458	5.287087	9.815973	0.33511	0.461379264
146	3.279373	1.241198	5.287087	9.807658	0.334369	0.460922595
147	3.269432	1.243128	5.287087	9.799647	0.333628	0.460481923
148	3.259581	1.245254	5.287087	9.791921	0.332885	0.460056245
149	3.249844	1.247569	5.287087	9.784499	0.332142	0.459646679
150	3.240197	1.25008	5.287087	9.777363	0.331398	0.459252293
151	3.230664	1.25278	5.287087	9.77053	0.330654	0.458874123
152	3.22122	1.255676	5.28708	9.76398	0.329909	0.45851130

	1		7	3		9
153	3.211892	1.25876	5.287087	9.757739	0.329164	0.458164804
154	3.202654	1.262042	5.287087	9.751782	0.328417	0.457833821
155	3.193529	1.265512	5.287087	9.746127	0.327672	0.457519229
156	3.184506	1.269174	4.705762	9.159441	0.347675	0.486239219
157	3.175574	1.273033	4.705762	9.154369	0.346892	0.485954531
158	3.166755	1.27708	4.705762	9.149597	0.346109	0.485686427
159	3.158028	1.281324	4.705762	9.145114	0.345324	0.485434303
160	3.149413	1.285756	4.705762	9.140931	0.34454	0.485198824
161	3.14089	1.290385	4.705762	9.137037	0.343754	0.484979459
162	3.132479	1.295202	4.705762	9.133443	0.342968	0.484776786
163	3.12416	1.300217	4.705762	9.130139	0.342181	0.484590347
164	3.115953	1.305418	4.705762	9.127134	0.341395	0.484420636
165	3.107839	1.310819	4.705762	9.12442	0.340607	0.484267268
166	3.099836	1.316405	4.705762	9.122003	0.33982	0.48413065
167	3.091926	1.322191	4.705762	9.119878	0.339031	0.484010472
168	3.084127	1.328162	4.705762	9.118051	0.338244	0.483907051
169	3.076421	1.334333	4.705762	9.116516	0.337456	0.483820155
170	3.068827	1.340689	4.705762	9.115277	0.336669	0.483750014
171	3.061325	1.347245	4.705762	9.114332	0.33588	0.483696467
172	3.053935	1.353986	4.705762	9.113682	0.335093	0.483659658
173	3.046638	1.360927	4.705762	9.113327	0.334306	0.483639503
174	3.039451	1.368053	4.705762	9.113266	0.333519	0.483636056
175	3.032358	1.37538	4.705762	9.1135	0.332733	0.483649308
176	3.025376	1.38289	4.176406	8.584672	0.352416	0.513504266
177	3.01848	1.390602	4.17640	8.58549	0.35158	0.51355093

	7		6	6		
178	3.011709	1.398497	4.176406	8.586613	0.350745	0.513614207
179	3.005024	1.406595	4.176406	8.588026	0.349909	0.51369424
180	2.99845	1.414875	4.176406	8.589732	0.349074	0.513790816
181	2.99197	1.423358	4.176406	8.591734	0.348238	0.513904152
182	2.9856	1.432023	4.176406	8.594029	0.347404	0.514033947
183	2.979324	1.440891	4.176406	8.596621	0.346569	0.514180493
184	2.973158	1.44994	4.176406	8.599505	0.345736	0.514343401
185	2.967087	1.459194	4.176406	8.602687	0.344902	0.514523037
186	2.961125	1.468628	4.176406	8.60616	0.34407	0.514718925
187	2.955258	1.478267	4.176406	8.609931	0.343238	0.514931503
188	2.9495	1.488087	4.176406	8.613993	0.342408	0.515160209
189	2.943837	1.498111	4.176406	8.618354	0.341578	0.515405557
190	2.938283	1.508315	4.176406	8.623004	0.340749	0.515666896
191	2.932824	1.518724	4.176406	8.627955	0.339921	0.515944813
192	2.927475	1.529313	4.176406	8.633194	0.339095	0.516238572
193	2.92222	1.540108	4.176406	8.638735	0.338269	0.516548832
194	2.917075	1.551082	4.176406	8.644563	0.337446	0.516874773
195	2.912025	1.562262	4.176406	8.650693	0.336623	0.517217126
196	2.907083	1.57362	4.176406	8.65711	0.335803	0.517574986
197	2.902238	1.585186	4.176406	8.66383	0.334983	0.517949157
198	2.8975	1.596929	4.176406	8.670836	0.334166	0.518338647
199	2.892859	1.60888	4.176406	8.678145	0.33335	0.518744335
200	2.888325	1.621008	4.176406	8.68574	0.332536	0.519165145
201	2.883888	1.633344	4.176406	8.693639	0.331724	0.519602026
202	2.87955	1.645857	4.17640	8.70182	0.330914	0.52005382

	9		6	2		1
203	2.875326	1.658578	4.176406	8.710311	0.330106	0.520521548
204	2.871201	1.671476	4.176406	8.719084	0.329301	0.521003971
205	2.867172	1.684583	4.176406	8.728162	0.328497	0.521502175
206	2.863251	1.697866	3.342642	7.903758	0.362264	0.577082021
207	2.859427	1.711358	3.342642	7.913426	0.361339	0.577598698
208	2.85571	1.725025	3.342642	7.923377	0.360416	0.578129162
209	2.85209	1.738902	3.342642	7.933634	0.359494	0.578674599
210	2.848577	1.752955	3.342642	7.944173	0.358574	0.57923356
211	2.845161	1.767217	3.342642	7.95502	0.357656	0.579807294
212	2.841852	1.781655	3.342642	7.966148	0.356741	0.580394276
213	2.838641	1.796303	3.342642	7.977585	0.355827	0.580995822
214	2.835536	1.811125	3.342642	7.989302	0.354917	0.581610333
215	2.832529	1.826158	3.342642	8.001329	0.354007	0.582239187
216	2.829628	1.841365	3.342642	8.013635	0.353102	0.582880714
217	2.826826	1.856783	3.342642	8.02625	0.352198	0.583536354
218	2.824129	1.872375	3.342642	8.039145	0.351297	0.584204368
219	2.821531	1.888179	3.342642	8.052351	0.350398	0.584886254
220	2.819038	1.904155	3.342642	8.065835	0.349504	0.585580207
221	2.816644	1.920344	3.342642	8.07963	0.348611	0.586287786
222	2.814355	1.936706	3.342642	8.093702	0.347722	0.587007116
223	2.812166	1.95328	3.342642	8.108087	0.346835	0.587739816
224	2.810081	1.970026	3.342642	8.122749	0.345952	0.588483947
225	2.808096	1.986986	3.342642	8.137723	0.345071	0.589241185
226	2.806215	2.004117	3.342642	8.152974	0.344195	0.590009527
227	2.80443	2.021462	3.342642	8.16853	0.343321	0.59079070

	4		2	8		5
228	2.802757	2.038978	3.342642	8.184377	0.342452	0.591582656
229	2.801181	2.056708	3.342642	8.200531	0.341585	0.592387166
230	2.799708	2.074609	3.342642	8.216959	0.340723	0.593202112
231	2.798336	2.092725	3.342642	8.233702	0.339864	0.594029335
232	2.797067	2.11101	3.342642	8.250719	0.339009	0.594866653
233	2.795899	2.129511	3.342642	8.268052	0.338157	0.59571596
234	2.794835	2.148182	3.342642	8.285658	0.33731	0.596575017
235	2.793871	2.167068	3.342642	8.303581	0.336466	0.59744577
236	2.793011	2.186123	2.702845	7.681979	0.36358	0.648157725
237	2.792252	2.205395	2.702845	7.700491	0.362607	0.649003558
238	2.791595	2.224835	2.702845	7.719275	0.36164	0.649857663
239	2.79104	2.244492	2.702845	7.738377	0.360675	0.650721968
240	2.790588	2.264317	2.702845	7.75775	0.359716	0.65159419
241	2.790237	2.284359	2.702845	7.777441	0.35876	0.652476301
242	2.789989	2.304568	2.702845	7.797402	0.35781	0.653365976
243	2.789843	2.324996	2.702845	7.817683	0.356863	0.654265228
244	2.789799	2.34559	2.702845	7.838234	0.355922	0.655171687
245	2.789856	2.366403	2.702845	7.859105	0.354984	0.65608741
246	2.790016	2.387383	2.702845	7.880244	0.354052	0.657009986
247	2.790279	2.408581	2.702845	7.901704	0.353124	0.65794151
248	2.790643	2.429945	2.702845	7.923433	0.352201	0.658879534
249	2.791109	2.451528	2.702845	7.945482	0.351283	0.65982619
250	2.791677	2.473277	2.702845	7.9678	0.35037	0.660778993
251	2.792348	2.495246	2.702845	7.990439	0.349461	0.661740112
252	2.79312	2.51738	2.70284	8.01334	0.348559	0.66270702

			5	5		8
253	2.793995	2.539734	2.702845	8.036574	0.34766	0.663681945
254	2.794972	2.562253	2.702845	8.060069	0.346768	0.66466231
255	2.796051	2.584992	2.702845	8.083888	0.345879	0.66565036
256	2.797231	2.607896	2.702845	8.107972	0.344998	0.666643514
257	2.798515	2.63102	2.702845	8.13238	0.34412	0.667644039
258	2.799899	2.654309	2.702845	8.157053	0.343249	0.668649325
259	2.801388	2.677818	2.702845	8.182051	0.342382	0.669661671
260	2.802976	2.701492	2.702845	8.207313	0.341522	0.670678438
261	2.804668	2.725387	2.702845	8.2329	0.340666	0.671701955
262	2.806461	2.749445	2.702845	8.258751	0.339817	0.672729558
263	2.808357	2.773725	2.702845	8.284928	0.338972	0.673763604
264	2.810354	2.798168	2.702845	8.311367	0.338134	0.674801405
265	2.812455	2.822834	2.702845	8.338134	0.3373	0.675845344
266	2.814656	2.847662	2.702845	8.365163	0.336474	0.676892711
267	2.816961	2.872713	2.702845	8.392519	0.335651	0.677945916
268	2.819366	2.897926	2.702845	8.420136	0.334836	0.679002226
269	2.821875	2.923362	2.702845	8.448082	0.334026	0.680064076
270	2.824484	2.94896	2.702845	8.476288	0.333222	0.681128715
271	2.827198	2.974781	2.702845	8.504824	0.332423	0.6821986
272	2.830011	3.000764	2.702845	8.533619	0.331631	0.683270962
273	2.832929	3.02697	2.702845	8.562744	0.330844	0.684348281
274	2.835946	3.053338	2.702845	8.592128	0.330063	0.685427771
275	2.839068	3.07993	2.702845	8.621843	0.329288	0.686511932
276	2.842289	3.106682	2.612597	8.561568	0.331982	0.694846008
277	2.84561	3.133659	2.61259	8.59187	0.331199	0.69592231

	6		7	2		9
278	2.849041	3.160796	2.612597	8.622434	0.330422	0.697000108
279	2.852572	3.188159	2.612597	8.653328	0.32965	0.698081877
280	2.856201	3.215681	2.612597	8.684479	0.328886	0.69916484
281	2.859937	3.243429	2.612597	8.715963	0.328126	0.700251513
282	2.86377	3.271336	2.612597	8.747702	0.327374	0.701339102
283	2.86771	3.299469	2.612597	8.779776	0.326627	0.702430137
284	2.871747	3.32776	2.612597	8.812104	0.325887	0.703521816
285	2.875891	3.356279	2.612597	8.844767	0.325152	0.704616684
286	2.880132	3.384955	2.612597	8.877684	0.324424	0.705711931
287	2.884481	3.413859	2.612597	8.910937	0.323701	0.706810113
288	2.888926	3.44292	2.612597	8.944443	0.322986	0.707908416
289	2.893479	3.47221	2.612597	8.978285	0.322275	0.709009407
290	2.898128	3.501656	2.612597	9.012381	0.321572	0.710110269
291	2.902886	3.53133	2.612597	9.046812	0.320874	0.711213577
292	2.907739	3.561161	2.612597	9.081497	0.320183	0.712316512
293	2.9127	3.591221	2.612597	9.116518	0.319497	0.713421658
294	2.917758	3.621437	2.612597	9.151791	0.318818	0.714526193
295	2.922924	3.651882	2.612597	9.187402	0.318145	0.71563271
296	2.928185	3.682482	2.612597	9.223264	0.317478	0.716738387
297	2.933555	3.713313	2.612597	9.259465	0.316817	0.717845822
298	2.939021	3.744298	2.612597	9.295915	0.316163	0.718952194
299	2.944595	3.775514	2.612597	9.332706	0.315514	0.720060107
300	2.950265	3.806884	2.612597	9.369745	0.314871	0.721166742
301	2.956043	3.838485	2.612597	9.407125	0.314235	0.722274706
302	2.96191	3.87024	2.61259	9.44475	0.313604	0.72338118

	7		7	4		4
303	2.967893	3.902187	2.612597	9.482677	0.31298	0.72448743
304	2.973978	3.934366	2.612597	9.520941	0.312362	0.7255947
305	2.980158	3.966698	2.612597	9.559453	0.31175	0.726700185

Appendix 6: Genetic parameter estimates from RRM2

DIM	Genetic variance	Permanent environmental	Residual Variance	Total variance	Heritability	Repeatability
5	5.367718	4.615988	6.842558	16.82626	0.319008	0.593341
6	5.332303	4.528287	6.842558	16.70315	0.319239	0.590343
7	5.297684	4.442399	6.842558	16.58264	0.319472	0.587366
8	5.263909	4.358376	6.842558	16.46484	0.319706	0.584414
9	5.23093	4.276123	6.842558	16.34961	0.319942	0.581485
10	5.19871	4.195626	6.842558	16.23689	0.320179	0.57858
11	5.167291	4.116896	6.842558	16.12675	0.320417	0.575701
12	5.136601	4.039834	6.842558	16.01899	0.320657	0.572847
13	5.106689	3.964508	6.842558	15.91375	0.320898	0.570022

14	5.077482	3.890817	6.842558	15.81086	0.321139	0.567224
15	5.049025	3.818794	6.842558	15.71038	0.321382	0.564456
16	5.021248	3.748358	6.842558	15.61216	0.321624	0.561716
17	4.994195	3.67954	6.842558	15.51629	0.321868	0.559008
18	4.9678	3.612277	6.842558	15.42263	0.322111	0.55633
19	4.942103	3.546569	6.842558	15.33123	0.322355	0.553685
20	4.917037	3.482352	6.842558	15.24195	0.322599	0.551071
21	4.892647	3.419673	6.842558	15.15488	0.322843	0.548491
22	4.868863	3.358424	6.842558	15.06985	0.323086	0.545944
23	4.845732	3.298665	6.842558	14.98695	0.32333	0.543432
24	4.823183	3.240305	6.842558	14.90605	0.323572	0.540954
25	4.801262	3.183375	6.842558	14.82719	0.323815	0.538513
26	4.7799	3.127798	6.842558	14.75026	0.324055	0.536106
27	4.759143	3.073605	6.842558	14.67531	0.324296	0.533737
28	4.738923	3.020722	6.842558	14.6022	0.324535	0.531402
29	4.719284	2.969179	6.842558	14.53102	0.324773	0.529107
30	4.700159	2.918902	6.842558	14.46162	0.325009	0.526847
31	4.681593	2.869921	6.842558	14.39407	0.325245	0.524627
32	4.663518	2.822173	6.842558	14.32825	0.325477	0.522443
33	4.64598	2.775667	6.842558	14.2642	0.325709	0.520299
34	4.628911	2.730353	6.842558	14.20182	0.325938	0.518192
35	4.612357	2.686239	6.842558	14.14115	0.326166	0.516125
36	4.596252	2.643274	6.363599	13.60313	0.337882	0.532196
37	4.580638	2.601478	6.363599	13.54571	0.338161	0.530213
38	4.565452	2.56078	6.363599	13.48983	0.338437	0.528267

39	4.550737	2.52121	6.363599	13.43555	0.338709	0.526361
40	4.53643	2.482699	6.363599	13.38273	0.338976	0.524492
41	4.522572	2.445275	6.363599	13.33145	0.339241	0.522663
42	4.509103	2.408872	6.363599	13.28157	0.339501	0.52087
43	4.496062	2.373516	6.363599	13.23318	0.339757	0.519118
44	4.483385	2.339149	6.363599	13.18613	0.340008	0.517402
45	4.471121	2.305784	6.363599	13.1405	0.340255	0.515726
46	4.459201	2.27337	6.363599	13.09617	0.340497	0.514087
47	4.447674	2.241921	6.363599	13.05319	0.340735	0.512487
48	4.436472	2.211385	6.363599	13.01146	0.340967	0.510923
49	4.425639	2.181783	6.363599	12.97102	0.341194	0.509399
50	4.415116	2.153052	6.363599	12.93177	0.341416	0.50791
51	4.404944	2.125218	6.363599	12.89376	0.341634	0.506459
52	4.395063	2.09822	6.363599	12.85688	0.341845	0.505043
53	4.385513	2.072084	6.363599	12.8212	0.342052	0.503666
54	4.376237	2.046749	6.363599	12.78659	0.342252	0.502322
55	4.367275	2.022241	6.363599	12.75311	0.342448	0.501016
56	4.358562	1.998503	6.363599	12.72066	0.342636	0.499743
57	4.350151	1.975555	6.363599	12.6893	0.34282	0.498507
58	4.341972	1.953343	6.363599	12.65891	0.342997	0.497303
59	4.334076	1.931888	6.363599	12.62956	0.343169	0.496135
60	4.326396	1.911137	6.363599	12.60113	0.343334	0.494998
61	4.318976	1.891113	6.363599	12.57369	0.343493	0.493896
62	4.31176	1.871758	6.363599	12.54712	0.343645	0.492824
63	4.304794	1.853096	6.363599	12.52149	0.343792	0.491786

64	4.29801	1.835075	6.363599	12.49668	0.343932	0.490777
65	4.291446	1.817718	6.363599	12.47276	0.344065	0.4898
66	4.285061	1.800968	5.741484	11.82751	0.362296	0.514565
67	4.278887	1.784852	5.741484	11.80522	0.362457	0.513649
68	4.272869	1.769315	5.741484	11.78367	0.362609	0.512759
69	4.267039	1.754381	5.741484	11.7629	0.362754	0.511899
70	4.261358	1.739998	5.741484	11.74284	0.36289	0.511065
71	4.255849	1.726188	5.741484	11.72352	0.363018	0.510259
72	4.250474	1.712902	5.741484	11.70486	0.363138	0.509479
73	4.245256	1.700161	5.741484	11.6869	0.363249	0.508725
74	4.240149	1.687915	5.741484	11.66955	0.363352	0.507994
75	4.235192	1.676188	5.741484	11.65286	0.363446	0.50729
76	4.230334	1.66493	5.741484	11.63675	0.363532	0.506607
77	4.22561	1.654163	5.741484	11.62126	0.36361	0.50595
78	4.22097	1.64384	5.741484	11.60629	0.363679	0.505313
79	4.216452	1.633981	5.741484	11.59192	0.363741	0.504699
80	4.211996	1.62454	5.741484	11.57802	0.363792	0.504105
81	4.207656	1.615541	5.741484	11.56468	0.363837	0.503533
82	4.203366	1.606934	5.741484	11.55178	0.363872	0.502979
83	4.199178	1.598744	5.741484	11.53941	0.363899	0.502445
84	4.195026	1.590924	5.741484	11.52743	0.363917	0.501929
85	4.190956	1.583494	5.741484	11.51593	0.363927	0.501431
86	4.186927	1.576417	5.741484	11.50483	0.363928	0.50095
87	4.182959	1.569704	5.741484	11.49415	0.363921	0.500486
88	4.179011	1.563319	5.741484	11.48381	0.363904	0.500037

89	4.17512	1.557278	5.741484	11.47388	0.36388	0.499604
90	4.171238	1.551544	5.741484	11.46427	0.363847	0.499184
91	4.167391	1.54613	5.741484	11.455	0.363805	0.498779
92	4.163552	1.541005	5.741484	11.44604	0.363755	0.498387
93	4.159746	1.536184	5.741484	11.43741	0.363696	0.498009
94	4.155918	1.531624	5.741484	11.42903	0.363628	0.49764
95	4.152121	1.527352	5.741484	11.42096	0.363553	0.497285
96	4.148292	1.523321	5.680706	11.35232	0.365414	0.4996
97	4.144474	1.519555	5.680706	11.34473	0.365321	0.499265
98	4.140622	1.516017	5.680706	11.33734	0.36522	0.498939
99	4.136782	1.512729	5.680706	11.33022	0.365111	0.498623
100	4.132889	1.509648	5.680706	11.32324	0.364992	0.498315
101	4.128986	1.506793	5.680706	11.31648	0.364865	0.498015
102	4.125021	1.504128	5.680706	11.30985	0.364728	0.497721
103	4.121047	1.501678	5.680706	11.30343	0.364584	0.497435
104	4.117012	1.499407	5.680706	11.29712	0.36443	0.497155
105	4.112949	1.49733	5.680706	11.29098	0.364268	0.496881
106	4.108806	1.49541	5.680706	11.28492	0.364097	0.496611
107	4.104635	1.493674	5.680706	11.27902	0.363918	0.496347
108	4.100377	1.492081	5.680706	11.27316	0.363729	0.496086
109	4.096072	1.490651	5.680706	11.26743	0.363532	0.495829
110	4.091692	1.489364	5.680706	11.26176	0.363326	0.495576
111	4.087248	1.488218	5.680706	11.25617	0.363112	0.495325
112	4.08271	1.487195	5.680706	11.25061	0.362888	0.495076
113	4.07811	1.486307	5.680706	11.24512	0.362656	0.494829

114	4.073409	1.48553	5.680706	11.23965	0.362414	0.494583
115	4.068628	1.484868	5.680706	11.2342	0.362164	0.494338
116	4.06375	1.484313	5.680706	11.22877	0.361905	0.494094
117	4.058796	1.483868	5.680706	11.22337	0.361638	0.49385
118	4.053717	1.483505	5.680706	11.21793	0.361361	0.493605
119	4.048566	1.483248	5.680706	11.21252	0.361075	0.49336
120	4.043284	1.483062	5.680706	11.20705	0.36078	0.493113
121	4.037923	1.482973	5.680706	11.2016	0.360477	0.492867
122	4.032426	1.482946	5.680706	11.19608	0.360164	0.492616
123	4.026832	1.482998	5.680706	11.19054	0.359843	0.492365
124	4.021108	1.483111	5.680706	11.18492	0.359511	0.49211
125	4.015282	1.483294	5.680706	11.17928	0.359172	0.491854
126	4.00932	1.48353	5.074315	10.56716	0.379413	0.519804
127	4.003251	1.483828	5.074315	10.56139	0.379046	0.519541
128	3.997042	1.484173	5.074315	10.55553	0.378668	0.519274
129	3.99071	1.484564	5.074315	10.54959	0.378281	0.519004
130	3.984244	1.485004	5.074315	10.54356	0.377884	0.518729
131	3.97765	1.485483	5.074315	10.53745	0.377478	0.518449
132	3.970919	1.486005	5.074315	10.53124	0.377061	0.518165
133	3.964056	1.486561	5.074315	10.52493	0.376635	0.517877
134	3.957041	1.487146	5.074315	10.5185	0.376198	0.517582
135	3.949914	1.487777	5.074315	10.51201	0.375753	0.517284
136	3.942618	1.488426	5.074315	10.50536	0.375296	0.516978
137	3.935196	1.489106	5.074315	10.49862	0.37483	0.516668
138	3.927614	1.489809	5.074315	10.49174	0.374353	0.516351

139	3.919891	1.490532	5.074315	10.48474	0.373866	0.516028
140	3.912018	1.491284	5.074315	10.47762	0.373369	0.5157
141	3.904012	1.492062	5.074315	10.47039	0.372862	0.515365
142	3.895842	1.492858	5.074315	10.46302	0.372344	0.515024
143	3.887525	1.493668	5.074315	10.45551	0.371816	0.514675
144	3.879044	1.494497	5.074315	10.44785	0.371277	0.51432
145	3.870436	1.495355	5.074315	10.44011	0.370728	0.513959
146	3.86165	1.496223	5.074315	10.43219	0.370167	0.513591
147	3.852725	1.497111	5.074315	10.42415	0.369596	0.513216
148	3.843633	1.498017	5.074315	10.41596	0.369014	0.512833
149	3.834399	1.498944	5.074315	10.40766	0.368421	0.512444
150	3.824999	1.499891	5.074315	10.3992	0.367816	0.512048
151	3.815456	1.500859	5.074315	10.39063	0.367202	0.511645
152	3.805746	1.501848	5.074315	10.38191	0.366575	0.511235
153	3.795893	1.50286	5.074315	10.37307	0.365937	0.510818
154	3.78586	1.503888	5.074315	10.36406	0.365287	0.510393
155	3.775697	1.504949	5.074315	10.35496	0.364627	0.509963
156	3.765367	1.506029	4.393677	9.665072	0.389585	0.545407
157	3.754881	1.507147	4.393677	9.655705	0.388877	0.544966
158	3.744242	1.508286	4.393677	9.646205	0.388157	0.544518
159	3.733437	1.50946	4.393677	9.636574	0.387424	0.544062
160	3.72249	1.510667	4.393677	9.626834	0.386679	0.543601
161	3.711379	1.511915	4.393677	9.616971	0.38592	0.543133
162	3.700127	1.513201	4.393677	9.607005	0.385149	0.542659
163	3.688712	1.514534	4.393677	9.596922	0.384364	0.542179

164	3.677159	1.515909	4.393677	9.586745	0.383567	0.541693
165	3.665444	1.517339	4.393677	9.57646	0.382756	0.5412
166	3.653581	1.51881	4.393677	9.566068	0.381931	0.540702
167	3.641571	1.520351	4.393677	9.555599	0.381093	0.540199
168	3.629427	1.521948	4.393677	9.545051	0.380242	0.539691
169	3.617115	1.523607	4.393677	9.534398	0.379375	0.539176
170	3.60467	1.52533	4.393677	9.523677	0.378496	0.538658
171	3.592074	1.527132	4.393677	9.512882	0.377601	0.538134
172	3.579359	1.529015	4.393677	9.502051	0.376693	0.537608
173	3.566484	1.530979	4.393677	9.49114	0.37577	0.537076
174	3.553483	1.533025	4.393677	9.480185	0.374833	0.536541
175	3.540337	1.535171	4.393677	9.469185	0.37388	0.536003
176	3.527057	1.537401	3.96102	9.025478	0.390789	0.561129
177	3.513648	1.53975	3.96102	9.014418	0.389781	0.560591
178	3.500121	1.542202	3.96102	9.003342	0.388758	0.56005
179	3.486445	1.544769	3.96102	8.992234	0.387717	0.559507
180	3.472668	1.547458	3.96102	8.981145	0.386662	0.558963
181	3.458747	1.550276	3.96102	8.970043	0.385589	0.558417
182	3.444729	1.553227	3.96102	8.958976	0.3845	0.557871
183	3.430574	1.556321	3.96102	8.947915	0.383394	0.557325
184	3.416314	1.559555	3.96102	8.936889	0.382271	0.556779
185	3.401935	1.562953	3.96102	8.925907	0.38113	0.556233
186	3.387457	1.566503	3.96102	8.91498	0.379974	0.555689
187	3.372865	1.570234	3.96102	8.904118	0.378798	0.555147
188	3.358179	1.574131	3.96102	8.89333	0.377607	0.554608

189	3.343387	1.578224	3.96102	8.882631	0.376396	0.554071
190	3.328497	1.582493	3.96102	8.87201	0.375168	0.553537
191	3.313517	1.586981	3.96102	8.861517	0.373922	0.553009
192	3.298446	1.591661	3.96102	8.851126	0.372658	0.552484
193	3.283292	1.596576	3.96102	8.840888	0.371376	0.551966
194	3.268055	1.601701	3.96102	8.830775	0.370076	0.551453
195	3.252731	1.607073	3.96102	8.820824	0.368756	0.550947
196	3.237352	1.612683	3.96102	8.811055	0.367419	0.550449
197	3.221885	1.618555	3.96102	8.801459	0.366063	0.549959
198	3.206359	1.624677	3.96102	8.792055	0.364688	0.549477
199	3.190764	1.631085	3.96102	8.782868	0.363294	0.549006
200	3.175118	1.637763	3.96102	8.7739	0.361882	0.548545
201	3.159401	1.644743	3.96102	8.765163	0.36045	0.548095
202	3.143652	1.652016	3.96102	8.756688	0.359	0.547658
203	3.127851	1.659618	3.96102	8.748488	0.35753	0.547234
204	3.112006	1.667524	3.96102	8.74055	0.356042	0.546823
205	3.09613	1.675785	3.96102	8.732934	0.354535	0.546427
206	3.080218	1.684372	3.265992	8.030583	0.383561	0.593306
207	3.064275	1.693331	3.265992	8.023598	0.381908	0.592952
208	3.048316	1.702644	3.265992	8.016952	0.380234	0.592614
209	3.032345	1.712354	3.265992	8.010692	0.378537	0.592296
210	3.016358	1.722437	3.265992	8.004788	0.376819	0.591995
211	3.00036	1.73294	3.265992	7.999292	0.375078	0.591715
212	2.984357	1.743839	3.265992	7.994188	0.373316	0.591454
213	2.968362	1.755185	3.265992	7.98954	0.371531	0.591216

214	2.952383	1.766954	3.265992	7.985329	0.369726	0.591001
215	2.936414	1.779193	3.265992	7.981599	0.367898	0.59081
216	2.920462	1.791877	3.265992	7.978332	0.366049	0.590642
217	2.904541	1.80506	3.265992	7.975594	0.364179	0.590502
218	2.888649	1.818714	3.265992	7.973356	0.362288	0.590387
219	2.87279	1.832893	3.265992	7.971675	0.360375	0.5903
220	2.856989	1.847572	3.265992	7.970553	0.358443	0.590243
221	2.841226	1.862801	3.265992	7.97002	0.356489	0.590215
222	2.825524	1.878557	3.265992	7.970073	0.354517	0.590218
223	2.80988	1.894894	3.265992	7.970766	0.352523	0.590254
224	2.79431	1.911784	3.265992	7.972087	0.350512	0.590322
225	2.778803	1.929285	3.265992	7.974081	0.348479	0.590424
226	2.763391	1.947368	3.265992	7.976752	0.346431	0.590561
227	2.748064	1.966091	3.265992	7.980148	0.344363	0.590735
228	2.732828	1.985427	3.265992	7.984248	0.342277	0.590946
229	2.7177	2.005433	3.265992	7.989125	0.340175	0.591195
230	2.702676	2.026082	3.265992	7.99475	0.338056	0.591483
231	2.687772	2.047432	3.265992	8.001197	0.335921	0.591812
232	2.672988	2.069457	3.265992	8.008437	0.333772	0.592181
233	2.658331	2.092216	3.265992	8.01654	0.331606	0.592593
234	2.643815	2.11568	3.265992	8.025488	0.329427	0.593048
235	2.629442	2.139912	3.265992	8.035347	0.327234	0.593547
236	2.615224	2.164881	2.476439	7.256543	0.360395	0.65873
237	2.601163	2.190651	2.476439	7.268253	0.35788	0.65928
238	2.587272	2.217191	2.476439	7.280902	0.355351	0.659872

239	2.573548	2.244572	2.476439	7.294559	0.352804	0.660509
240	2.560016	2.272751	2.476439	7.309206	0.350245	0.661189
241	2.546667	2.301807	2.476439	7.324913	0.347672	0.661916
242	2.533525	2.331696	2.476439	7.34166	0.345089	0.662687
243	2.520583	2.362498	2.476439	7.35952	0.342493	0.663505
244	2.507857	2.394174	2.476439	7.378469	0.339889	0.66437
245	2.495354	2.426794	2.476439	7.398586	0.337274	0.665282
246	2.48309	2.460318	2.476439	7.419846	0.334655	0.666241
247	2.471059	2.494829	2.476439	7.442327	0.332028	0.667249
248	2.459273	2.530293	2.476439	7.466005	0.329396	0.668305
249	2.447749	2.566772	2.476439	7.49096	0.32676	0.66941
250	2.436492	2.604234	2.476439	7.517165	0.324124	0.670562
251	2.42551	2.642756	2.476439	7.544704	0.321485	0.671765
252	2.414807	2.682306	2.476439	7.573552	0.318847	0.673015
253	2.404401	2.722949	2.476439	7.60379	0.316211	0.674315
254	2.394294	2.764661	2.476439	7.635393	0.313578	0.675663
255	2.384502	2.807504	2.476439	7.668445	0.31095	0.677061
256	2.375026	2.851457	2.476439	7.702921	0.308328	0.678507
257	2.36588	2.896591	2.476439	7.73891	0.305712	0.680002
258	2.357073	2.942866	2.476439	7.776378	0.303107	0.681543
259	2.348616	2.990365	2.476439	7.815419	0.300511	0.683134
260	2.340516	3.039046	2.476439	7.856001	0.297927	0.684771
261	2.332785	3.088993	2.476439	7.898218	0.295356	0.686456
262	2.325432	3.140165	2.476439	7.942035	0.292801	0.688186
263	2.318467	3.192646	2.476439	7.987552	0.29026	0.689963

264	2.311896	3.246405	2.476439	8.03474	0.287738	0.691784
265	2.305737	3.301508	2.476439	8.083684	0.285233	0.69365
266	2.299992	3.357932	2.476439	8.134363	0.28275	0.695558
267	2.29468	3.415744	2.476439	8.186863	0.280288	0.697511
268	2.289802	3.474923	2.476439	8.241164	0.277849	0.699504
269	2.285375	3.535547	2.476439	8.297361	0.275434	0.701539
270	2.281406	3.59757	2.476439	8.355416	0.273045	0.703613
271	2.27791	3.661086	2.476439	8.415435	0.270682	0.705727
272	2.274892	3.726047	2.476439	8.477378	0.268349	0.707877
273	2.272369	3.792547	2.476439	8.541355	0.266043	0.710065
274	2.270346	3.860538	2.476439	8.607322	0.263769	0.712287
275	2.268839	3.930116	2.476439	8.675394	0.261526	0.714545
276	2.267853	4.001249	2.071734	8.340836	0.271898	0.751616
277	2.267407	4.074002	2.071734	8.413143	0.269508	0.75375
278	2.267505	4.148357	2.071734	8.487596	0.267155	0.75591
279	2.268165	4.224382	2.071734	8.564281	0.26484	0.758096
280	2.269391	4.302059	2.071734	8.643184	0.262564	0.760304
281	2.271203	4.381472	2.071734	8.724409	0.260327	0.762536
282	2.273604	4.462569	2.071734	8.807907	0.258132	0.764787
283	2.276614	4.545455	2.071734	8.893803	0.255978	0.767059
284	2.280237	4.630074	2.071734	8.982045	0.253866	0.769347
285	2.284492	4.716533	2.071734	9.072759	0.251797	0.771653
286	2.289384	4.804776	2.071734	9.165895	0.249772	0.773974
287	2.294933	4.894912	2.071734	9.261579	0.247791	0.776309
288	2.301143	4.986884	2.071734	9.35976	0.245855	0.778655

289	2.308035	5.080822	2.071734	9.460591	0.243963	0.781014
290	2.315611	5.176628	2.071734	9.563973	0.242118	0.783381
291	2.323895	5.274455	2.071734	9.670084	0.240318	0.785758
292	2.332889	5.374224	2.071734	9.778847	0.238565	0.788141
293	2.342613	5.476025	2.071734	9.890372	0.236858	0.79053
294	2.353074	5.579844	2.071734	10.00465	0.235198	0.792923
295	2.364293	5.685774	2.071734	10.1218	0.233584	0.79532
296	2.376273	5.793753	2.071734	10.24176	0.232018	0.797717
297	2.389036	5.9039	2.071734	10.36467	0.230498	0.800116
298	2.402585	6.016151	2.071734	10.49047	0.229025	0.802513
299	2.416948	6.130652	2.071734	10.61933	0.227599	0.804909
300	2.43212	6.247288	2.071734	10.75114	0.22622	0.807301
301	2.44813	6.366206	2.071734	10.88607	0.224886	0.809689
302	2.464982	6.487368	2.071734	11.02408	0.2236	0.812072
303	2.482688	6.610797	2.071734	11.16522	0.222359	0.814448
304	2.501277	6.736623	2.071734	11.30963	0.221163	0.816817
305	2.520746	6.864753	2.071734	11.45723	0.220013	0.819177