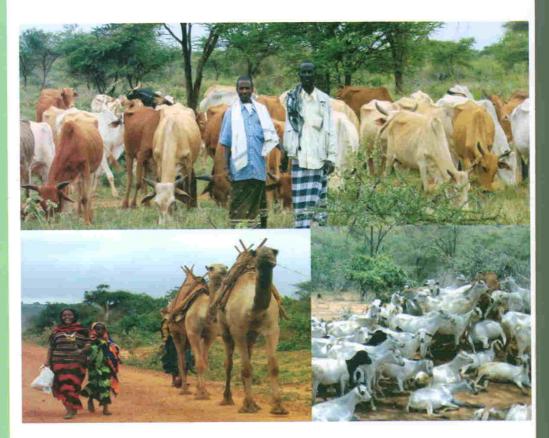
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Application of Random Regression Model (RRM) in Dairy Cattle Genetic Evaluation

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Abstract

Data for milk production, fertility, growth and survivability of dairy cows provide an example of repeated measures or longitudinal data, the essential feature of which is the presence of correlations between tests on the same animal. Longitudinal data need a special statistical treatment because of their covariance pattern which will vary depending on the assumption of analysis. Besides most statistical analysis methods in Africa including Ethiopia results in failure to fully account for the systematic environmental effects. Modelling the covariance structure of repeated measurements correctly is of importance for drawing correct inference from the data. It is important to explore the potential of any statistical and computing technique which allows a direct and more efficient utilization of all available records for genetic evaluation of dairy cattle. Hence, Random Regression Model (RRM) is potentially applicable to evaluate longitudinal data of dairy cattle. Several alternatives have been proposed and these include fractional polynomials and linear and Bsplines depending on the nature of the data and evaluation context. The model also enables to account both genetic and environment variation precisely based on different function and order of fit. This review traces nature of RR model its application and advantages over others model. The paper discusses how to model lactation curve using test day records, survival analysis, genetic by environment interaction studies with different alternatives such as functions order of fit. The need to initiate and popularize the model in Ethiopia is also indicated.

Key words: Dairy Cattle, Genetic Evaluation, Longitudinal Data, Random Regression, Test Day Records

Introduction

Data for milk production, fertility, growth and survivability of dairy cows provide an example of repeated measures or longitudinal data, the essential feature of which is the presence of correlations between measurements on the same animal. Repeated observations measured along a trajectory (time) and the mean and covariance between measurements change gradually along the trajectory. Genetic correlations between repeated measurements usually tended to decreases the time between them increased.

It is important to explore the potential of any statistical and computing technique which allows a direct and more efficient utilization of all available records for genetic evaluation of dairy cattle. For example various methods have been used to analyse milk production and related records which represent longitudinal data. In Ethiopia Haile et al. (2009) and Effa et al. (2011)

have used the approach where records at various stages of lactation are assumed to be independent. The assumption that the data are independent is questionable since measurements are performed on the same animal. Besides lactation curves have been fitted at a phenotypic level and the parameters of the curve have subsequently been analysed as new traits. However, this approach results in failure to fully account for the systematic environmental effects (VanRaden, 1997). Therefore, repeated measurements/longitudinal data need a special statistical treatment since their covariance pattern varies depending on the methods of analysis.

Modelling the covariance structure of repeated measurements correctly is of importance for drawing correct inference from the data. Hence, Random Regression Model (RRM) is potentially applicable in dairy cattle genetic evaluation. It was first implemented in Canada (Schaeffer et al., 2000) in 1999 and several countries that are members of Inter-bull have since adopted various forms of the methodology, including Belgium, Germany, the Netherlands, Italy, Finland, Denmark and Sweden (Inter-bull, 2009). Lack of appropriate recording system, expertise in the field of animal breeding and/or Biometrics is a major limitation to apply the model in genetic evaluation in most African countries like Ethiopia. But, there is still a need to initiate and popularize the model so that more accurate genetic predictions can be made than what can be obtained using the conventional analytical models. Therefore, the objective of the paper is to review available information on RR model and its application in particular.

Random Regression Model and Genetic Evaluation of Dairy Cattle

Random Regression Model

Random Regression Model (RRM) is are intended for use on longitudinal data or 'repeated' records situation where observations for a trait are collected several times during the course of animal life (Hill and Brotherstone,1999).

The general concept of using RR for analysis of covariance in an animal breeding context was suggested by Henderson (1982). Kirkpatrick et al. (1994) introduced the infinite-dimensional model for traits measured repeatedly per individual, and suggested to model genetic covariances of trajectories through covariance functions. However, initial applications of the RRM were in genetic evaluation of dairy cows, using records from individual test-days to model the lactation curve (Schaeffer & Dekkers, 1994). Since then, the RRM has become a standard for analyses of repeated measured records from animal breeding schemes. Other areas of animal breeding that have already utilized RRM include conformation traits (Uribe et al., 2000), body condition scores (Sasaki et al., 2010), feed intake (Kebede and Gebertsadik, 2010); growth in pigs (Lorenzo Bermejo, 2003), sheep (Lewis & Brotherstone, 2002) and beef cattle (Meyer, 2005) and litter size in pigs (Lukovic et al., 2004). The RRM has also been used for analysis of survival data (Veerkamp et al., 2001; Sasaki et al., 2010) and for assessing genotype by environment interactions using a continuum of an environmental parameter as covariance functions in reaction norms (Shariati et al., 2007).

History of Random Regression Models in Dairy Cattle Genetic Evaluation

Dairy cattle genetic evaluation was significantly move to Random Regression Model (RRM) with increasing in accuracy of genetic evaluations over the sire model that was used previously (Bilal and Khan, 2009). The models have been applied to existing test day records. In addition to providing the usual evaluations for production traits on a 305-day basis, the test day model also provides evaluations for persistency of lactation.

In RRM approach, the additive genetic values (estimated breeding values, EBV) of animals are usually obtained from mixed model analyses. For the trait under consideration, a linear regression of observations on indicator variables is performed. Animals' additive genetic effects are fitted as random effects. Because the functions of time, such as DIM, can be readily modelled in the mixed model framework (Henderson, 1982), trajectories (e.g. lactation curve) can be described. The co-variables are usually nonlinear functions such as polynomials or splines relating time to the traits e.g. milk, fat or protein yield. Fitting sets of RR coefficients for each individual random factor (e.g. additive genetic and permanent environmental effects) produces the estimates of the corresponding trajectories (Schaffer, 2003; Dzomba et al., 2010).

Table 1. Trend's in methods of dairy cattle genetic evaluation

Year	Methods of Evaluations	Particular features			
1974	Sire model(SM)	 Consideration of the merit of herd-mates, 2) inclusion of genetic groups based on pedigree index, 3) improved weighting of information. 			
1989	Animal Model (AM)	It considered all relatives, no matter how distant, and all animals of a breed, male and female, were evaluated simultaneously.			
1993	Test Day Model (TDM)	A TDM allows for a more exact specification and consideration of the environment (a day vs. lactation). Often, it includes consideration of persistency of lactation and rate of maturity.			
1993	Repeatability Model (RPM)	Consecutive test-day samples from the same lactation are considered as repeated observations on the same trait, and a permanent environmental effect accounts for environmental similarities between different test-days within the same lactation. A major disadvantage of the repeatability model is the heterogeneity of the residual variance during the lactation.			
2000	Random Regression Model (RRM)	Random regression test day model allows the fitting of lactation curves to individual lactations. Because curve parameters are treated as random variables, reasonable estimates are obtained even with few data points.			

Application of Random Regression Model

Test Day Records

Several reviews on the use of RRM for the analysis of test day records of dairy cattle have been given by (Bohamanova et al., 2008; Dzomba et al., 2010). Research still continues on determining the order of fit for the random regressions for additive genetic and permanent environmental effects that explains the most variation in the observations. For the evaluation of TD records, the RR test-day animal model is considered the most appealing statistically. It is often used to fit the RR coefficients in a linear model to obtain genetic parameters and breeding values. There are two approaches to the RR model (RRM): RR on lactation curve functions (e.g. the Wilmink's function) or RR on polynomials or splines (Dzomba et al., 2010). The number of parameters that can be fitted to describe a lactation curve is flexible with the RR where a lactation curve function is used. Jamrozik & Schaeffer (2002) found that the TDM with Legendre polynomials outperformed the TDM with a lactation curve function, considering the same number of parameters in terms of statistics on the goodness of fit.

Several alternatives have been proposed and these include fractional polynomials and linear and B-splines. Splines are curves constructed from piece-wise lower degree polynomials which are joined smoothly at selected points (knots). White et al. (1999) used cubic splines, while Torres & Quaas (2001) used B-splines with 10 knots in separate RR analyses of test-day records of dairy cows. Bohmanova et al. (2008) concluded that splines model with 6 knots had the best overall performance compared with Legendre polynomials of order 4 and 3 alternative of liner spline with 4,5 and 6 knot for production trait and somatic cell count. Too many knots would increase model complexity, while too few knots would reduce accuracy in estimates (Meyer, 2005). It is important to compare RR models with available data using lactation curve functions, orthogonal polynomials and splines.

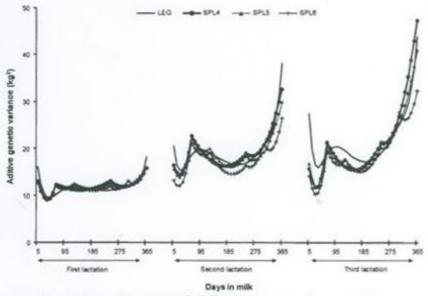


Figure 1.Lactation curve with different functions; (Sources: Bohmanova et al. (2008))

Partitioning Variance with Random Regression Model

The first estimates of variance components for test-day milk yields obtained by RRM were published by Jamrozik & Schaeffer (1997). The RRM were used for modeling genetic effects only. Meyer & Hill (1997) and Meyer (1998) demonstrated the use of covariance functions to model additive genetic and permanent environmental effects in random regression TDMs. The covariance function describes the covariance structure of an infinite-dimension character, such as test-day milk yields, as a function of time. The covariance function is equivalent to a RRM if the same functions are used (Meyer & Hill, 1997; Van der Werf et al., 1998). The equivalence of the RRM with the covariance function is useful when analyzing data observed at many time periods, because the number of regression coefficients determines the number of covariance to be estimated for each source of variation in a RRM. In a univariate RRM, k regression coefficients result in k (k+1)/2 covariance estimates. The covariance function is used to reduce the rank of the covariance matrix from n, the number of traits, to k, the number of functions, when starting from a multiple trait approach (Meyer & Fitzpatrick, 2005).

The further development of the variance component estimation by RRM included modeling of permanent environmental effects by random regressions (Van der Werf et al., 1998; Olori et al., 1999; Rekaya et al., 1999; Strabel & Misztal, 1999). In addition, other authors modeled the heterogeneity of residual variance across the lactations (Jamrozik & Schaeffer, 1997; Jamrozik et al., 1998; Brotherstone et al., 2000; Jaffrezic et al., 2000).

Parameters obtained in various models and with various data sets showed great variability in both average values and shapes of trajectories (Misztal et al., 2000). The heritability estimates of the first lactation milk yield for particular DIM resulting from RR models ranged between 0.14 (Strabel & Misztal, 1999) and 0.51 (Olori et al., 1999). Some authors reported high heritability at the beginning and at the end of lactation (Jamrozik & Schaeffer, 1997; Olori et al., 1999; Kettunen et al., 2000). Other authors found the highest heritability in the middle of lactation (e.g. Swalve, 1995; Rekaya et al., 1999; Liu et al., 2000; Pool et al., 2000; Jacobsen et al., 2002; Duet et al., 2003).

Standard mixed-model-based variance component procedures (i.e. Restricted maximum Likelihood: REML or Bayesian methods based on Markov chain Monte Carlo methodology: MCMC) can be used to estimate covariance functions directly from the data (Jensen, 2001). High computational demands limit the size of the datasets and the nature of the models that can be analyzed using REML, but algorithms for multivariate analyses via AIREML are readily adapted to the estimation of covariance among random regression coefficients (Meyer & Kirkpatrick, 2005).

Modelling Environmental Effects in the Random Regression Model

Milk production is influenced by exactly the same environmental factors whether a TDM or lactation model is used in genetic evaluation. However, for a TDM, the stage of lactation is an important consideration, because of the curvilinear relationship that exists between the stage of lactation and milk production (Swalve, 1995; 2000). The TDMs often use types of covariates

or mathematical functions, in a regression, to account for stage of lactation. Meyer (2005a) and Meyer & Kirkpatrick (2005) noted that the resultant lactation curve parameters can be considered as examples of 'function-valued traits' implying that mathematical functions are in use.

The adoption of TDM over the lactation model replaced the use of herd-year-season (HYS) with herd-test-date (HTD). The HTD accounts for the effects of herd and the year and the season of production whereas HYS effect is commonly used to account for the effects of the individual herd, the year, and the season of calving and the interactions among them. With a TDM, further effects that can be fitted in the analysis include age at calving, parity, and pregnancy (Swalve, 1995).

The random regression TDM can account for many environmental factors that could affect cows differently during the lactation (Schaeffer & Deckers, 1994). The lactation curve is split into two parts: a fixed part (average lactation curve) and a random animal specific part (deviation from the average curve) (Figure 2) whereas the conventional methods couldn't separate it. To account for the variability within lactation stage, an appropriate sub-model is fitted on stage of lactation, nested within parts of the model that account for environmental effects. There are profound differences in the manner in which environmental variation is accounted for with RRM in respect to definition of subgroups for fixed regression on the stage of lactation (Zavadilova et al., 2005). Frequently used factors are season of calving and/or classes of age at calving (Reents et al., 1998; Strabel & Misztal, 1999; Lidauer et al., 2000; Schaeffer et al., 2000). Other models used include the effects of days carried calf (Lidauer et al., 2000). For most developing countries including Ethiopia, it is important to investigate how best the information collected when testing herds can be used in genetic analysis to account for the environmental variation. Mostert et al. (2006) defined a fixed regression TD-model which passed the necessary trend validation tests required by Inter-bull to ensure that the model sufficiently accounts for all environmental effects. Such studies can also attempt to recommend inclusion of valuable variables that the current milk recording system ignores or encourage inclusion of some traits such as fertility measures in the routine genetic evaluations.

Persistency of Lactation

Dairy breeders focus on modeling the individual genetic curves of the cows and estimating genetic parameters of the lactation curves to select for lactation yields or persistency (Shanks et al., 1981; Danell, 1982; Ferris et al., 1985; Gengler, 1996; Jamrozik & Schaeffer, 1997). Although the definition of persistency varies, generally it refers to the rate of decline in production after peak milk yield production has been reached (Swalve & Gengler, 1999). High persistency is associated with a slow rate of decline in production whereas low persistency is associated with a rapid rate of decline. Persistent cows are more desirable because they are more efficient in roughage usage, suffer less metabolic stress due to high peak yield, and are thus more disease-resistant (Solkner & Fuchs, 1987). Genetic modification of the lactation curves are concerned with the artificial redistribution of total lactation responses among different stages of the lactation (Lin & Togashi, 2005). In a recent study, Mostert et al. (2008) laid out the framework for inclusion of persistency of lactation in genetic evaluation of South African dairy cattle

based on the Canadian Persistency Index. As a result, persistency of production has been implemented in routine genetic evaluations thereby highlighting the economic importance of persistency.

In describing the persistency of milk production during lactation, the choice of a parameter that gives a correct description of the shape of a lactation curve is important. It is therefore important to develop an evaluation method in which genetic differences in persistency can be evaluated on a routine basis.

A key issue in genetic evaluation of persistency is trait definition. Gengler (1995; 1996) identified three types of measures of persistency which are: measures based on ratios of yields, measures based on variation of yields, and measures developed out of functions that describe lactation yields. There is, however, no clear consensus on how best to mathematically model persistency. The procedure most widely used to measure lactation persistency nowadays is based on the by-product of the random regression test day model. Druet et al. (2005) showed that the first and second eigenvectors of the estimated genetic covariance matrix in a random regression model may serve as proxies for yield and persistency. Use of these eigenvectors in random regression test-day models is computationally advantageous but there is still no clear biological interpretation of the eigenvectors.

Advantages of RR Test-Day Models

Advantages of RR test-day models over other approaches of evaluating test-day records are now widely acknowledged (Bohmanova et al., 2008; Hammami et al., 2008). The genetic component of the lactation curve can be modelled by fitting regression coefficients for each animal, commonly referred to as random regression (RR) coefficients (Schaeffer & Dekkers, 1994). The additive genetic solutions can be extracted from the BV estimates for the RR coefficients (Jamrozik et al., 1997). It becomes possible to genetically rank animals for each TD yield by estimating a BV of each animal for each TD yield. The estimated BV is given as a product of the RR coefficients and the days in milk (DIM) dependent covariates. Monitoring of management of individual herds and of individual cows within a herd is also an added advantage through the simple comparison between actual and expected production (Dzomba et al., 2010). The same authors list the advantage of RR test day model over the other.

- This type of model provides a continuous treatment of observation over time and is able to incorporate heterogeneous variances and covariance among measures along time (including days that were not sampled) with a potentially reduced number of parameters compared with the multiple trait approach.
- Every record contributes information at the value of the control variable at which it is measured. Arbitrary or inappropriate corrections for the differences in the control variable are therefore rendered useless.
- With regards to estimation of variance components, random regression models
 facilitate parsimonious description of changing and potentially complex covariance
 structures, thereby utilizing the data more efficiently and generating breeding values of
 higher accuracies.

- 4. Because the lactation curve is allowed to differ for each cow, this facilitates accounting for the variability in persistency and makes possible the prediction of evaluations for persistency, thereby providing additional information for selection.
- The RRM for TD yields can account more precisely for environmental factors that could affect cows differently during lactation.
- Due to emphasis on more yield information, a RRM results in top animals which are less related and hence results in reduced rates of inbreeding compared to lactation models.
- 7. The RRM also allows a cow to be evaluated on the basis of any number of TD records during lactation. Related to this, as only eight to 10 TD yields per cow per lactation may be collected, this could result in lower costs of recording (Schaeffer et al., 2000). For example, in conventional calculation sub-period yields or aggregated lactation yield per cow can be used, which will then be evaluated statistically with a simple variance analysis based on averaged sub-period milk yields is marked by the following disadvantages:
 - a) Complicate and incomplete lactation records of cows will have the same weighting in the analysis.
 - b) Possible assumption on the significance of differences between sub-period yields can be caused by different environmental effects on the test days.
 - c) Due to the calculation of average values, the number of daily milk yields per cow is lost, and as a result, the degrees of freedom for comparison of the group average will be reduced.
 - d) Dependencies between repeated yields of a cow from different sub-periods of the lactation are not taken into account, where as in random regression model, each lactation curve could be plotted independently (Figure 2). Besides, variance due to additive genetics (A), permanent environment (Pe), temporary environment (t) and dam could be plotted.

Table 2. Milk yield per lactation by conventional analysis

	Number of cows		LSMEANS		
Sub-period [Days in milk]	Control	Experimental group	Control	Experimental group	p
5-100	73	59	35.9	39.2	< 0.0001
101-200	38	60	33.9	34.4	0.5630
201-300	18	31	30.2	30.9	0.5801
5-300	89	83	34.4	36.2	0.0129

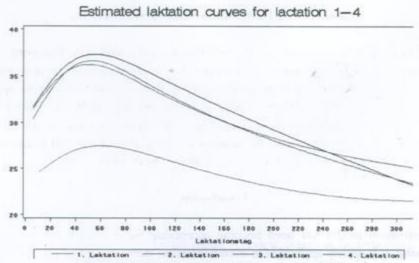
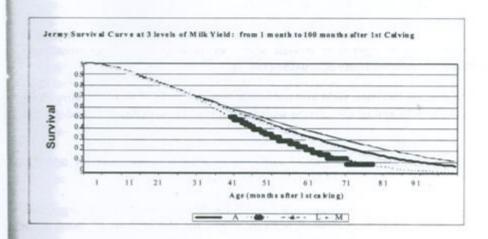


Figure 2. Estimation of lactation curve by RRM

Survival Analyses

Survival is a longitudinal trait that can be measured many times throughout an animal's life, but only the point at which an animal dies or culled is usually recorded in the data. Survival analyses are typically undertaken using a non-liner Proportional Hazard (PH) model (Schaeffer, 2003). However, Veerkamp et al., (1999) proposed that RRM could be used for survival analysis. At any given point in time an animal is either alive (1) or dead (0) (Figure 3). The survival 'curve' for an individual animal is a straight line at the value 1 from the birth until the animals culled, after which a value of 0 is assigned and continuous as a straight line to the end of the observation period. Survival curves can vary depending on the production levels and type trait scores of the individual animal. Other factors influencing the survival curve include province, year and season of birth as well as herd environment and management practices (Galbraith and Schaeffer, 2003).



Genotype by Environment Interaction Studies

A genotype by environment interaction implies that animals would rank differently in different environments. If those environments can be ordered such as by a temperature-humidity index (THI), or by elevation, or by average herd production, then a RRM could be applied with regressions on these variables rather than on time or age. RRM are useful when the environments cover a range of different conditions rather than just a few categories (Schaeffer, 2003). Ravagnolo and Misztal (2000); Brűqemann et al. (2011) used the THI to obtain different heritability and different rankings of animals at different heat stress levels.

Conclusion

Random regression model has been become acceptable for dairy cattle genetic evaluation internationally. It is widely applicable to model lactation curve using test day records, survival analysis, genetic by environment interaction studies, feed intake, and growth and fertility trait. The model accounts all environmental factors precisely and it clearly indicates individual difference along the time at which the trait is observed. Even if there is a limitation to apply the model as a means of genetic evaluation in most African countries, it is important to initiate and popularize the model and incorporate it as national genetic evaluation system.

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