Agriculture and Natural Resources 50 (2016) 64–70

Contents lists available at ScienceDirect

Agriculture and Natural Resources

journal homepage: http://www.journals.elsevier.com/agriculture-and-natural-resources/

Original article

Estimation of genetic parameters using a random regression monthly test-day model in an Ethiopian dairy cattle population

Gebregziabher Gebreyohannes,[a] Skorn Koonawootrittriron,[a,*] Mauricio A. Elzo,[b] Thanathip Suwanasopee[a]

[a] Department of Animal Science, Faculty of Agriculture, Kasetsart University, Bangkok 10900, Thailand
[b] Department of Animal Sciences, University of Florida, Gainesville, FL 32611-0910, USA

ARTICLE INFO

Article history:
Received 6 August 2014
Accepted 19 June 2015
Available online 10 February 2016

Keywords:
Milk yield
Modified incomplete gamma
Random regression
Test-day

ABSTRACT

Monthly test-day milk records (n = 50,839) from 2045 cows born from 312 sires and 1169 dams in Bako, Debre Zeit and Holetta (Ethiopia, 1977 to 2010) were used to estimate the variance components and genetic parameters for monthly test-day milk yield. Cows were Horro (H), Boran (B), Friesian (F) crossbreds, Jersey (J) crossbreds, and Simmental (S) crossbreds. Lactations were modeled with a log-transformed, modified, incomplete, gamma function. The random regression, animal repeatability model considered herd-year-test-day subclass, parity, H, B, F, J, and S cow fractions, F × B, F × H, J × B, J × H, S × B and S × H cow heterozygosities as fixed effects. Random effects were additive genetic, permanent environmental and residual. Variance components were estimated using restricted maximum likelihood procedures. Additive genetic, permanent environmental and phenotypic variances, heritabilities (0.17–0.42) and repeatabilities (0.84–0.94) for test-day milk yields increased as lactation progressed. Additive genetic, permanent environmental and phenotypic correlations were higher between adjacent than non-adjacent monthly test-days, and decreased as interval between test-days increased. The results suggested that a random regression, animal repeatability model using a modified, incomplete, gamma function would be appropriate for genetic evaluation in this multibreed population.

Introduction

Selection for milk yield in dairy cattle is generally based on the analysis of 305 d lactation records. Test-day milk yields are used to estimate 305 d lactation yield. The accuracy of 305 d yields depends on the number of test-day records, the number of days between tests and the methods of estimating 305 d yield. However, genetic evaluation in developing countries is constrained by the lack of an appropriate data recording system. The use of test-day data would offer practical solutions where there is a lack of necessary infrastructure and resources required for milk recording throughout the lactation period.

Models that use 305 d lactation milk yield do not account for the changes in environmental factors within 305 d of lactation. Test-day models, however, allow more accurate estimation of environmental effects from including the influence of a particular day of recording, account for variation in the numbers of tests recorded per animal, enable optimal use of information from all test-days (especially for lactations with long intervals from calving to the first test-day or between test-days) and greater stability of bull evaluations through accounting for genetic differences among daughters in the shape of the lactation curve and maturity rate (Swalve, 1995; Wiggans and Goddard, 1997).

Test-day records are expressions of a trait that change over time. Genetic correlations between individual test-days and 305 d milk yield ranged from 0.78 to 1.00 (Machado et al., 1999). Ptak and Schaeffer (1993) indicated that a genetic evaluation using four or more test-days yield per lactation is more accurate than from just one 305 d record. Estimated breeding values for 305 d and test-day yields and comparison of both sets of breeding values indicated only minor changes in sire ranking (Swalve, 1995). Similarly, a strong positive rank correlation was observed between the ranking of sires and cows on the basis of test-day and 305 d yield (Kaya et al., 2003; Sawalha et al., 2005).

* Corresponding author.
E-mail address: agrskk@ku.ac.th (S. Koonawootrittriron).

http://dx.doi.org/10.1016/j.anres.2015.06.002

Variance components and genetic parameters are needed for a genetic improvement program to predict selection response, to choose among breeding plans and to predict the breeding values of candidates for genetic selection. The methods of estimation of variance components and genetic parameters depend on the type of data. Random regression models are widely used for the estimation of variance components and prediction of breeding value for traits repeatedly recorded over time because they are more flexible and accurate than multiple trait models (Cobuci et al., 2005). Random regression models predict breeding values for cumulative milk yield throughout the lactation and for milk yield at any specific day of lactation in contrast to multi-trait models that only permit point predictions (Bignardi et al., 2011). The estimated genetic parameters depend on the type of regression functions utilized and the covariance structures assumed for animal additive genetic, permanent environment and residual effects in random regression models (Bignardi et al., 2011). Many different models (for example, Legendre polynomials, splines and lactation curve functions) have been proposed for test-day regression. However, it is unlikely that a single "best model" exists because local circumstances determine which effects should be included in the model. In principle, the model that maximizes genetic progress in the population should be chosen for genetic evaluation (Jensen, 2001). The objective of this study was to estimate genetic parameters for monthly test-day milk yields in an Ethiopian multibreed dairy cattle population using a random regression, animal repeatability model.

Materials and methods

Description of the study area, animals and breeding system

The study was based on monthly test-day milk data from the Bako, Debre Zeit and Holetta Research Centers, Ethiopia. Details of the research centers have been reported elsewhere (Gebreyohannes, 2013).

Data and statistical analysis

Lactation milk yields for the period 1977 to 2010 for Bako and Holetta and from 1989 to 2006 for the Debre Zeit research center were used for the study. Monthly test-day milk data were extracted from the daily records of each cow for every 30 day interval starting from the date of calving. The dataset used for this study consisted of 50,839 monthly test-day records. The data were from 2045 cows born from 312 sires and 1169 dams. Records from only parities 1 to 5 were included in the analysis. Lactations shorter than 90 d (less than three monthly test-day records) were excluded from the analysis.

Different functions can be used in regression models. To be suitable for a random regression model, a function must be linear in the parameters and should have as few parameters as possible (Jakobsen et al., 2002). The modified, incomplete, gamma function (MIG) was chosen for this study because it was found to accurately fit monthly test-day milk data and provide excellent predictions of lactation milk yields (Gebreyohannes, 2013). The MIG is represented as $y_t = ate^{-ct}$, where y_t is the monthly test-day milk yield (in kilograms) at time t (in days) after calving, and a and c are parameters of the function. The MIG function was log-transformed to a linear form ($ln(y/t) = ln(a) + (-ct)$) with the intercept equal to $ln(a)$ and the slope equal to $-c$. This log-transformed MIG function was used to model random, animal genetic and permanent environmental effects in the random regression, animal repeatability model.

The random regression, animal repeatability model included the fixed effects of year-season and parity subclasses, regression on the Horro (H), Boran (B), Friesian (F), Jersey (J), and Simmental (S) breed fraction of the cow, regression on F × B, F × H, J × B, J × H, S × B and S × H heterozygosity fractions of the cows and the animal additive genetic, permanent environmental and residual random effects. Animal additive genetic and permanent environmental effects were modeled using a log-transformed MIG function. The residual variance was assumed to be constant throughout the lactation.

The random regression animal repeatability model used here can be described using Equation (1):

$$y_{jkmt} = HTM_j + P_k + \beta DIM_t + \sum_{i=1}^{5} f(g_{im})g_{it} + \sum_{i=1}^{5} f(h_{im})h_{it} + \sum_{n=0}^{1} a_{mn}z_{mtn} + \sum_{n=0}^{1} pe_{mn}z_{mtn} + e_{jkmt} \quad (1)$$

where: y_{jkmt} represents $ln(y/t)$ of milk recorded from cow m on monthly test-day t in herd-year- test-day subclass j, and parity subclass k. The HTM_j is the fixed effect of the jth herd-year-monthly test-day subclass (j = 1 to 1017); P_k is the fixed effect of parity subclass (k = 1 to 5), and β is the regression coefficient for DIM_t, where DIM_t represents the days in milk at day t after calving (t = 30, 60, 90, 120, 150, 180, 210, 240, 270 and 300 d). The g_{im} are additive breed regression coefficients, and the h_{im} are heterosis regression coefficients. The $f(g_{im})$ is the ith breed fraction of cow m (i = 1, …, 5; B, H, F, J and S), and $f(h_{im})$ is the ith heterozygosity for cow m (i = 1, …, 6; F × B, F × H, J × B, J × H, S × B and S × H). The ith breed fraction for cow m was computed as $f(g_{im}) = 0.5(p_i^s + p_i^d)$ and the ith heterozygosity for cow m was computed as $f(h)im = p_i^s p_j^d + p_i^d p_j^s$, where p_i^s and p_i^d denote the proportion of breed i or j in the sire and dam of cow m (Dickerson, 1973; Elzo and Famula, 1985; Koch et al., 1985). The a_{mn} are the random regression coefficients for animal additive genetic effects for cow m, the pe_{mn} are the random regression coefficients for permanent environmental effects for cow m, and e_{lmtjk} is the residual associated with each test-day observation. The z_{mtn} represent the nth coefficient of the log-transformed MIG function for monthly test-day records at time t for animal m (i.e., $z_{mt0} = 1$, and $z_{mt1} = t$).

The random regression model in matrix notation can be described using Equation (2):

$$y = X\beta + Qg + Z_1 a + Z_2 pe + e \quad (2)$$

where $\boldsymbol{y}$ is the vector of $ln(y/t)$ of monthly test-day observations on day t, β is a the vector of fixed effects for herd-year-test-day subclasses (htm), parity subclasses and fixed regression of milk yield on days of lactation, g is the vector of fixed cow breed and heterosis effects, a is the vector of random regression coefficients for animal additive genetic effects, pe is the vector of random regression coefficients for permanent environmental effects, X is the matrix relating observations to fixed effects, Q is the matrix relating observations to cow breed effects (through B, H, F, J, and S breed fractions of the cows) and cow heterosis effects (through F × B, F × H, J × B, J × H, S × B and S × H heterozygosity fractions of the cows). Matrices Z_1 and Z_2 are incidence matrices that relate observations to random regression coefficients for the animal and permanent environmental effects, respectively; and $\boldsymbol{e}$ is the vector of residuals. The expected value of y is $X\beta + Qg$. The expected values of random animal additive genetic, permanent environmental and residual effects is zero. The variance of the vector of random regression coefficients for animal additive genetic effects is $G \otimes A$, the variance of vector of random regression coefficients for permanent environmental effects is $P \otimes I$ and the variance of the vector of residuals is $R = I\sigma_e^2$, where G and P are 2 × 2 matrices of variances and covariances between random regression coefficients for animal additive genetic effects and for permanent environmental effects,

respectively, A is the numerator relationship matrix, I is an identity matrix, $\otimes$ is a Kronecker product and σ_e^2 is the residual variance common to all monthly test-days. Variance components for additive genetic and permanent environmental random regression coefficients and residual variances were estimated using an Average Information Restricted Maximum Likelihood (AI-REML) procedure of the ASREML software (Gilmour et al., 2009).

The additive genetic variance for *ln(y/t)* at test-day *i* ($\sigma^2_{a(i)}$) was computed as $\sigma^2_{a(i)} = t_i G t_i'$ and the additive genetic covariance between *ln(y/t)* at test-days *i* and *j* $\sigma_{a(i,j)}$ as $\sigma_{a(i,j)} = t_i G t_j'$ Similarly, the permanent environmental variance for *ln(y/t)* at test-day *i*($\sigma^2_{pe(i)}$) was computed as $\sigma^2_{pe(i)} = t_i P t_t'$, and the permanent environmental covariance between *ln(y/t)* at test-day *i* and *j* ($\sigma_{pe(i,j)}$) was computed as $\sigma_{pc(i,j)} = t_i P t_j'$, where t_i is the *i*th row vector of the matrix of monthly test-day coefficients of the log-transformed MIG function (T). The size of matrix T was 10 × 2, where 10 = number of test-days considered, and 2 = the number of parameters linear log-transformed MIG function (i.e., intercept and slope). The *i*th row vector of T had two values: 1 and t, where t = 30, 60, 90, 120, 150, 180, 210, 240, 270 and 300. Heritabilities (h_i^2) and repeatabilities (r_i) for *ln(y/t)* at test-day ***i*** and additive genetic correlations ($r_{a(i,j)}$) between *ln(y/t)* at test-days *i* and *j* were calculated using Equations (3)–(5):

$$h_i^2 = \frac{\sigma^2_{a(i)}}{\sigma^2_{a(i)} + \sigma^2_{pe(i)} + \sigma^2_e} \quad (3)$$

$$r_i = \frac{\sigma^2_{a(i)} + \sigma^2_{pe(i)}}{\sigma^2_{a(i)} + \sigma^2_{pe(i)} + \sigma^2_e} \quad (4)$$

$$r_{a(i,j)} = \frac{\sigma_{a(i,j)}}{\sqrt{\sigma^2_{a(i)} \times \sigma^2_{a(j)}}} \quad (5)$$

Permanent environmental and phenotypic correlations were computed using expressions similar to the one for additive, genetic correlations but involving permanent environmental and phenotypic variances and covariances, respectively. Computations for estimates of additive genetic, permanent environmental and phenotypic variances and covariances as well as heritabilities and repeatabilities were carried out using PROC IML of the Statistical Analysis System (SAS, 2003).

Results and discussion

Additive genetic, permanent environment, and phenotypic variances

A log-transformed MIG function was used to model the lactation trajectory for both the random animal additive genetic and permanent environmental effects. Varona et al. (1998) suggested that a desirable feature of a prediction equation for lactation curves would be a biological interpretation of the parameters of the curve. The log-transformed MIG function has two parameters (intercept and slope), is linear, simple to fit and the parameters have biological interpretations related to the initial milk yield and the rate of decline from peak yield. Although more complicated models are potentially more accurate, parameters for these models would be harder to estimate (Strabel and Misztal, 1999).

The covariance between the regression coefficients (intercept and slope) for animal additive genetic effects (1.38 $(\ln(kg/d))^2$) was higher than for permanent environmental effects (1.11 $(\ln(kg/d))^2$) while the variances for the intercept (4.314 vs. 6.879 $(\ln(kg/d))^2$) and slope (0.571 vs. 0.817 $(\ln(kg/d))^2$) for animal additive genetic effects were lower than the corresponding variances for permanent environmental effects. The residual variance was 0.138 $(\ln(kg/d))^2$. The genetic correlation between the intercept (related to the initial milk yield) and slope (related to the rate of drop in milk yield after peak yield) was positive (0.88). The correlation between the intercept and the slope for animal additive genetic effects (0.88) was higher than the correlation for permanent environmental effects (0.47). Both correlations suggested that cows that started their lactation at a higher level had a faster rate of decline in milk yield after the peak of lactation (that is, lower persistency of lactation). A similar genetic correlation (0.48) was found between parameters *a* (parameter related to the initial milk yield) and *c* (parameter related to the rate of decline from the peak) of the incomplete gamma function in Spanish Friesian dairy cattle (Varona et al., 1998). Conversely, Cobuci et al. (2005) found a negative correlation (−0.40) between the parameters for the initial milk yield and the rate of decrease in the milk yield after the peak of the Wilmink function in first-parity Holsteins indicating that cows with lower peak yields tended to have lower declining rates of production (that is, higher persistency of lactation).

Animal additive genetic, permanent environmental and phenotypic variances and covariances were estimated for all log-transformed monthly test-day milk yields (thatis, *ln(y/t)*). Animal additive genetic variances (0.14–1.00 $(\ln(kg/d))^2$; Table 1), permanent environmental variances (0.54–1.23 $(\ln(kg/d))^2$; Table 2) and phenotypic variances (0.82–2.37 $(\ln(kg/d))^2$; Table 3) increased as lactation progressed. Thus, the last monthly test-day (300 d) had the highest estimates of additive genetic, permanent environmental and phenotypic variances whereas the first test-day (30 d) had the lowest estimates. Permanent environmental variances (Table 2) were larger than additive genetic variances (Table 1) for all monthly test-days indicating that permanent environmental effects had a higher influence on the variation of milk yields among cows in this multibreed population than additive genetic effects.

Animal additive genetic covariances (0.16–0.92 $(\ln(kg/d))^2$; Table 1), permanent environmental covariances (0.49–1.15 $(\ln(kg/d))^2$; Table 2) and phenotypic covariances (0.69–2.07 $(\ln(kg/d))^2$; Table 3) between different log-transformed monthly test-day milk yields increased as the interval between test-days increased, except for the permanent environmental covariance between the first test-day and the other test-days. The higher phenotypic variances and covariances in the later test-days could be partly attributed to breed variation in lactation length and persistency. This population was composed of cows from different breeds that varied in their genetic potential for daily milk yield, lactation milk yield, and lactation length. The Friesian crossbred, Jersey crossbred and Simmental crossbred cows had higher values for daily milk yield and lactation milk yield, and longer lactation lengths than the Horro and Boran. In addition, Horro and Boran cows had lower persistency than crossbred cows which resulted in higher variability of phenotypic and genotypic variances and covariances during the later test-days. The decrease in the number of cows with records as lactation progressed due to dry off could also have contributed to higher variances during the later test-days.

Different results have been reported (Strabel et al., 2005; Zavadilova et al., 2005; El Faro et al., 2008) in relation to the trend in the animal additive genetic, permanent environmental and phenotypic variances. Higher genetic and permanent environmental variances for particular days in milk at the beginning and at the end of lactation were reported for Czech Holstein cattle (Zavadilova et al., 2005) and Polish Black and White cattle (Strabel et al., 2005). Conversely, higher phenotypic, animal additive genetic, permanent environmental and residual variances at the beginning of the lactation that decreased thereafter were reported by El Faro et al. (2008).

Table 1
Additive genetic variances (bold diagonal; $(\ln(kg/d))^2$) and covariances (below diagonal; $(\ln(kg/d))^2$) for log-transformed, monthly test-day, milk yields (*ln(y/t)*).

Monthly test-day	Monthly test-day									
	30	60	90	120	150	180	210	240	270	300
30	**0.14**									
60	0.16	**0.18**								
90	0.17	0.20	**0.23**							
120	0.19	0.23	0.27	**0.30**						
150	0.21	0.25	0.30	0.34	**0.38**					
180	0.22	0.28	0.33	0.38	0.43	**0.48**				
210	0.24	0.30	0.36	0.42	0.47	0.53	**0.59**			
240	0.26	0.32	0.39	0.45	0.52	0.58	0.65	**0.71**		
270	0.27	0.35	0.42	0.49	0.56	0.63	0.71	0.78	**0.85**	
300	0.29	0.37	0.45	0.53	0.61	0.69	0.76	0.84	0.92	**1.00**

Table 2
Permanent environmental variances (bold diagonal; $(\ln(kg/d))^2$) and covariances (below diagonal; $(\ln(kg/d))^2$) for log-transformed, monthly test-day, milk yields (*ln(y/t)*).

Monthly test-day	Monthly test-day									
	30	60	90	120	150	180	210	240	270	300
30	**0.54**									
60	0.54	**0.54**								
90	0.53	0.54	**0.56**							
120	0.52	0.55	0.57	**0.59**						
150	0.52	0.55	0.58	0.62	**0.65**					
180	0.51	0.55	0.60	0.64	0.68	**0.73**				
210	0.50	0.56	0.61	0.66	0.72	0.77	**0.82**			
240	0.50	0.56	0.63	0.69	0.75	0.81	0.88	**0.94**		
270	0.49	0.57	0.64	0.71	0.78	0.86	0.93	1.00	**1.08**	
300	0.49	0.57	0.65	0.74	0.82	0.90	0.98	1.07	1.15	**1.23**

Table 3
Phenotypic variances (bold diagonal; $(\ln(kg/d))^2$) and covariances (below diagonal; $(\ln(kg/d))^2$) for log-transformed, monthly test-day, milk yields (*ln(y/t)*).

Monthly test-day	Monthly test-day									
	30	60	90	120	150	180	210	240	270	300
30	**0.82**									
60	0.69	**0.86**								
90	0.70	0.75	**0.93**							
120	0.71	0.77	0.84	**1.03**						
150	0.72	0.80	0.88	0.96	**1.17**					
180	0.74	0.83	0.92	1.02	1.11	**1.35**				
210	0.75	0.86	0.97	1.08	1.19	1.30	**1.55**			
240	0.76	0.88	1.01	1.14	1.27	1.40	1.53	**1.79**		
270	0.77	0.91	1.06	1.20	1.35	1.49	1.64	1.78	**2.06**	
300	0.78	0.94	1.10	1.26	1.42	1.59	1.75	1.91	2.07	**2.37**

The lower variance at the beginning of lactation (Fig. 1) could be partly attributed to the variety of lactation curve functions used for random regression models. The log-transformed MIG function here, the incomplete gamma function in Varona et al. (1998), and the Wilmink function in Cobuci et al. (2005) resulted in different variances and covariances. Similarly, a comparison made between a random regression model with both random and fixed regressions fitted by Legendre polynomials and linear splines for production traits in Canadian Holstein cows resulted in lower estimates of variances at the extremes of the lactation for models with splines than with Legendre polynomials (Bohmanova et al., 2008). The stage that is most difficult to fit in a lactation curve is the period from calving to peak. After the peak yield, the curve is almost linear requiring only a rate of drop from peak yield to the end of lactation. The higher genetic, permanent environmental and phenotypic variances at the beginning of lactation reported in various studies (Cobuci et al., 2005; Strabel et al., 2005; Zavadilova et al., 2005; El Faro et al., 2008) could be attributed to problems in goodness of fit of functions during the early stages of a lactation. Here, the

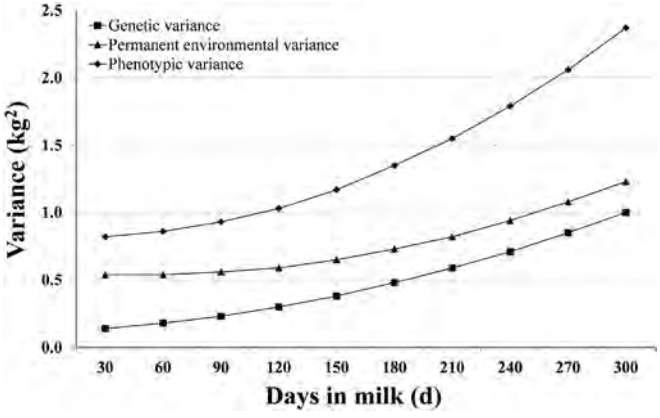

Fig. 1. Additive genetic, permanent environmental and phenotypic variances for log-transformed monthly test-day, milk yields (*ln(y/t)*).

population had shorter days to peak and the MIG function provided the best fit to the data which resulted in lower variances at the beginning of the lactation.

The residual variance was assumed to be constant (0.137 kg^2) during lactation. In agreement with the present study, Cobuci et al. (2005) also considered a constant residual variance. Use of a constant variance simplified the model. Olori et al. (1999) indicated that when the residual variance was assumed to be constant, its estimate was approximately the mean of the estimates obtained by allowing the residual variance to vary. However, Bignardi et al. (2011) reported that models containing a homogeneous residual variance provided the worst fit irrespective of the parametric functions used to model random effects. Both studies (Olori et al., 1999; Bignardi et al., 2011) suggested the need for a heterogeneous variance structure for the residual effect because the residual variance tended to differ during lactation. Thus, although the heritabilities and repeatabilities obtained here were in agreement with other studies in the literature, future research in Ethiopia should consider random regression models with heterogeneous residual variances.

Heritabilities, repeatabilities and genetic, permanent environmental and phenotypic correlations

Heritability estimates for *ln(y/t)* ranged from 0.17 for the first test-day recorded 30-d after calving to 0.42 for the last test-day recorded 300 d after calving (Table 4, Fig. 2). Similar ranges of heritability estimates for test-day milk yields using random regression models were obtained in Czech Holstein model (0.13–0.52; Zavadilova et al., 2005) and England (0.31–0.51; Olori et al., 1999). However, the heritabilities estimated here were higher than those reported for first lactation (0.14–0.19) and second lactation (0.10–0.16) Polish Black and White cattle (Strabel and Misztal, 1999).

Considerable variation in heritability estimates have been reported in the literature due to differences in populations, methods of analysis and especially how the trait was defined (Machado et al., 1999). The values of genetic parameters estimated with random regression models are influenced by the regression functions and the covariance structure of animal additive genetic, permanent environmental and residual effects (Bignardi et al., 2011). The higher heritability estimates for *ln(y/t)* (0.17–0.42) obtained here could be partly attributed to a high degree of genetic variation in this multibreed population. Genetic variances were expected to be higher in a mixed population of Boran, Horro, Friesian crossbreds, Jersey crossbreds and Simmental crossbreds than in a single-breed population. The longer lactation lengths of Friesian crossbred, Jersey crossbreed and Simmental crossbred cows (Gebreyohannes et al., 2012) relative to Boran and Horro cows may have increased the genetic variation for monthly test-day milk yields in this population resulting in higher heritability estimates throughout lactation.

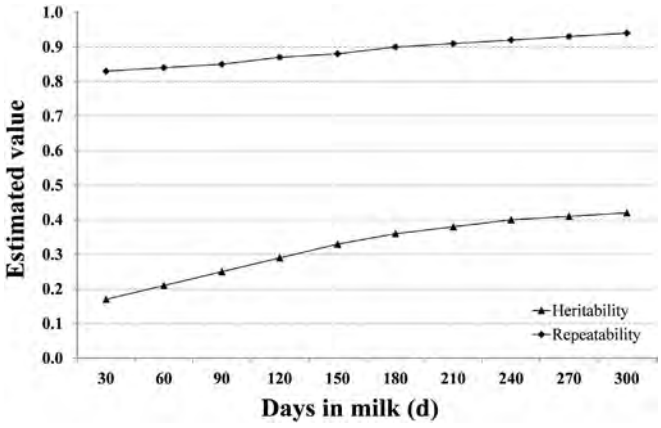

Fig. 2. Heritability and repeatability estimates of for log-transformed monthly test-day, milk yields (*ln(y/t)*).

The monthly test-day milk yield is defined as the milk yield recorded at monthly intervals starting soon after calving. However, research studies have used different test-day intervals. For example, El Faro et al. (2008) used weekly test-days whereas Gengler et al. (1999) defined four lactation stages of 75 d each, starting on day 6 and the test-day that was nearest to the center of the lactation stage (d 43, 118, 193, or 268) was retained. These variations in the definition of test-day resulted in heritability estimates ranging from 0.09 (12th week) to 0.32 (42nd week) with higher estimates at the end of lactation for native Brazilian Caracu heifers (El Faro et al. 2008) and mean heritability estimates of 0.19 for Holstein Friesian cows (Gengler et al., 1999).

The 30 d uniform test-day interval in the present study resulted in heritability estimates for *ln(y/t)* ranging from 0.17 to 0.42. These heritabilities suggested that this multibreed population would be able to be genetically improved by selection. Swalve (1995) noted that yields defined as the average yield in a standardized 30 d interval resulted in higher estimates of heritability than for a non-standardized interval due to lower residual variance estimates. The use of standardized intervals can remove some of the problems that arise when different intervals between test-days are used, especially between calving and the first test-day (Swalve, 1995).

Although the trend in heritability estimates for *ln(y/t)* showed a steady increase from the first to the last test-day (Table 4; Fig. 1), three different trends over test-days have been reported in the literature, with an increase in heritability with an increase in test-day (Gengler et al., 1999; Cubuci et al., 2005; Zavadilova et al., 2005; Guzzo et al., 2009), lower heritability at the beginning and end of lactation and higher in the middle of the lactation (Takma and Akbas, 2007; Nazari et al., 2010) and lower heritability at the peak of lactation, increasing toward the middle of the second part

Table 4
Heritabilities (bold diagonal), genetic correlations (above diagonal) and phenotypic correlations (below diagonal) for monthly test-day, milk yields.

Monthly test-day	Monthly test-day									
	30	60	90	120	150	180	210	240	270	300
30	**0.17**	0.99	0.96	0.92	0.89	0.86	0.84	0.81	0.79	0.78
60	0.83	**0.21**	0.99	0.97	0.95	0.93	0.92	0.90	0.88	0.87
90	0.81	0.84	**0.25**	1.00	0.98	0.97	0.96	0.95	0.94	0.93
120	0.78	0.82	0.85	**0.29**	1.00	0.99	0.98	0.97	0.97	0.96
150	0.74	0.80	0.84	0.87	**0.33**	1.00	0.99	0.99	0.98	0.98
180	0.70	0.77	0.83	0.86	0.89	**0.36**	1.00	1.00	0.99	0.99
210	0.66	0.74	0.81	0.85	0.88	0.90	**0.38**	1.00	1.00	0.99
240	0.62	0.71	0.78	0.84	0.88	0.90	0.91	**0.40**	1.00	1.00
270	0.59	0.69	0.76	0.82	0.87	0.89	0.91	0.93	**0.41**	1.00
300	0.56	0.66	0.74	0.81	0.85	0.89	0.91	0.93	0.94	**0.42**

Table 5
Repeatabilities (bold diagonal) and permanent environmental correlations (below diagonal) for monthly test-day, milk yields.

Monthly test-day	Monthly test-day									
	30	60	90	120	150	180	210	240	270	300
30	**0.84**									
60	0.99	**0.85**								
90	0.96	0.99	**0.85**							
120	0.92	0.97	0.99	**0.87**						
150	0.87	0.93	0.97	0.99	**0.88**					
180	0.81	0.89	0.94	0.98	0.99	**0.90**				
210	0.76	0.84	0.90	0.95	0.98	1.00	**0.91**			
240	0.70	0.79	0.86	0.92	0.96	0.98	1.00	**0.92**		
270	0.65	0.74	0.83	0.89	0.94	0.97	0.99	1.00	**0.93**	
300	0.60	0.70	0.79	0.86	0.91	0.95	0.98	0.99	1.00	**0.94**

of the lactation, and then dropping to rise again at the end (Strabel and Misztal, 1999). Nazari et al. (2010) in their study of first lactation Najdi cattle using test-day milk data obtained a lower heritability estimate for milk yield at the beginning (0.15) of the lactation and increased towards the middle of the lactation, reached a maximum (0.34) in the fifth month of lactation and then decreased toward the end of the lactation. Strabel and Misztal (1999) reported heritabilities ranging from 0.13 to 0.17 for most of the lactation, but they approached 0.20 at the end of lactation from a single-parity model. Cobuci et al. (2005) reported an increase in heritability estimates for test-day milk yields (0.14–0.31) as the first lactation progressed in Holsteins. However, Guzzo et al. (2009) reported heritability values ranging from 0.15 to 0.34 with lower values at the beginning and end of the lactation in the Rendena breed. The lower heritability estimated during the first test-day in the current study agreed with the reports of Gengler et al. (1999) and Guzzo et al. (2009), but the higher heritability at the last test-day contradicted the report of Machado et al. (1999) who found higher heritabilities during mid-lactation (0.24–0.32). Similarly, Takma and Akbas (2007) reported higher heritability estimates for test-day milk yields in the middle of the lactation (0.07–0.32).

Repeatabilities for $ln(y/t)$ showed a trend similar to heritabilities for $ln(y/t)$ with a slight increase with the advance of lactation, primarily due to increases in both the animal additive genetic and permanent environmental variances (Table 5; Fig. 2). El Faro et al. (2008) attributed the higher estimates of heritability at the beginning and toward the end of the lactation to difficulties in modeling the variances at the extremes of the lactation partly due to the biological processes that occur at the beginning of lactation and the smaller number of records at the end. For Zebu and tropical native breeds, both reasons can be even more important. In general, these animals have not been as intensively selected for milk production as Holsteins and population sizes are smaller. In addition, it is usually necessary to keep the calf with the dam during milking and short lactations are frequent.

Additive genetic correlations between $ln(y/t)$ in consecutive test-days ranged from 0.78 to 1.00 and decreased as intervals between test-days increased. The lowest genetic correlation (0.78) was observed between the first and last test-day (Table 5). Higher additive genetic correlations for milk yields between consecutive test-days and lower as test-day intervals increased were also found in cattle populations in Turkey (Takma and Akbas, 2007), New Zealand (Vanderick et al., 2009), and Brazil (Bignardi et al., 2011).

Permanent environmental correlations (0.60–1.00; Table 5) and phenotypic correlations (0.56–94; Table 4, below diagonal) were consistently equal or lower than genetic correlations (0.78–1.00; Table 4, above diagonal) for $ln(y/t)$ across all test-days. However, genetic, permanent environmental and phenotypic correlations for $ln(y/t)$ showed similar trends throughout the lactation. Correlations between $ln(y/t)$ from adjacent test-days were higher than from non-adjacent test-days (Tables 4 and 5), in agreement with several studies (Olori et al., 1999; Cobuci et al., 2005; Zavadilova et al., 2005; Takma and Akbas, 2007). Also in agreement with these studies, the high, positive genetic correlations observed in this population, even at the extremes of the lactation trajectory, suggested that selection for increased milk yield in early lactation would have a positive effect on yield in late lactation. However, other researchers (El Faro et al., 2008; Bignardi et al., 2011) reported negative genetic correlations between the initial and final test-days for some of the models they compared and attributed this to the difficulty of modeling the initial test-days milk yields of lactation.

This research showed that a random regression, animal repeatability model using a log-transformed, modified, incomplete gamma function to account for random additive genetic and permanent environment effects yielded reasonable estimates of heritabilities, repeatabilities, genetic, permanent environmental and phenotypic correlations. This random regression, animal repeatability model could be used as an initial model for the implementation of a genetic improvement program in this multibreed Ethiopian dairy cattle population. Future research in Ethiopia should consider records from different parities as multiple traits and account for the heterogeneity of residual variances and covariances.

Conflict of Interest

No conflicts of interest influenced this research.

Acknowledgments

The authors would like to acknowledge the Rural Capacity Building Project of the Ethiopian Ministry of Agriculture and Rural Development for the financial support and the Tigray Agricultural Research Institute for the study leave offered to the first author. The study is based on data collected in the Holetta Research Center of the Ethiopian Institute of Agriculture Research, the Bako Research Center of the Oromia Agricultural Research Institute and the Debre Zeit Research Station of the International Livestock Research Institute (ILRI). The authors are grateful to all institutions.

References

Bignardi, A.B., El Faro, L., Torres Junior, R.A.A., Cardoso, V.L., Machado, P.F., Albuquerque, L.G. 2011. Random regression models using different functions to model test-day milk yield of Brazilian Holstein cows. Genet. Mol. Res. 10: 3565–3575.

Bohmanova, J., Miglior, F., Jamrozik, J., Misztal, I., Sullivan, P.G. 2008. Comparison of random regression models with Legendre polynomials and linear splines for production traits and somatic cell score of Canadian Holstein cows. J. Dairy Sci. 91: 3627–3638.

Cobuci, J.R., Euclydes, R.F., Lopes, P.S., Costa, C.N., Torres, R.de A., Pereira, C.S. 2005. Estimation of genetic parameters for test-day milk yield in Holstein cows using a random regression model. Genet. Mol. Biol. 28: 75–83.

Dickerson, G. 1973. Inbreeding and heterosis in animals. In: Proceeding of Animal Breeding and Genetics Symposium in Honor of Dr. J. L. Lush. Champaign, IL, USA, pp. 54–77.
El Faro, L., Cardoso, V.L., de Albuquerque, L.G. 2008. Variance component estimates applying random regression models for test-day milk yield in Caracu heifers (*Bos taurus Artiodactyla, Bovidae*). Genet. Mol. Biol. 31: 665–673.
Elzo, M.A., Famula, T.R. 1985. Multibreed sire evaluation procedures within a country. J. Anim. Sci. 60: 942–952.
Gebreyohannes, G., Koonawootrittriron, S., Elzo, M.A., Suwanasopee, T. 2012. Impact of crossbreeding on production and reproduction traits in an Ethiopian dairy cattle population. In: Proceedings of the 15th AAAP Animal Science Congress. Thammasat University, Bangkok, Thailand.
Gebreyohannes, G. 2013. Fitness of lactation curve functions to daily and monthly test-day milk data in an Ethiopian dairy cattle population. Kasetsart J. Nat. Sci. 47: 60–73.
Gengler, N., Tijani, A., Wiggans, G.R., Van Tassell, C.P., Philpot, J.C. 1999. Estimation of (co)variances of test day yields for first lactation Holsteins in the United States. J. Dairy Sci. 82: 225.e1–e14.
Gilmour, A.R., Cullis, B.R., Welham, S.J., Thompson, R. 2009. ASREML Discovery Reference Manual. University of Adelaide, Adelaide, SA, Australia.
Guzzo, N., Sartori, C., Mantovani, R. 2009. Test day-milk yields variance component estimation using repeatability or random regression models in the Rendena breed. Ital. J. Anim. Sci. 8: 71–73.
Jakobsen, J.H., Madsen, P., Jensen, J., Pedersen, J., Christensen, L.G., Sorensen, D.A. 2002. Genetic parameters for milk production and persistency for Danish Holsteins estimated in random regression models using REML. J. Dairy Sci. 85: 1607–1616.
Jensen, J. 2001. Genetic evaluation of dairy cattle using test-day models. J. Dairy Sci. 84: 2803–2812.
Kaya, I., Akbas, Y., Uzmay, C. 2003. Estimation of breeding values for dairy cattle using test-day milk yields. Turk. J. Vet. Anim. Sci. 27: 459–464.
Koch, R.M., Dickerson, G.E., Cundiff, L.V., Gregory, K.E. 1985. Heterosis retained in advanced generations of crosses among Angus and Hereford cattle. J. Anim. Sci. 60: 1117–1132.
Machado, S.G., Freitas, M.A.R., Gadini, C.H. 1999. Genetic parameters of test day milk yields of Holstein cows. Genet. Mol. Biol. 22: 383–386.
Nazari, M., Nassiri, M.T.B., Fayazi, J., Tabatabaei, S. 2010. Estimation of breeding values of Najdi cattle breed using random regression model. J. Anim. Vet. Adv. 9: 726–729.
Olori, V.E., Hill, W.G., McGuirk, B.J., Brotherstone, S. 1999. Estimating variance components for test day milk records by restricted maximum likelihood with a random regression animal model. Livest. Prod. Sci. 61: 53–63.
Ptak, E., Schaeffer, L.R. 1993. Use of test-day yields for genetic evaluation of dairy sires and cows. Livest. Prod. Sci. 34: 23–35.
SAS 2003. SAS OnlineDoc 9.1.3. SAS Institute Inc, Cary, NC, USA.
Sawalha, R.M., Keown, J.F., Kachman, S.D., VanVleck, L.D. 2005. Genetic evaluation of dairy cattle with test-day models with autoregressive covariance structures and with a 305-day model. J. Dairy Sci. 88: 3346–3353.
Strabel, T., Misztal, I. 1999. Genetic parameters for first and second lactation milk yields of polish black and white cattle with random regression test-day models. J. Dairy Sci. 82: 2805–2810.
Strabel, T., Szyda, J., Ptak, E., Jamrozik, J. 2005. Comparison of random regression test-day models for Polish black and white cattle. J. Dairy Sci. 88: 3688–3699.
Swalve, H.H. 1995. The effect of test day models on the estimation of genetic parameters and breeding values for dairy yield traits. J. Dairy Sci. 78: 929–938.
Takma, C., Akbas, Y. 2007. Estimates of genetic parameters for test day milk yields of a Holstein Friesian herd in Turkey with random regression models. Arch. Tierz 50: 327–336.
Vanderick, S., Harris, B.L., Pryce, J.E., Gengler, N. 2009. Estimation of test-day model (co)variance components across breeds using New Zealand dairy cattle data. J. Dairy Sci. 92: 1240–1252.
Varona, L., Moreno, C., Cortes, L.A.G., Altarriba, J. 1998. Bayesian analysis of Wood's lactation curve for Spanish dairy cows. J. Dairy Sci. 81: 1469–1478.
Wiggans, G.R., Goddard, M.E. 1997. A computationally feasible test-day model for genetic evaluation of yield traits in the United States. J. Dairy Sci. 80: 1795–1800.
Zavadilova, L., Jamrozik, J., Schaeffer, L.R. 2005. Genetic parameters for test-day model with random regressions for production traits of Czech Holstein cattle. Czech J. Anim. Sci. 50: 142–154.