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Genetic Analysis of Wood's Lactation Curve for Iranian Holstein Heifers

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Abstract: Genetic aspects of the lactation curve of Iranian Holstein heifers were studied with the use of Wood's incomplete gamma function ($y_t = at^b(\exp)^{-ct}$). Data comprised 179,460 monthly test day milk records from 17,946 Iranian Holstein dairy heifers calving between 1986 and 2001 and distributed in 287 herds. Wood's incomplete gamma function parameters (a, b and c) were initially estimated for individual cows using SAS programme and subsequently along with some production characteristics including peak time (b/c), peak yield ($a(b/c)^b(\exp)^{-b}$), persistency $-(b+1)\text{Log}_e c$ and 305 day lactation milk yield were subjected to a multivariate Animal Model to estimate genetic parameters of seven traits using MTC programme. Based on the results, it was revealed that heritability estimates for the parameters of Wood's incomplete gamma function (0.1, 0.03 and 0.05 for a, b and c, respectively), peak time (0.1) and persistency (0.08) were low indicating that these traits were substantially influenced by the environmental factors and as a result additive genetic variation between animals for these traits was not remarkable suggesting that direct selection may not meaningfully change the shape of the lactation curve. In this study, the heritability estimates of peak yield (0.28) and 305 day milk yield (0.29) were found to be approximately the same.

Key words: Lactation curve, wood's incomplete gamma function, Iranian holsteins

INTRODUCTION

The production of milk and its components varies during different months of lactation. Moreover, milk production traits follow a curvilinear pattern over the course of lactation. The knowledge of the lactation curve can provide a worthwhile information source about the pattern of milk production traits which in turn would be used for herd breeding and management decisions (Perochon *et al.*, 1996; Val-Arreola *et al.*, 2004; Lin and Togashi, 2005; Macciotta *et al.*, 2005). Over the past three decades, many studies have been undertaken to apply different mathematical models to obtain more accurate prediction of the shape of the lactation curve. The incomplete gamma function has been proposed by Wood (1967) to model the lactation curve of milk. The parameters of Wood's incomplete gamma function are usually estimated by least squares technique using a logarithmic transformation of the function (Tekerli *et al.*, 2000; Macciotta *et al.*, 2005) or a non-linear regression (Kellogg *et al.*, 1977; Congleton and Everett, 1980a). Weighted regression was also proposed as an alternative procedure to non-linear regression for estimating the lactation curve parameters of Wood's incomplete gamma function (Cobby and Le Du, 1978). Other research workers have also used different non-linear functions to model lactation curve and estimate corresponding parameters

(Ali and Schaeffer, 1987; Morant and Gnanasakthy, 1989; Ramirez *et al.*, 1994; Castillo *et al.*, 2002; Macciotta *et al.*, 2005). Grossman *et al.* (1986) extended the incomplete gamma function by including sine and cosine terms to take account of seasonal variations other than season of calving. Batra (1986) and Batra *et al.* (1987) compared this extended function to the inverse polynomial function and concluded that a better fit can be provided by the inverse polynomial function. Grossman and Koops (1988) used a multiphasic non-linear function in the analysis of lactation curves and concluded that the diphasic function has smaller, more symmetric and less correlated residuals than the incomplete gamma function. Nelder (1966) proposed the inverse quadratic polynomial function to model lactation curve. This function is $y_t = t/(a+bt+ct^2)$ or alternatively $y_t^{-1} = a/t+b+ct^2$ where t is days in milk and a, b and c are the lactation parameters to be estimated. Also, two non-linear functions proposed by Wilmink (1987), Ali and Schaeffer (1987) are $y_t = a+b(\exp)^{-0.05t}+ct$ and $y_t = a+b(t/305)+c(t/305)^2+d(\log 305/t)+e(\log 305/t)^2$, respectively. These functions have been also widely used by many research workers in phenotypic (Dedkova and Nemkova, 2003) and genetic (Jamrozik and Schaeffer, 1997; Jamrozik *et al.*, 1997; Kaya *et al.*, 2003) evaluation based on test day models to take account of the shape of the lactation curve in dairy cows. Pollott (2000) proposed a biological approach (based on the processes occurring

during pregnancy and lactation in mammary gland) to analysis lactation curve of milk yield using a 7 parameter non-linear function which could be over-parametrised when monthly test day records are used. As pointed out by Olori *et al.* (1999) the effectiveness of mathematical models is mainly based on how well they can predict daily yield with lower errors whilst taking into account factors affecting the lactation curve. Other criteria for the selection of optimal models could be based on the mean absolute errors of prediction and variances of the errors (Scott *et al.*, 1996).

It has also been well documented that the lactation curve is influenced by environmental factors such as herd, year of calving, parity, age of calving and season of calving (Auran, 1973, 1974; Schaeffer and Burnside, 1976; Wood, 1976; Congleton and Everett, 1980b; Danell, 1982; Grossman *et al.*, 1986; Keown *et al.*, 1986; Tekerli *et al.*, 2000). As described by many research workers e.g., Schaeffer and Burnside (1976) the shape of lactation is largely influenced by herd management. The cows that are raised in higher yielding herds have higher peak production and more persistency when compared with low herd production cows (Keown *et al.*, 1986). The lactation curve is also influenced by seasonal variations (Castillo *et al.*, 2002). For instance, the cows calving in late spring or in the beginning of summer have a lactation curve which reaches a lower peak level than winter calvers (Wood, 1969; Rao and Sundaresan, 1979; Poso *et al.*, 1996). Other than environmental factors, the shape of the lactation curve is also affected by genetic variation among animals.

As pointed out by Lin and Togashi (2005), geneticists focus on modeling the individual genetic curves and estimating genetic parameters of the lactation curves, to select for lactation yields or persistency. The main purpose of the present research was to analyse genetic aspects of the lactation curve for Iranian Holstein heifers based on application of Wood's incomplete gamma function with the use of a multivariate Animal Model.

MATERIALS AND METHODS

The Animal Breeding Centre of Iran provided the raw data used in this research. In the present study an initial data set comprised of 457,576 first lactation monthly test day milk records. The data was first edited based on the number of monthly test days and interval between consecutive test days for individual cows (trice a day milking). The interval between consecutive test days was set up to be maximum 60 days. Furthermore, from computational point of view, only cows with complete

first lactation which had 10 monthly test day records were utilized to obtain a better estimation of the lactation curve parameters for individual cows. The edited data set consisted of 179,460 monthly test day milk yields belonging to 17,946 first lactations of Iranian Holstein heifers in 287 herds and calved from 1986 to 2001. Some descriptive statistics of the data are presented in Table 1.

The current milk recording scheme in Iran is generally based upon monthly supervising of the dairy herds. Although daily weighing is the most appropriate method of milk recording (in particular to calculate total lactation yield), this method of recording is highly time consuming and costly especially when the size of dairy herds is large (Wood, 1974). For this reason, in many countries each test day record is taken regularly at monthly intervals. In Fig. 1, the shape of the lactation curve for the Iranian heifers is given. As shown in the figure, average daily milk yield increased from the beginning of lactation towards peak time and afterwards it decreased gradually towards the end of lactation. The trajectory indicates that milk yield of a cow changes during the course of the lactation.

To describe the lactation curve and associated production characteristics, Wood's incomplete gamma function was applied in this study. This function, which has been widely used by many researchers (Kellogg *et al.*, 1977; Cobby and Le Du, 1978; Shanks *et al.*, 1981; Ferris *et al.*, 1985; Batra *et al.*, 1987; Gama *et al.*, 1994; Scott *et al.*, 1996; Varona *et al.*, 1998; Tozer and Huffaker, 1999; Rekaya *et al.*, 2000; Val-Arreola *et al.*, 2004;

Table 1: Some descriptive statistics of data set

Month of lactation	Days in milk (d)			Daily milk yield (kg)		
	Mean	SD	CV (%)	Mean	SD	CV (%)
1	14.01	6.737	48.08	23.69	5.819	24.56
2	44.45	6.595	14.83	25.96	5.240	20.18
3	74.72	6.817	9.12	28.24	5.611	19.86
4	105.17	6.590	6.26	27.88	5.710	20.48
5	135.47	6.819	5.03	27.12	5.715	21.07
6	165.93	6.620	3.98	26.28	5.710	21.72
7	196.23	6.843	3.48	25.41	5.676	22.33
8	226.70	6.653	2.93	24.53	5.620	22.91
9	256.99	6.894	2.68	23.48	5.552	23.64
10	287.42	6.722	2.33	22.15	5.576	25.17

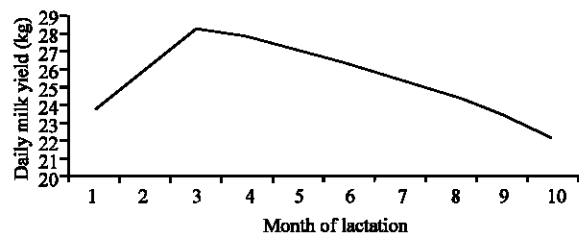


Fig. 1: The phenotypic shape of the lactation curve

Macciotta *et al.*, 2005) to study phenotypic and genetic aspects of the lactation curve, is of the following form:

$$y_t = at^b (\exp)^{-ct} \quad (1)$$

Where y_t is the average daily milk yield in kg at t^{th} month of lactation, a is the parameter associated with overall scale of production, t is the month of lactation, b is the parameter associated with increase rate of yield during the inclining phase until peak time, c is the parameter associated with the decreasing rate of yield during the declining phase until the end of lactation and \exp is the base of the natural logarithm and was set up as 2.71828 in the function. The parameters b and c are related to pre-peak and post-peak curvature, respectively (Wood, 1976). Due to the method of herd recording, a monthly model was applied rather than a daily or a weekly representation. Most herds in Iran are recorded on average, once a month i.e., every 4 weeks (the average interval between two consecutive tests was about 30 days, Table 1). Thus as pointed out by Tozer and Huffaker (1999) a monthly representation of milk production would more accurately estimate the herd recording data. Kellogg *et al.* (1977) also used the same model on monthly test day records of Holstein dairy cows. When test day records are collected once a week, a weekly model is usually used to fit the lactation curve by Wood's incomplete gamma function (Rao and Sundaresan, 1979; Batra, 1986; Olori *et al.*, 1999). Initially, the parameters of Wood's incomplete gamma function for whole data set were estimated by non-linear procedure of SAS programme (SAS Institute Inc., 1989) using Gauss-Newton method (which is based on Taylor Series) until iterated estimates converged. Priors (starting grids) needed for non-linear analysis, were first estimated by fitting the Wood's function in form of log-linear.

In the next step, Wood's incomplete gamma function was fitted to the monthly test day milk yields of individual cows at first calving. With respect to the large number of data, weighted linear regression analysis (which is an alternative to non-linear estimation) with weighting proportional to the squares of the untransformed milk yields (Cobby and Le Du, 1978) was implemented to estimate the lactation curve parameters of Wood's incomplete gamma function for individual cows. After discarding atypical lactation curves (negative b or c), production characteristics, which are some functions of the estimated lactation curve parameters, were subsequently calculated using the following equations:

- Peak time (PT) was calculated as b/c (2)

- Peak yield (PY) at the peak time was calculated as

$$PY = a(b/c)^b (e)^{-c(b/c)} = a(b/c)^b e^{-b} \quad (3)$$

- Persistency (Per) was calculated as

$$Per = \log_e c^{-(b+1)} = -(b+1) * \log_e c \quad (4)$$

In order to improve normality and avoid instability associated with estimated small values of c parameter, the natural logarithm (\log_e) of persistency measure ($c^{-(b+1)}$, Wood, 1967) was used (Rekaya *et al.*, 2000).

Estimated lactation curve parameters (a , b and c), production characteristics (PT, PY and Per) and 305 day milk (M305) yields of all first lactation cows were fitted in a multivariate (seven variates) Animal Model to estimate genetic and phenotypic parameters. Estimation of phenotypic and genetic parameters of the lactation curve traits was restricted to first lactation records because the largest number of records (after discarding atypical lactation curves) pertained to this lactation and selection would not bias the estimates. Furthermore, selection in dairy cattle is mostly based on first lactation records. The multivariate Animal Model was as follows:

$$y_{ijk} = HYS_{ik} + \sum_{R=1}^2 \beta_R * (A_{ijk})^R + \sum_{R=1}^2 \delta_R * (LL_{ijk})^R + a_{jk} + e_{ijk} \quad (5)$$

Where y_{ijk} is the record of the k^{th} trait ($a, b, c, PT, PY, Per, M305$) of the j^{th} cow, HYS_{ik} is the fixed effect of the i^{th} contemporary group of Herd-Year-Season of calving on the k^{th} trait, A_{ijk} is the covariate of calving age (month), LL_{ijk} is the covariate of lactation length (day), β and δ are the linear and quadratic partial non-orthogonal regression coefficients for the corresponding covariates in the model, Σ is the summation notation for each covariate, a_{jk} is the random effect of additive genetic merit of the j^{th} cow on the k^{th} trait and e_{ijk} is the random residual effect associated with y_{ijk} and it is assumed to be distributed as $N(0, R \otimes 1)$.

In matrix notation this equation can be re-written as follows:

$$Y = X\beta + Zu + e \quad (6)$$

Where y is a column vector of observations for the traits ($a, b, c, PT, PY, Per, M305$)^T;

X is a known design matrix relating elements of β to each y ;

β is an unknown column vector of fixed effects of herd-year-season of calving, linear and quadratic regression coefficients for age of calving and lactation length;

Z is a known design matrix of 0 and 1 relating elements of u to elements y;

u is an unknown column vector of random effect of additive genetic effect of the animals (cows, dams and sires);

e is an unknown column vector of random effect of residuals.

Under a no selection model the expectations of u and e are null (Henderson, 1988):

$$E \begin{bmatrix} y \\ u \\ e \end{bmatrix} = \begin{bmatrix} X\beta \\ 0 \\ 0 \end{bmatrix} \quad (7)$$

Variance and covariance matrix between y, u and e is as follows:

$$V \begin{bmatrix} y \\ u \\ e \end{bmatrix} = \begin{bmatrix} V & ZG \otimes A & R \otimes I \\ & G \otimes A & 0 \\ & & R \otimes I \end{bmatrix} \quad (8)$$

Where G, R and V are additive genetic, residual and phenotypic variance and covariance matrices, respectively. Matrix A (a symmetric matrix of additive genetic relationships among animals) is the Numerator Relationship Matrix (NRM) of order N*N of animals to be evaluated. Also, $V = ZG \otimes AZ^T + R \otimes I$ in which I is an identity matrix. The symbol \otimes stands for Kronecker product operator. The additive genetic variance-covariance matrix of G is:

$$G_{7 \times 7} = \begin{bmatrix} g_{11} & g_{12} & g_{13} & g_{14} & g_{15} & g_{16} & g_{17} \\ g_{21} & g_{22} & g_{23} & g_{24} & g_{25} & g_{26} & g_{27} \\ g_{31} & g_{32} & g_{33} & g_{34} & g_{35} & g_{36} & g_{37} \\ g_{41} & g_{42} & g_{43} & g_{44} & g_{45} & g_{46} & g_{47} \\ g_{51} & g_{52} & g_{53} & g_{54} & g_{55} & g_{56} & g_{57} \\ g_{61} & g_{62} & g_{63} & g_{64} & g_{65} & g_{66} & g_{67} \\ g_{71} & g_{72} & g_{73} & g_{74} & g_{75} & g_{76} & g_{77} \end{bmatrix} \quad (9)$$

Where g with the same subscript (diagonals) denotes additive genetic variance component ($g_{11}, g_{22}, \dots, g_{77}$) and with a different subscript (off-diagonals) denotes additive genetic covariance component between traits. Residual variance-covariance matrix R is:

$$R_{7 \times 7} = \begin{bmatrix} r_{11} & r_{12} & r_{13} & r_{14} & r_{15} & r_{16} & r_{17} \\ r_{21} & r_{22} & r_{23} & r_{24} & r_{25} & r_{26} & r_{27} \\ r_{31} & r_{32} & r_{33} & r_{34} & r_{35} & r_{36} & r_{37} \\ r_{41} & r_{42} & r_{43} & r_{44} & r_{45} & r_{46} & r_{47} \\ r_{51} & r_{52} & r_{53} & r_{54} & r_{55} & r_{56} & r_{57} \\ r_{61} & r_{62} & r_{63} & r_{64} & r_{65} & r_{66} & r_{67} \\ r_{71} & r_{72} & r_{73} & r_{74} & r_{75} & r_{76} & r_{77} \end{bmatrix} \quad (10)$$

Where r with the same subscript (diagonals) denotes residual variance component ($r_{11}, r_{22}, \dots, r_{77}$) and with a different subscript (off-diagonals) denotes residual covariance component between traits.

In the Animal Model used to estimate variance and covariance components, design matrices were equal due to having the same levels of fixed and random effects for all traits. Variance and covariance components for additive genetic (G) and residual (R) random effects between traits were estimated by MTCAFS (or MTC) programme (Misztal, 1994) using EMREML (Expectation Maximisation REstricted Maximum Likelihood) algorithm and canonical transformation. The EM-REML procedure, as described by Misztal and Perez-Enciso (1993), needs the first derivative of the residual likelihood for the maximisation and it is computationally more demanding than DFREML (Derivative Free REstricted Maximum Likelihood) developed by Graser *et al.* (1987) procedure. However, as all traits were available for all individuals cows, design matrices for the fixed and random effects were equal for all traits by which canonical transformation would be feasible to convert multivariate analysis to a series of corresponding univariate analyses (Meyer, 1989) which could result in a less computational effort.

Genetic parameters were subsequently calculated using REML estimated additive genetic and residual variance and covariance components. Heritability (in narrow sense) was obtained based on the following equations (Falconer and Mackay, 1996):

$$(\text{Heritability}) h_N^2 = \frac{V_A}{V_P} \quad (11)$$

Where V_A and V_P are additive genetic (breeding value) and phenotypic variances (equal to summation of additive genetic and residual variances) of the corresponding trait, respectively. To obtain phenotypic and genetic correlations between traits the following equations were also used:

$$(\text{Phenotypic Correlation}) r_p = \frac{\text{Cov}_{P,XY}}{\sigma_P \times \sigma_P Y} \quad (12)$$

$$\text{(Additive Genetic Correlation)} r_A = \frac{\text{Cov}_{Axy}}{\sigma_{Ax}\sigma_{Ay}} \quad (13)$$

Where $\text{Cov}_{p,xy}$ and $\text{Cov}_{A,xy}$ are phenotypic and additive genetic covariance between trait x and y, $\sigma_{p,x}$ and $\sigma_{p,y}$ are phenotypic standard deviations of the traits, $\sigma_{A,x}$ and $\sigma_{A,y}$ are additive genetic standard deviations of the traits.

RESULTS

Based upon the estimated lactation curve parameters as well as production characteristics obtained from the fitted typical lactations (which had positive b and c parameters), overall mathematical means for the traits studied in the present research included a, b, c, PT, PY, Per and M305 were 25.47, 0.389 and 0.104 kg, 3.72 months, 29.02, 3.249 and 7448 kg, respectively.

Heritability estimates of the lactation curve parameters of Wood's incomplete gamma function (a, b and c), production characteristics (PT, PY and Per) as well as 305 day milk yield are presented in Fig. 2. The point estimates of the heritabilities of the lactation curve parameters of Wood's incomplete gamma function ranged from 0.03 to 0.10 indicating that there is no considerable genetic variation for the parameters a, b and c. Heritability estimates of production characteristics were 0.10, 0.28 and 0.08 for peak time, peak yield and persistency, respectively. The heritability estimate of 0.29 was obtained for 305 day milk yield.

Phenotypic and genetic correlation estimates among the lactation curve parameters, production characteristics and 305 day milk yield are presented in the Table 2 as lower and upper diagonals, respectively. From the results, the genetic correlations between the first parameter of Wood's incomplete gamma function (a) and other traits ranged from -0.09 to 0.84 and the corresponding phenotypic correlations ranged from -0.54 to 0.67. For the second parameter of Wood's incomplete gamma function (b), genetic and phenotypic correlations ranged from 0.03 to 0.64 and -0.31 to 0.86, respectively. The third parameter of Wood's incomplete gamma function (c) had a high negative genetic correlation with persistency (-0.72) and a very low positive genetic correlation with peak yield (0.05). The range of phenotypic correlations between parameter c and the other traits was from -0.68 to 0.10. Peak time had positive genetic correlations with peak yield, persistency and 305 day milk yield and ranged from 0.49 to 0.92 while its phenotypic correlations ranged from 0.00 to 0.58. Although peak yield had a negative phenotypic (-0.11) correlation with persistency it was positively genetically correlated this trait. A very high

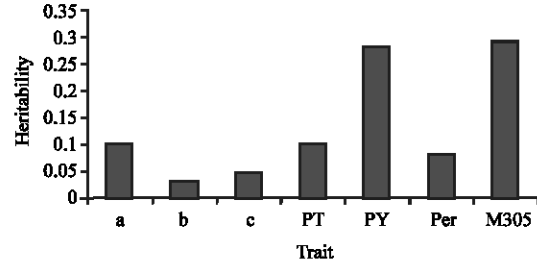


Fig. 2: Multivariate REML estimates of heritability of lactation curve parameters, production characteristics and 305 day milk yields for cows calving at first parity

Table 2: Multivariate REML estimates of additive genetic (above diagonal) and phenotypic (under diagonal) correlations among the lactation curve parameters of Wood's incomplete gamma function¹, production characteristics and 305 day milk yields using first parity records

Trait	a	b	c	PT	PY	Per	M305
a	1.00	0.11	0.16	-0.02	0.84	-0.09	0.74
b	-0.51	1.00	0.64	0.41	0.44	0.03	0.37
c	-0.19	0.86	1.00	-0.41	0.05	-0.72	-0.14
PT	-0.54	0.37	-0.04	1.00	0.49	0.92	0.64
PY	0.67	0.07	0.10	0.00	1.00	0.34	0.98
Per	-0.27	-0.31	-0.68	0.58	-0.11	1.00	0.53
M305	0.56	-0.08	-0.20	0.18	0.91	0.23	1.00

Fitted as $y_i = a^b(\exp)^{-ct}$ for all monthly test day records of individual cows

genetic correlation (0.98) was revealed between peak and 305 day milk yields. Both genetic (0.53) and phenotypic (0.23) correlations were positive between persistency and 305 day milk yield.

DISCUSSION

A sound knowledge of the lactation curve is an important issue in dairy cattle breeding because the pattern of how a cow produces milk over the lactation course could determine a cow's biological and economic efficiency and enable dairy farmers to manage cows according to their lactation characteristics (Grossman and Koops, 1988; Tozer and Huffaker, 1999). Furthermore, knowing the genetic relationship between lactation curve traits, each animal breeder would be able to select cows based on performance records of the lactation course.

In this research, phenotypic and genetic parameters of Wood's incomplete gamma function, production characteristics and 305 day milk yields of first parity Iranian Holstein cows were estimated by implementing a multivariate Animal Model. Generally, low heritability estimates were obtained for the parameters of Wood's incomplete gamma function and peak time suggesting that these traits were substantially influenced by the environmental factors and genetic variation between cows for these traits was low. This implies that direct selection for the lactation curve parameters may not change the

shape of the lactation curve effectively and successfully (Grossman *et al.*, 1986). In this study, persistency measure was defined as the natural logarithm of $c^{-(b+1)}$ as described by Wood (1967). However, some researchers have used other measures of persistency. Danell (1982), for instance, used the proportion of total milk yield at the second trimester of lactation (91-180 days) to total milk yield at the first trimester of lactation (1-90 days). The heritability of persistency obtained in the present study was 0.08. Low values of heritability were also obtained by other previous studies such as Rao and Sundaresan (1979) Shanks *et al.* (1981), Ferris *et al.* (1985), Batra *et al.* (1987) and Rekaya *et al.* (2000) who defined the persistency measure based on Wood's incomplete gamma function. The heritability of time of peak yield was also low (0.10) but within the range of estimates found by the other research workers.

Total lactation milk yield has been found to be associated with a high peak yield in dairy cows (Balaine *et al.*, 1970; Ferris *et al.*, 1985; Gama *et al.*, 1994), while genetic correlations between 305 day milk yield and persistency tend to be positive but low or moderate (Balaine *et al.*, 1970; Schneeberger, 1981; Ferris *et al.*, 1985; Gama *et al.*, 1994). The genetic correlation between peak yield and persistency is generally lower than the correlation between total yield and persistency (Balaine *et al.*, 1970; Shanks *et al.*, 1981; Ferris *et al.*, 1985; Gama *et al.*, 1994). Persistency had negative phenotypic (-0.11) and positive genetic correlations (0.34) with peak yield. This implies that higher peak yield in dairy cows is genetically associated with higher persistency.

In contrast to phenotypic correlations, positive genetic correlations were found between the first parameter and both b and c parameters. This implies that selection for higher values of a would result in higher rates of inclining and declining slopes of the lactation curve which in turn leads to lower persistency due to a negative genetic correlation between a and persistency (-0.09). The positive genetic correlations between a and b (0.11) and a and c (0.16) are in disagreement with those reported by Schneeberger (1981) and Ferris *et al.* (1985) and are in agreement with those reported by Varona *et al.* (1998). According to the negative estimated phenotypic correlations between a and b as well as c, cows with a higher level of production tend to have phenotypically lactation curves with a long ascending (b) and lower rate of descending (c) phases during the lactation which are in agreement with Schneeberger (1981) Ferris *et al.* (1985); Gama *et al.* (1994) Varona *et al.* (1998) and Tekerli *et al.* (2000). The positive phenotypic correlation (0.86) between the second and third parameters of the lactation curve indicates that cows with higher ascending slopes of milk

production would be expected to have a higher rate of decline of milk production after peak at the phenotypic level (Tekerli *et al.*, 2000). The positive phenotypic correlation (0.58) between peak time and persistency indicates that cows that reach peak yield later during lactation would have higher persistency.

Genetic correlations between parameters of Wood's incomplete gamma function (a, b and c) and production characteristics (PT, PY and Per) ranged from very low to very high values. The first parameter (a) had negative and very low genetic correlations with persistency and peak time (-0.09, -0.02, respectively), positive and high genetic correlations with 305 day milk production (0.74) and a very high positive genetic correlation with peak yield (0.84). With respect to genetic structure of the correlations among lactation curve parameters and total 305 day milk yield, it can be therefore concluded that genetic selection for 305 day milk yield would result in an increased level of production (a), ascent to peak yield (b) and a decreased descent from peak (c). Selection on genetic merit for parameter a would result in lower persistency, later and higher peak yield and a small correlated response in total lactation yield. The first parameter of the lactation curve (a) can be therefore considered as a useful early predictor of this correlated response and would bring a substantial reduction in the generation interval in dairy cattle genetic evaluation. However, with respect to its negative genetic correlation (-0.09) with persistency, selection for higher yields at the beginning of lactation could have undesirable effects in practical breeding programmes.

The second parameter of Wood's incomplete gamma function (b), which is associated with the ascending phase of the lactation, was relatively highly correlated with peak yield (genetic correlation of 0.44) and moderately correlated with 305 day milk production yield (0.37) indicating that selection on b would improve peak and total milk yield. The third parameter of Wood's incomplete gamma function (c), associated with the decline of the lactation curve, had a high negative genetic correlation with persistency (-0.72) indicating that selection for small values of (c) would result in an improved lactation persistency. The inverse relationship between the rate of decline and persistency has been also pointed out by the previous researchers (Togashi and Lin, 2004) and as mentioned by Solkner and Fuchs (1987), a cow with a higher persistency tends to incur less feed, health and reproduction costs. A high positive genetic correlation (0.64) was found between parameters b and c implying that cows with higher incline slope of lactation tend to have a higher decline of milk production after peak time which is in agreement with results obtained by Schneeberger (1981).

Estimated genetic correlations between parameters of Wood's incomplete gamma function and production characteristics from the present study are in rather agreement with previous studies (Shanks *et al.*, 1981; Ferris *et al.*, 1985; Gama *et al.*, 1994; Rekaya *et al.*, 2000). High genetic merit for persistency seems to be associated with low values for the third parameter of the lactation curve. A large positive genetic correlation between 305 day and peak yield has also been found in most studies (Ferris *et al.*, 1985; Rekaya *et al.*, 2000). Genetic correlation between persistency and the second parameter of the lactation curve was found to be positive which is in disagreement with Shanks *et al.* (1981) and Gama *et al.* (1994). The genetic correlation between the third parameter of the lactation curve and 305 day milk yield was low and negative (-0.14) which is similar to the results reported by Shanks *et al.* (1981), Ferris *et al.* (1985) and Gama *et al.* (1994).

Genetic correlations between 305 day milk yield and the other production characteristics were 0.64 for peak time, 0.98 for peak yield and 0.53 for persistency. Therefore, selection for total yield of lactation would be expected to result in lactations with higher peak production and later peaks. However, due to low heritability of persistency, correlated response for this trait would be expected to be inconsiderable as direct selection on 305 day milk yield is practised. Persistency had a low and positive genetic correlation with peak yield (0.34) and a large and positive genetic correlation with peak time (0.92) indicating that more persistent cows are expected to have higher and later peak yield genetically. Based on the estimated genetic correlations, selection for 305 day milk yield will not significantly affect persistency but would result in higher peak yield and later timing of peak lactations. Selection for increased value of the first or second parameters of the Wood's incomplete gamma function would result in higher 305 day milk yield but decreased persistency to a somewhat due to a little negative genetic correlation between first lactation curve parameter and persistency. With respect to the negative genetic correlation between the third parameter and 305 day milk yield, selection for lower values of *c* would result in higher 305 day lactation yield through higher persistency.

Recently there has been a considerable interest in using test day models to analyse individual test day records for genetic evaluation of dairy cows as a replacement for the traditional use of estimating accumulated 305 day lactation yields in a lactation model (Mayeres *et al.*, 2004). Canada, for example, officially has adopted and implemented random regression test day model in 1999 to replace lactation model (Schaeffer *et al.*, 2000). In a practical situation, as genetic evaluation of

dairy cattle is undertaken using monthly test day records in a test day model, the parametric models like Wood's incomplete gamma function, Wilmink's function or polynomial regression functions (Jamrozik and Schaeffer, 1997; Jamrozik *et al.*, 1997; Kaya *et al.*, 2003) or orthogonal legendre polynomials in covariance function (Meyer and Hill, 1997; Druet *et al.*, 2003) could be used in the model (as fixed and random regressions) to take account of the shape of the lactation curve for individual cows at the genetic level (Swalve, 2000). However, particular attention should be given to the number of monthly test day records available for each cow. This is due to the fact that the accuracy of estimation of genetic parameters and prediction of breeding values are affected to a great extent by the number of test day records available for each cow during the lactation course.

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REFERENCES

- Ali, T.E. and L.R. Schaeffer, 1987. Accounting for covariances among test day milk yields in dairy cows. *Can. J. Anim. Sci.*, 67: 637-644.
- Auran, T., 1973. Studies on monthly and cumulative monthly milk yield records. I. The effect of age, month of calving, herd and length of first test period. *Acta Agric. Scandinavica*, 23: 189-199.
- Auran, T., 1974. Studies on monthly and cumulative monthly milk yield records. II. The effect of calving interval and stage in pregnancy. *Acta Agric. Scandinavica*, 24: 339-348.
- Balaine, D.S., G.S. Gill and R.M. Acharya, 1970. Effectiveness of the components of lactation in selecting for milk production in Haryana cattle. *J. Dairy Sci.*, 53: 1064-1068.
- Batra, T.R., 1986. Comparison of two mathematical models in fitting lactation curves for pureline and crossline dairy cows. *Can. J. Anim. Sci.*, 66: 405-414.
- Batra, T.R., C.Y. Lin, A.J. McAllister, A.J. Lee, G.L. Roy, J.A. Vesely, J.M. Wauthy and K.A. Winter, 1987. Multitrait estimation of genetic parameters of lactation curves in Holstein heifers. *J. Dairy Sci.*, 70: 2105-2111.
- Castillo, G., N.P.P. Macciotta, A. Carretta and A. Cappio-Borlino, 2002. Effect of age and calving season on lactation curves of milk production traits in Italian water buffaloes. *J. Dairy Sci.*, 85: 1298-1306.

- Cobby, J.M. and Le Du, Y.L.P. 1978. On fitting curves to lactation data. *Anim. Prod.*, 26: 127-133.
- Congleton, W.R. Jr. and R.W. Everett, 1980a. Error and bias in using the incomplete gamma function to describe lactation curves. *J. Dairy Sci.*, 63: 101-108.
- Congleton, W.R. Jr. and R.W. Everett, 1980b. Application of the incomplete gamma function to predict cumulative milk production. *J. Dairy Sci.*, 63: 109-119.
- Danell, B., 1982. Studies on lactation yield and individual test day yields of Swedish dairy cows. III. Persistency of milk yield and its correlation with lactation yield. *Acta Agric. Scandinavica*, 32: 93-101.
- Dedkova, L. and E. Nemcova, 2003. Factors affecting the shape of lactation curves of Holstein cows in the Czech Republic. *Czech J. Anim. Sci.*, 48: 395-402.
- Druet, T., F. Jaffrezic, D. Boichard and V. Ducrocq, 2003. Modeling lactation curves and estimation of genetic parameters for first lactation test day records of French Holstein cows. *J. Dairy Sci.*, 86: 2480-2490.
- Falconer, D.S. and T.F.C. Mackay, 1996. *Introduction to Quantitative Genetics*. 4th Edn. Longman, Harlow, Essex.
- Ferris, T.A., I.L. Mao and C.R. Anderson, 1985. Selecting for lactation curve and milk yield in dairy cattle. *J. Dairy Sci.*, 68: 1438-1448.
- Gama, L.T., R.N. Carolino, A.A. Cruz and M.I. Carolino, 1994. Genetic parameters estimates for shape of the lactation curve in dairy cattle. In *Proceedings of the 5th World Congress on Genetics Applied to Livestock Production*, Guelph, Ontario, Canada, 17: 132-135.
- Graser, H.U., S.P. Smith and B. Tier, 1987. A derivative-free approach for estimating variance components in animal models by restricted maximum likelihood. *J. Animal Sci.*, 64: 1362-1370.
- Grossman, M., A.L. Kuck and H.W. Norton, 1986. Lactation curves of purebred and crossbred dairy cattle. *J. Dairy Sci.*, 69: 195-203.
- Grossman, M. and W.J. Koops, 1988. Multiphasic analysis of lactation curves in dairy cattle. *J. Dairy Sci.*, 71: 1598-1608.
- Henderson, C.R., 1988. Theoretical basis and computational methods for a number of different animal models. *J. Dairy Sci.*, 71: 1-16.
- Jamrozik, J. and L.R. Schaeffer, 1997. Estimates of genetic parameters for a test day model with random regressions for yield traits of first lactation Holsteins. *J. Dairy Sci.*, 80: 762-770.
- Jamrozik, J., L.R. Schaeffer and J.C.M. Dekkers, 1997. Genetic evaluation of dairy cattle using test day yields and random regression model. *J. Dairy Sci.*, 80: 1217-1226.
- Kaya, I., Y. Akbas and C. Uzmay, 2003. Estimation of breeding values for dairy cattle using test day milk yields. *Turk. J. Vet. Anim. Sci.*, 27: 459-464.
- Kellogg, D.W., N.S. Urquhart and A.J. Ortega, 1977. Estimating Holstein lactation curves with a Gamma curve. *J. Dairy Sci.*, 60: 1308-1315.
- Keown, J.F., R.W. Everett, N.B. Empet and L.H. Wadell, 1986. Lactation curves. *J. Dairy Sci.*, 69: 769-781.
- Lin, C.Y. and K. Togashi, 2005. Maximization of lactation milk production without decreasing persistency. *J. Dairy Sci.*, 88: 2975-2980.
- Macciotta, N.P.P., D. Vicario and A. Cappio-Borlino, 2005. Detection of different shapes of lactation curves for milk yield in dairy cattle by empirical mathematical models. *J. Dairy Sci.*, 88: 1178-1191.
- Mayeres, P., J. Stoll, J. Bormann, R. Reents and N. Gengler, 2004. Prediction of daily milk, fat and protein production by a random regression test day model. *J. Dairy Sci.*, 87: 1925-1933.
- Meyer, K., 1989. Estimation of Genetic Parameters. In *Evolution and Animal Breeding* (Hill, W.G. and F.C. Mackay, Eds.), CAB International, pp: 161-167.
- Meyer, K. and W.G. Hill, 1997. Estimation of genetic and phenotypic covariance functions for longitudinal or 'repeated' records by restricted maximum likelihood. *Livestock Prod. Sci.*, 47: 185-200.
- Misztal, I., 1994. Comparison of software packages in animal breeding. In *Proceedings of the 5th World Congress on Genetics Applied to Livestock Production*, Guelph, Ontario, Canada, 22: 3-10.
- Misztal, I. and M. Perez-Enciso, 1993. Sparse matrix inversion for restricted maximum likelihood estimation of variance components by expectation-maximization. *J. Dairy Sci.*, 76: 1479-1483.
- Morant, S.V. and A. Gnanasakthy, 1989. A new approach to the mathematical formulation of lactation curves. *Anim. Prod.*, 49: 151-162.
- Nelder, J.A., 1966. Inverse polynomials, a useful group of multi-factor response functions. *Biometrics*, 22: 128-141.
- Olori, V.E., S. Brotherstone, W.G. Hill and B.J. McGuirk, 1999. Fit of standard models of the lactation curve to weekly records of milk production of cows in a single herd. *Livestock Prod. Sci.*, 58: 55-63.
- Perochon, L., J.B. Coulon and F. Lescourret, 1996. Modelling lactation curves of dairy cows with emphasis on individual variability. *Anim. Sci.*, 63: 189-200.
- Pollott, G.E., 2000. A biological approach to lactation curve analysis for milk yield. *J. Dairy Sci.*, 83: 2448-2458.

- Poso, J., E.A. Mantysaari and A. Kettunen, 1996. Estimation of genetic parameters of test day production in Finnish Ayrshire cows. In Proceedings of the INTERBULL Annual Meeting, Veldhoven, The Netherlands, 23-24 June 1996, No. 14: 45-48.
- Ramirez, R., G. Ramirez and R. Nunez-Dominguez, 1994. Comparison of equations and estimation procedures of lactation curves in Angus, Brown Swiss and their crosses. In Proceedings of the 5th World Congress on Genetics Applied to Livestock Production, Guelph, Ontario, Canada, 17: 136-139.
- Rao, M.K. and D. Sundaresan, 1979. Influence of environment and heredity on the shape of lactation curves in Sahiwal cows. *J. Agric. Sci.*, 92: 393-401.
- Rekaya, R., M.J. Carabano and M.A. Toro, 2000. Bayesian analysis of lactation curves of Holstein-Friesian cattle using a nonlinear model. *J. Dairy Sci.*, 83: 2691-2701.
- SAS Institute Inc., 1989. SAS/STAT. User's Guide. Version 6th Edn., Cary, NC: SAS Institute Inc., Vol. 1 and 2.
- Schaeffer, L.R. and E.B. Burnside, 1976. Estimating the shape of the lactation curve. *Can. J. Anim. Sci.*, 56: 157-170.
- Schaeffer, L., J. Jamrozik, G.J. Kistemaker and B.J. Van Doormaal, 2000. Experience with a test day model. *J. Dairy Sci.*, 83: 1135-1144.
- Schneeberger, M., 1981. Inheritance of lactation curve in Swiss Brown cattle. *J. Dairy Sci.*, 64: 475-483.
- Scott, T.A., B. Yandell, L. Zepeda, R.D. Shaver and T.R. Smith, 1996. Use of lactation curves for analysis of milk production data. *J. Dairy Sci.*, 79: 1885-1894.
- Shanks, R.D., P.J. Berger, A.E. Freeman and F.N. Dickinson, 1981. Genetic aspects of lactation curves. *J. Dairy Sci.*, 64: 1852-1860.
- Solkner, J. and W. Fuchs, 1987. A comparison of different measures of persistency with special respect to variation of test-day milk yields. *Livestock Prod. Sci.*, 16: 305-319.
- Swalve, H.H., 2000. Theoretical basis and computational methods for different test day genetic evaluation methods. *J. Dairy Sci.*, 83: 1115-1124.
- Tekerli, M., Z. Akinci, I. Dogan and A. Akcan, 2000. Factors affecting the shape of lactation curves of Holstein cows from the Balikesir province of Turkey. *J. Dairy Sci.*, 83: 1381-1386.
- Togashi, K. and C.Y. Lin, 2004. Efficiency of different selection criteria for persistency and lactation milk yield. *J. Dairy Sci.*, 87: 1528-1535.
- Tozer, P.R. and R.G. Huffaker, 1999. Mathematical equations to describe lactation curves for Holstein-Friesian cows in New South Wales. *Aus. J. Agric. Res.*, 50: 431-440.
- Val-Arreola, D., E. Kebreab, J. Dijkstra and J. France, 2004. Study of the lactation curve in dairy cattle on farms in central Mexico. *J. Dairy Sci.*, 87: 3789-3799.
- Varona, L., C. Moreno, Garcia L.A. Cortes and J. Altarriba, 1998. Bayesian analysis of wood's lactation curve for Spanish dairy cows. *J. Dairy Sci.*, 81: 1469-1478.
- Wilmink, J.B.M., 1987. Adjustment of test day milk, fat and protein yield for age, season and stage of lactation. *Livestock Prod. Sci.*, 16: 335-348.
- Wood, P.D.P., 1967. Algebraic model of the lactation curve in cattle. *Nature*, 216: 164-165.
- Wood, P.D.P., 1969. Factors affecting the shape of the lactation curve in cattle. *Anim. Prod.*, 11: 307-316.
- Wood, P.D.P., 1974. A note on the estimation of total lactation yield from production on a single day. *Anim. Prod.*, 19: 393-396.
- Wood, P.D.P., 1976. Algebraic models of the lactation curves for milk, fat and protein production with estimates of seasonal variation. *Anim. Prod.*, 22: 35-40.