

LACTATION CURVE OF HOLSTEIN FRIESIAN COWS IN THE KINGDOM OF SAUDI ARABIA

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Summary

Monthly test day production for 12,020 records, were collected from six of the largest specialized dairy farms located in central region of the Kingdom of Saudi Arabia. The records described lactating cows in four parities and two seasons of calving. Monthly test day records were fitted using Wood's model $At^b e^{-ct}$ with multiple and additive error term. Linear and non-linear regression models were used to find the estimates of the parameters necessary to draw the lactation curves. The shape of the lactation curves of different parities showed that third lactation has the highest peak (43.08 kg) for linear regression model and (42.08 kg) for non-linear regression model. Fourth lactation has the lowest peak (24.00 kg) for linear regression model and (25.64 kg) for non-linear regression model. Cows of second and third lactations reached the peak at 58 day for both linear and non-linear regression models. Cows of first lactation were more persistent and had late peak at 68 and 67 days for both models respectively. While, third lactation cows were lower persistent and had early peak at 58 day for both models. Cows calved at winter months have higher starting values (A), higher ascending slope (b) and higher descending slope (c).

Least square means of milk yield of the first four parities and for overall data were 6,653, 7,659, 7,482, 6,988 and 7,614 kg respectively. The corresponding lactation period were 358, 367, 350, 363 and 364 days respectively.

(Key Words : Lactation Curve, Non Linear Model, Persistency, Milk Yield, Lactation Period)

Introduction

Lactation curve is the figure that illustrates the configuration of milk yields over the lactation period. Estimating the parameters of the mathematical model of that curve is an important approach for several reasons, namely: 1-Provision the pattern of cumulative production curve so that extension factors for incomplete lactation can be computed. 2-Finding the effect of systematic factors like age and month of calving on the shape of lactation curve. 3-Prediction of a cow 305-day milk and fat production that would help dairy breeders in (a) Evaluating cow genetic potential, (b) Culling the low producing cows, (c) Selecting herd replacements, and (d)

Evaluating sire in progeny testing program. 4-The mathematical model of the lactation curve is an essential component of system analysis scheme as well as economic analysis. 5-Determination of the turning point (peak) of the lactation curve is important for carrying out feeding experiment throughout the descending phase of the lactation curve. 6-Computing genetic parameters like heritability, repeatability and genetic correlation for the curve parameters will assist in selection of lactation with desired shape.

The most widely used model to describe the lactation curve was the one proposed by Wood (1967) to fit the curve of a cow with three parameters of incomplete gamma function such that, $y_t = At^b \exp^{-ct}$ where y_t represents the milk yield in time t , the parameters can be estimated after log transformation, from a multiple regression of $\ln(y)$ on $\ln(t)$ and t .

Several studies used non-linear technique to describe the lactation curve. Kellog et al. (1977) used an intrinsically non-linear regression model to validate the assumption that a cow's production has equal variance

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Received November 7, 1995

Accepted February 28, 1996

throughout the 10 month lactation, they fitted three parameters using non-linear model: $y_t = \beta_1 t^{\beta_2} \exp^{-\beta_3 t} + E_t$ where y_t is the milk yield at specific month (t). The model fitted adequately monthly milk records for individual cows and measured the means of 36 cows within lactation. The first part of Kellogg's model is the deterministic part which is the model used by Wood and was described as the incomplete gamma function. Cobby and Le Du (1978) found that the fitted curve by Wood's model using log least squares did not describe the data over the whole lactation, while Non-linear least squares fitted the data better for most of the lactation and reduced residual mean square by about 14%. Grossman et al. (1986) corrected for the day of the year by multiplying Wood's equation $A t^b e^{-ct}$ time a correction factor: $\{1 + u \sin(x) + v \cos(x)\}$ where x is the day of the year, t is the day of lactation and A , b , c , u and v are parameters of the curve. Ferris et al. (1985) used Marquardt's method for non-linear regression to fit a first order non-linear approximate model as follows: $y_t = \ln(a) + b \ln(t) + ct + e/y^2$

The objectives of this study were: 1-Fit the data of monthly milk yield of six Dairy Farms in Saudi Arabia using Incomplete Gamma function by linear and non-linear technique to find the best estimate of the parameters of the lactation curve. 2-Determine the effect of non-genetic factors like farm, parity and season of calving on the lactation curve. 3-Draw the confidence or inference band of the lactation curve using the estimated parameters derived from the two models.

Materials and Methods

The data used in this study consisted of 12,020 monthly test day milk records (kg/day) collected from six of the largest, specialized dairy farms located in the central region of the Kingdom of Saudi Arabia: Masstock, Nadec, Azizeah, Abnai, AL-Khajj and King Saud University dairy farm. Each record set has the following information: Farm number, cow number, birth date, calving date, lactation period, total milk yield and the milk yield of one specified day for each month of lactation.

Data were collected during the period 1980 to 1992 and included cows calved in two seasons 1-Winter (S1): for cows calved during October to March and 2- Summer (S2): for cows calved in April until September. The number of records for first, second, third and fourth lactations or greater were 3,793, 3,500, 2,470 and 2,257 respectively.

Each lactation included records with a wide range of age at calving. Therefore, age of calving was classified

into categories such that; Age of calving ranged from 18 to 42 month for first lactation; 30 to 54 for second lactation; 44 to 68 for third lactation; 56 to 80 for fourth lactation or greater. Each age of calving category was divided into 4 intervals, 6 month each.

Records with a lactation period < 100 days or > 550 days were excluded from the analysis. The range of lactation period was chosen because the frequency distribution has shown that 73% of the records have lactation period longer than 300 days.

Monthly milk records for overall data and for different parities and season of calving were fitted using:

1-Linear regression model such that milk yield: $y_t = A t^b \exp^{-ct} E(t)$ where $E(t)$ represents a multiplicative random error- $N(0, \sigma^2 I)$.

2-Non-linear regression model such that milk yield: $y_t = f(X_t, \theta) + E_t$ where E_t is the additive random- $N(0, \sigma^2 I)$ and $f(X_t, \theta) = A t^b e^{-ct}$.

Marquardt's method was used to estimate the parameters by non-linear model because Marquardt is equivalent to performing a series of ridge regression which correct for collinearity or near singularity problems that arise from the correlation between the parameters of the lactation curve (Bates and Watts, 1988).

The parameters A , b and c of linear and non-linear regression models were used to estimate some functions which are important in lactation curve study and have biological meaning; like time of peak, maximum milk yield (peak yield) and persistency. Environmental effects like farm, season of calving (summer and winter) and age of calving within lactation were removed from the parameters A , b and c by fitting a linear model that used the parameter as a dependent variable and environmental effects as independent variables.

Inference or confidence bands for the curve of the overall data were computed for linear and non-linear regression models according to method given by Bates and Watts (1988).

Regression, non-linear and GLM procedures of SAS (1986) was used to carry out the statistical analysis.

Results and Discussion

Fitting the data by incomplete gamma function yielded negative estimates of c (about 11% of records) and negative estimates of b (about 2%). These atypical lactation curve would have peaked before calving and therefore were removed from the analysis. Similar situation was observed by Ferris et al. (1985). Excluding the records from the analysis can be explained by the following: If the initial rising portion of a certain curve is

short or information on this portion of the curve is missing, linear and non-linear regression will estimate a negative b , then function t^b , which is the rising components of the curve, will decrease with large values of t . Also, if some months on the descending phase have higher yield than the first peak i.e., curve with multiple peaks or the curve is short with missing monthly test yield after 100 days the model will result on negative estimate of the parameter c . In both situations (negative b or c) the resulting curve will have a negative slope for all days in milk and predict peak production b/c before freshening. Curves of this shape are characterized by a large amount of bias in predicting milk yield. Congleton and Everett (1980) found that negative estimates for b and c were more common for lactations with a first test day 30 days or more after freshening than for lactations with a first test day within 10 days after freshening.

As the pattern of milk yield changes over the lactation period, it is important to investigate the impact of the parameters on determining the shape of the curve within and across lactations. The parameter A is a multiplier and changes the height of the curve across lactations. However, it has no effect on the shape of the lactation curve. Table 1 shows that least square estimate of the parameter A of first lactation has lower values than those of other lactations. However, least square estimate of measure for the ascending slope (b) was the lowest on the fourth lactation. Parameter c which is a measure of descending slope showed a minimal variation from lactation to lactation for linear regression model.

TABLE 1. LEAST SQUARE MEANS AND STANDARD ERRORS OF THE PARAMETERS OF THE LACTATION CURVE FROM LINEAR REGRESSION MODELS FOR OVERALL DATA AND DIFFERENT PARITIES AND TWO SEASONS OF CALVING

	A	b	c
Overall	13.3882 ± 1.045	0.3200 ± .0122	0.0051 ± .0001
L1	12.0140 ± 1.064	0.2932 ± .0171	0.0043 ± .0002
L2	16.7264 ± 1.070	0.2511 ± .0194	0.0043 ± .0002
L3	13.5127 ± 1.086	0.3826 ± .0237	0.0066 ± .0004
≥ L4	13.1821 ± 1.033	0.1976 ± .0099	0.0034 ± .0003
S1	14.8774 ± 1.069	0.3371 ± .0186	0.0063 ± .0002
S2	14.2867 ± 1.063	0.3202 ± .0169	0.0055 ± .0002

Least square estimates of the parameters from non-linear regression model as given in tabel 2, indicate that both parameters A and b have lower values in fourth

lactation than other lactations. However, parameter c has its lowest value at first lactation. Least square estimates of A , b and c for lactation curve of overall data were 13.3882 ± 1.045, 0.3200 ± .0122 and 0.0051 ± .0001 for linear regression model and were 16.1106 ± .8350, 0.2650 ± .0235 and 0.0046 ± .00033 for non-linear regression model respectively.

TABLE 2. LEAST SQUARE MEANS AND STANDARD ERRORS OF THE PARAMETERS OF THE LACTATION CURVE FROM NON-LINEAR REGRESSION MODELS FOR OVERALL DATA AND DIFFERENT PARITIES AND TWO SEASONS OF CALVING

	A	b	c
Overall	16.1106 ± 0.835	0.2650 ± .0235	0.0046 ± .00033
L1	18.2627 ± 1.158	0.1950 ± .0297	0.0029 ± .00034
L2	17.3470 ± 1.171	0.2275 ± .0336	0.0038 ± .00049
L3	19.7320 ± 1.595	0.2479 ± .0326	0.0043 ± .00038
≥ L4	15.3186 ± 1.402	0.1764 ± .0292	0.0035 ± .00050
S1	15.9333 ± 1.095	0.3108 ± .0278	0.0056 ± .00038
S2	15.5662 ± 1.080	0.2927 ± .0291	0.0050 ± .00042

The magnitude of least square estimates of the curve parameters is important in explaining the discrepancy among the shape of the curves of different parities, which due to peak time, peak yield and persistency. Table 3 and (figures 1 and 2) show that third lactation has the highest peak : 43.08 kg for linear regression model and 42.08 kg

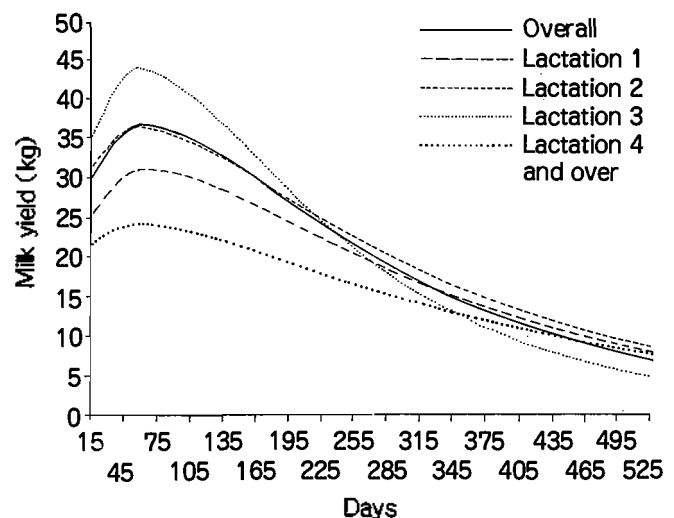


Figure 1. Lactation curve for different parities and overall data from fitting linear regression model.

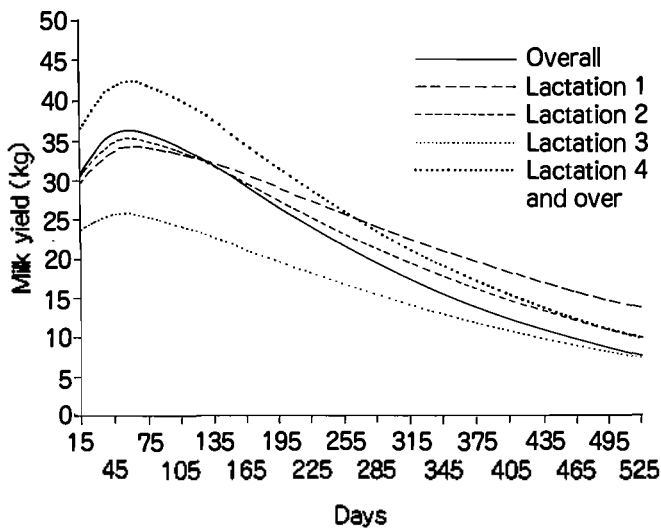


Figure 2. Lactation curve for different parities and overall data from fitting non-linear regression model.

for non-linear regression model. While, fourth lactation has the lowest peak : 24.00 kg for linear regression model and 25.64 kg for non-linear regression model. Cows of second and third lactations reached that peak at 58 day for linear regression model and at day 60 and 58 for non-linear regression model. Cows of first lactation have late peak at 68 day and 67 day for both models, so the time of peak for curves of different lactations lies in the range of 45 to 70 days as reported by previous studies, such as Appleman et al. (1969), Lamb and McGilliard (1960), Madden et al. (1955), Mahadevan (1951) and Kellog et al. (1977). Figures 1 and 2 show that first lactation has the lowest rate of decline, however, third lactation has the highest peak and rapid decline i.e. low persistency, a property that has been noticed by previous studies like Kellog et al. (1977) and Ferris et al. (1985).

On the other hand, with incomplete Gamma function, cows that have fast ascending (large b) and low descending (small c) are more persistent and are expected to have a higher peak because of the relation in peak equation : $\{A (b/c)^b \text{Exp} (-b)\}$. If two cows have the same A and b , peak yield indicate persistency because of the relationship of c in the peak equation, so the cow with higher peak will have smaller c and more persistent. Ferris et al. (1985) mentioned that these may not be true biologically they recommended using a more flexible equation that allow rate of ascent, peak, time of peak and persistency to be independent.

The curve of the overall data has been intermediate among the curves of other lactations. The curves of

different parities have a long descending phase which is mainly due to a long lactation period since dairy farms in Saudi Arabia do not dry their cows on 305 day of milk, but let them milk for a period greater than 500 days. The length of lactation period (> 305 days) in Holstein cows in Saudi Arabia is mainly due to : 1-Low conception rate, Salah and Mogawer (1990^a) found the conception rate to be 45% in two herds in Saudi Arabia. 2-Long days open, in another study, Salah and Mogawer (1990^b) estimated the average length of 'days open' to be as long as 140 days. Tables 1 and 2 show that estimates for winter season were higher for linear regression. Non-linear regression showed that winter season started at a high level (high A), with low rate of inclining (low b) and low rate of declining (low c). The results were concordant for both models. Figures (3 and 4) illustrate that cows calving at winter months have higher starting values (A), higher ascending slope (b) and higher descending slope (c) than cows calved at summer months. Moreover, table 3 shows that cows calved in winter have higher peak for linear (40.43 kg) and non-linear (40.67 kg) and lower persistency than cows calved in summer, and this was mainly because cows calved in the winter season reached summer 180 days after calving, the opposite situation occurred for cows calved in summer months.

The R^2 values were greater than 0.90 for linear and non-linear regression models. First order autocorrelation among residuals ranged from -0.054 to -0.08 . All values of Durbin Watson were above 2, which indicates an autocorrelation of zero.

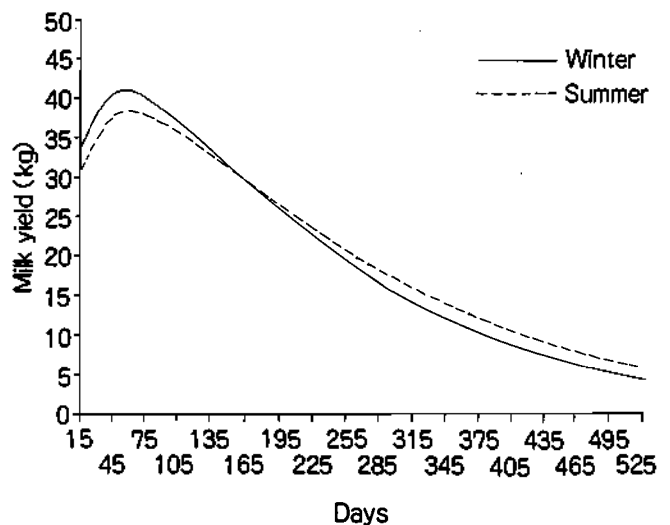


Figure 3. Lactation curve for cows calved in winter and summer from fitting linear regression model.

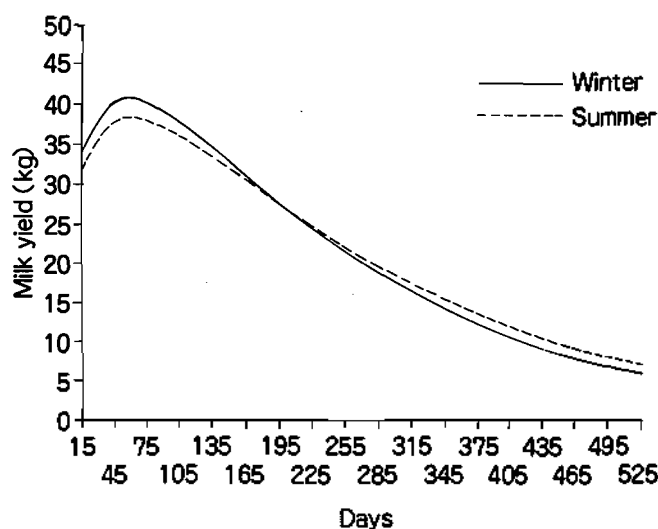


Figure 4. Lactation curve for cows calved in winter and summer from fitting non-linear regression model.

TABLE 3. MAXIMUM MILK YIELD (MMY), DAY OF PEAK AND PERSISTENCY BY PARITIES AND SEASON OF CALVING FROM FITTING LINEAR AND NON-LINEAR REGRESSION MODELS

	Linear			Non-linear		
	MMY	peak (day)	persistency	MMY	peak (day)	persistency
Overall	36.36	62.75	6.97	36.19	57.61	6.81
L1	30.86	68.19	7.05	34.14	67.24	6.98
L2	35.85	58.40	6.82	35.05	59.87	6.84
L3	43.08	57.97	6.94	42.08	57.65	6.80
≥ L4	24.00	58.12	6.81	25.64	50.40	6.65
S1	40.43	53.51	6.78	40.67	55.50	6.80
S2	37.74	58.22	6.87	38.23	58.54	6.85

Maximum milk yield = $A(b/c)^b \exp^{-b}$.

Peak (day) = b/c .

persistency = $c^{-(b+1)}$.

Relationship between the parameters of the lactation curve :

Table 4 shows the correlation coefficients between the parameter of the component of the lactation curve. High negative correlation was found between the parameters A and b for linear $-0.95 < r_{Ab} < -0.92$ and for non-linear $-0.88 < r_{Ab} < -0.82$. Moderate negative correlations were found between A and c for linear $-0.61 < r_{Ac} < -0.55$ and for non-linear $-0.56 < r_{Ac} < -0.50$. High positive correlation was obtained between b and c for

linear $0.73 < r_{bc} < 0.78$ and for non-linear $0.65 < r_{bc} < 0.83$. The estimates of correlation coefficients between the parameters agreed in magnitude and sign with those found by Strandberg and Lundberg (1991), the correlations were close to each other for both models.

TABLE 4. CORRELATION COEFFICIENTS BETWEEN THE PARAMETERS OF LACTATION CURVE FROM LINEAR AND NON-LINEAR REGRESSION MODELS

	Linear			Non-linear		
	r_{Ab}	r_{Ac}	r_{bc}	r_{Ab}	r_{Ac}	r_{bc}
Overall	-0.95	-0.60	0.78	-0.82	-0.56	0.83
L1	-0.94	-0.57	0.74	-0.82	-0.56	0.81
L2	-0.95	-0.61	0.77	-0.84	-0.52	0.75
L3	-0.95	-0.55	0.73	-0.87	-0.50	0.65
≥ L4	-0.92	-0.55	0.77	-0.88	-0.51	0.75
S1	-0.94	-0.59	0.78	-0.86	-0.52	0.74
S2	-0.95	-0.60	0.76	-0.87	-0.53	0.73

The relation between the parameters of the lactation curve and consequently between the function of these parameters are important in determining desirable change of shape of the lactation curve to meet certain management strategy as described by Ferris et al. (1985). For example if one is concerned about cows which are more efficient in utilization of feed during the early part of lactation, then selection should be for increased rate of ascent to the peak (b) or increased rate of ascent as well as peak yield $\{A(b/c)^b e^{-b}\}$ while ignoring persistency $c^{-(b+1)}$ in later lactation. Another strategy is to increase initial production (A) and increase persistency while decreasing peak will result in flattening curve. Finally large value of (b/c) i.e. late peak will reduce stress and allow body reserve of the cow to be used gradually and slowly.

The effect of farm, season of calving and age of calving on the parameters :

Tables 5 and 6 show that, Farm has a highly significant effect of the parameters of the lactation curve (A, b and c) for different parities and for overall data. Season of calving has showed significant effect mainly on the parameters b and c of the lactation curve for first and second parity and for overall data. Similar results were found in several previous researches, such as Wood (1969 and 1976), Papajcsik (1977), Kellog et al. (1977), Grossman et al. (1986) and Grossman and Koops (1988).

TABLE 5. THE EFFECT OF FARM (FN), SEASON OF CALVING (S) AND AGE OF CALVING WITHIN LACTATION (AGC/L) ON THE PARAMETERS OF LACTATION CURVE FOR OVERALL DATA AND FOR DIFFERENT PARITIES (L1-L4) FROM LINEAR REGRESSION MODELS

1-Parameter A :

Source	df	F-Value				Overall
		L1	L2	L3	≥ L4	
FN	5	52.92**	35.48**	21.62**	23.88**	149.26**
S	1	1.15	0.08	2.41	2.92	0.59
AGC/L	3	1.15	2.55*	0.08	1.42	1.1 ¹
MSE		0.50798	0.63087	0.625337	0.334999	0.58026

* (p < .05). ** (p < .01).

2-Parameter b :

Source	df	F-Value				Overall
		L1	L2	L3	≥ L4	
FN	5	62.78**	52.55**	18.44**	12.73**	151.**
S	1	3.11*	3.9*	0.01	0.01	3.18*
AGC/L	3	3.21*	1.44	0.27	1.37	0.21 ¹
MSE		0.038024	0.051727	0.0514225	0.307989	0.044526

* (p < .05). ** (p < .01).

3-Parameter c :

Source	df	F-Value				Overall
		L1	L2	L3	≥ L4	
FN	5	73.2**	67.84**	22.62**	8.82**	167.**
S	1	14.71**	5.24*	0.16	1.27	31.97**
AGC/L	3	13.89**	0.13	0.44	0.87	0.72 ¹
MSE		0.0000068	0.0000117	0.0000118	0.0000079	0.0000072

* (p < .05). ** (p < .01). ¹: df = 12.

TABLE 6. THE EFFECT OF FARM (FN), SEASON OF CALVING (S) AND AGE OF CALVING WITHIN LACTATION (AGC/L) ON THE PARAMETERS OF LACTATION CURVE FOR OVERALL DATA AND FOR DIFFERENT PARITIES (L1-L4) FROM NON-LINEAR REGRESSION MODELS

1-Parameter A :

Source	df	F-Value				Overall
		L1	L2	L3	≥ L4	
FN	5	24.29**	16.89**	5.00**	1.88	36.92**
S	1	5.79**	15.67**	0.07	0.14	0.5
AGC/L	3	1.55	3.06	0.58	1.64	2.65* ¹
MSE		76.758	77.162	87.277	43.383	58.068

* (p < .05). ** (p < .01).

2-Parameter b :

Source	df	F-Value				
		L1	L2	L3	≥ L4	Overall
FN	5	35.99**	23.47**	3.96**	6.39**	50.32**
S	1	4.59*	9.99**	0.17	0.01	3.55*
AGC/L	3	1.60	0.60	0.74	2.04	1.35 ¹
MSE		0.0507	0.063	0.0364	0.019	0.040

* (p < .05). ** (p < .01).

3-Parameter c :

Source	df	F-Value.				
		L1	L2	L3	≥ L4	Overall
FN	5	40.85**	29.34**	4.48**	5.55**	43.51**
S	1	11.05**	6.27**	0.26	0.01	4.98**
AGC/L	3	4.29**	0.56	1.29	0.97	3.60** ¹
MSE		0.0000067	0.0000139	0.0000048	0.0000056	0.0000082

* (p < .05). ** (p < .01). ¹: df = 12.

Age of calving within lactation has not shown a consistent significant effect on the parameters of the curves of different parities or for the curve of overall data. The significant effect of farm, season of calving and age of calving has been excepted on milk yield and lactation period as shown in tables 7 and 8. Least square means of milk yield of the first four parities and for overall data were 6,653, 7,659, 7,482, 6,988 and 7,614 kg, respectively. Lactation period for the four parities and for overall data were 358, 367, 350, 363 and 364 days, respectively. Mansour (1992) found that 305-day milk yield was 6,113, 6,806, 7,129, 7,145, 7,038 for the first, second, third, fourth and fifth lactation or more. The author did not correct the milk yield for the length of lactation period. Low production of milk yield of Holstein cows can be attributed at least in part to direct effect of

high environmental temperature prevailing in Saudi Arabia which remains above the thermoneutral temperature of lactating Holsteins (21 °C) for at least 8 months of the year on milk synthesis (AL-Haidary A. 1989). Milk production of exotic temperate-evolved Holstein cows transferred to hot regions is known to decline. This decline have been ascribed to heat-induced suppression of thyroid activity along with many other physiological changes (including alteration of thermal and other hormonal energy and water balance) necessary to minimize the rise in body temperature (Collier et al., 1981, and Johnson 1965).

Confidence bands :

Confidence bands (or inference bands), were computed for the lactation curve of the overall data using parameters obtained from fitting linear and non-linear regression

TABLE 7. THE EFFECT OF FARM (FN), SEASON OF CALVING (S) AND AGE OF CALVING WITHIN LACTATION (AGC/L) ON THE MILK YIELD FOR OVERALL DATA AND FOR DIFFERENT PARITIES (L1-L4)

Source	df	F-Value				
		L1	L2	L3	≥ L4	Overall
FN	5	81.54**	71.01**	71.22**	70.36**	214.15**
S	1	14.05**	0.53	18.15**	0.01	5.04*
AGC/L	3	1.67**	3.10*	1.28	0.66	2.26
MSE		4.479E±06	5.737E±06	6.330E±06	3.792E±06	8.748E±06

* (p < .05). ** (p < .01).

TABLE 8. THE EFFECT OF FARM (FN), SEASON OF CALVING (S) AND AGE OF CALVING WITHIN LACTATION (AGC/L) ON THE LACTATION PERIOD FOR OVERALL DATA AND FOR DIFFERENT PARITIES (L1-L4)

Source	df	F-Value					Overall
		L1	L2	L3	≥ L4		
FN	5	105.07**	38.97**	14.98**	6.39**	117.09**	
S	1	38.98**	88.22**	18.95**	50.57**	308.51**	
AGC/L	3	6.29**	1.56	1.23	0.35	16.44**	
MSE		6,604.2	4,887.5	6,644.7	5,685.1	6,145.9	

* ($p < .05$). ** ($p < .01$).

models using least square regression, (figures 5 and 6). The bands, upper and lower band, were wide for the early part of the lactation curve to reach the maximum width or largest variability at peak time, then the bands narrowed gradually after peak to be close to the points of the fitting curve at the end of the lactation. Different band width is mainly explained by the amount of variation at different stages of the lactation curve, Since the individual variation is more manifested at early stage of lactation where the cow has the high ability and urge to produce milk. At later stage of the curve, low level of milk production has been accompanied by low individual variation, where most cows are going towards drying off. Mean square error, from fitting milk yield of each month of the overall lactation for farm, season of calving and age of calving within lactation, decreased gradually from 48.058 in the first month to 14.409 in the 18th month. These results are

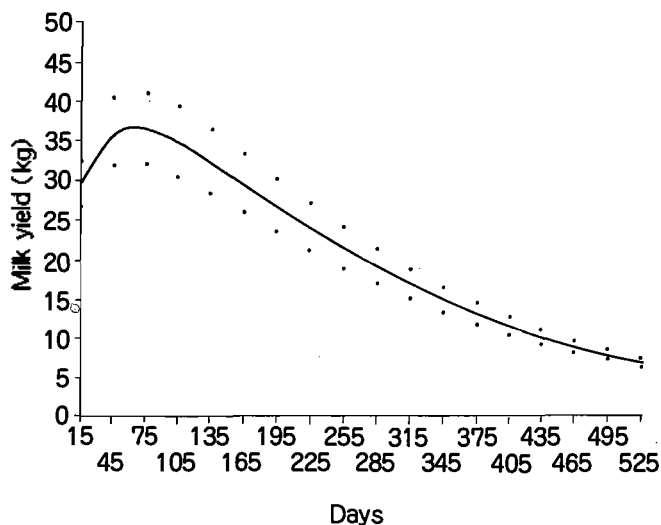


Figure 5. Confidence band for different parities and overall data from fitting linear regression model.

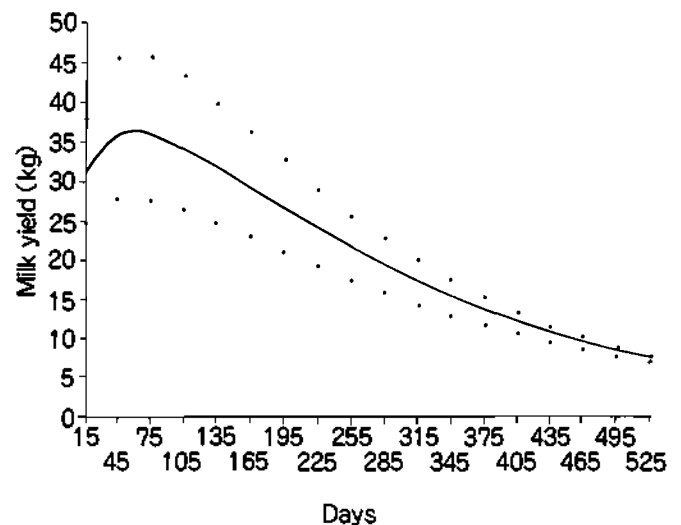


Figure 6. Confidence band for different parities and overall data from fitting non-linear regression model.

in agreement with Madden et al. (1955), who found permanent differences between cows to be more important early in lactation and less important as the lactation progressed. Congleton (1980) and Cobby and Le Du (1978) found more variability around the predicted lactation curve at peak production. Wider bands have been observed from fitting non-linear regression models than linear regression model and this is mainly due to relatively large standard errors for the parameters A, b and c obtained from the non-linear model.

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