Comparison of models for describing the lactation curves of Chios sheep using daily records obtained from an automatic milking system

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Abstract. The objectives of this study were: (i) to compare five models (Wood, Cobby & Le Du, Wilmink, Cappio Borlino, Djikstra) for describing the lactation curve of Chios sheep, (ii) to identify variation in lactation parameters related to environmental factors (season) and animal factors (parity). A data base on 61,705 recordings of daily milk production obtained from an automatic milking system was used. The lactation models were individually adjusted for each lactation. Analysis of variance was performed for the comparison of the parameter estimates. The goodness of fit measures used for comparisons of the models was the coefficient of determination (R^2), mean of mean square error (MMSE), Akaike information criterion (AIC), corrected Akaike information criterion (AICc) and Bayesian information criterion (BIC). Wood model had the lowest values for information criteria (MMSE = 347.4681, AIC = 1,056.436, AICc = 1,056.733, BIC = 1,063.856) and the highest value for the coefficient of determination (R^2=0.79). The highest values for information criteria were found for Djikstra's model (MMSE = 636.6438, AIC = 1,076.621, AICc = 1,077.117, BIC = 1,086.582) having the same time the lowest value for the coefficient of determination (R^2=0.59). Overall, Wood (1967) model showed the best adjustment. Despite of being more recent, the model by Djikstra (1997) mechanist based and with a higher number of parameters showed a low convergence for the data used. Wood model (1967) has a greater advantage of producing a good fit measurement with only three parameters.

Keywords: lactation curve, Chios sheep, daily milk yield, environmental effects

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1. Introduction

The term lactation curve refers to a graphic representation of the ratios between milk production and lactation time (Sherchand et al., 1995). Equations that describe milk production in time provide summary information, which is useful in making management (nutrition) and breeding (culling) decisions, in simulating dairy enterprise and in genetic breeding programs.

The lactation curve is also important because its wide characterization of the animal production throughout lactation allows to estimate the peak yield, the time of peak, days in milk, the total milk yield (Ferreira & Bearzoti, 2003).

There is a lack of studies on the complete lactation of dairy sheep and this is partly due to the fact that in most dairy sheep production systems, lambs are allowed to suck for at least 30 days post lambing and milk recording starts only after the weaning. However, in some dairy sheep flocks operated under intensive management, the common practice is to milk the ewes from the start of the lactation. Lambs are moved from their mothers at lambing into an artificial rearing unit. To study the lactation curve of dairy sheep, several papers dealt specifically with the application of Wood's (1967) model to various sheep breeds (Torres-Hernadez and Hohenboken, 1980, Cappio-Borlino et al, 1989, Sakul and Boylan, 1992, Groenewald et al, 1995, 1996, Portolano et al, 1996a). The first attempts to mathematically represent the lactation curve were made by Brody et al. (1923) and Brody et al. (1924). However, only after the development of the model of the Wood (1967) did the use of lactation curve models become more popular. Since then, many researchers have attempted to develop lactation curve models from empirical conceptions (Cobby Le Du, 1978, Wilmink, 1987, Cappio Borlino et al, 1995) or mechanist conceptions (Djikstra et al, 1997). The major limitations of the Wood curve are the poor fit especially around the lactation peak (Cobby Le Du, 1978) and the large margin of error for the estimation of total milk yield. On the other hand Wood (1967) model has the advantage of estimating three parameters a, b, c which can easily be linked to the biology of the lactation curve. This has rendered the Wood (1967) model the most widely used function for the description of the lactation phenomenon. Advances in modeling, however, provided models which represent biological processes occurring in the mammary gland. Djikstra et al. (1997) developed a mechanistic model that describes proliferation and death of mammary gland cells during pregnancy and lactation. The mechanistic representation provides an understanding of factors controlling the variation in milk production throughout lactation that cannot be attained with most empirical models. However, greater complications arise when using a mechanistic model. For instance, non-limited supply of nutrients to the mammary gland needs to be assumed for simplification.

The objectives of the current study were to compare five models (Wood, Cobby & Le Du, Wilmink, Cappio Borlino, Djikstra) for describing the lactation curve of Chios sheep and to identify effects of season and parity on the lactation curve parameters.

2 Materials and methods

Database

The data used in the current study consist of 61705 recordings of daily milk production of a Chios sheep herd obtained from an automatic milking system. The first milk recording was between 10 and 40 days after parturition, minimum and maximum lactation lengths were 101 and 260 days. In this flock, for a period of time lambs were weaned immediately after parturition but then due to the high mortality rates, lambs were suckled by their mother and weaning was on average 40 days after parturition. The data were ranked according to the lactation number, into first, second, third or greater.

Lactation models

Five models were used in the current study to describe lactation curves. The models are: Wood (1967), Cobby & Le Du (1978), Wilmink (1987), Cappio Borlino (1995) and the mechanist based model by Djikstra (1997). Wood's equation is:

$$y = a\, t^{b} e^{-c\,t} \qquad \textbf{(1)}$$

Where y is milk production (gr/day) at time t of lactation (days), and a, b and c are parameters that determine the shape and scale of the curve. The parameter a is related to the milk yield after parturition, b is the inclining slope parameter and c is the declining slope parameter.

The Cobby & Le Du model is:

$$y = a\text{-}bt - ae^{-c\,t} \qquad \textbf{(2)}$$

Where y is milk production (gr/day) at time t of lactation (days), and a, b and c are parameters that determine the shape and scale of the curve. The parameter a is related to a milk yield, b is the inclining slope parameter and c is the declining slope parameter.

Wilmink's equation is:

$$y = a - be^{-k\,t} - ct \qquad \textbf{(3)}$$

Where y is milk production (gr/day) at time t of lactation (days), and a, b and c are parameters that determine the shape and scale of the curve. The parameter a is related to the level of the milk production, b is the milk yield before peak and c is the declining slope parameter, k is related to peak day of peak milk yield.

The Cappio Borlino model is:

$$y = a\, n^{\,be - c\,n} \qquad \textbf{(4)}$$

Where y is milk production (gr/day) at time t of lactation (days), and a, b and c are parameters that determine the shape and scale of the curve. The parameter a is related to the milk yield after parturition, b is the inclining slope parameter and c is the declining slope parameter.

Dkjikstra's equation is:

$$y= m*\exp[(m_1/k')(1-\exp(-k'*t))-l*t] \qquad \textbf{(5)}$$

Where m is the initial rate of milk production (gr/day) at parturition. The parameters m_1 and l are defined as the specific rates of secretory mammary cell proliferation at parturition and of death respectively, k' is a decay parameter associated with reduction in cell proliferation capacity with time.

Statistical analysis

The models were fitted by non-linear regression to the data described above using PROC NLIN statement of the statistical package SAS (SAS 1999). This non linear regression method is preferred to that of log-linear transformation, because the reduction of weighting of higher yields when using the log scale may lead to a greater lack of fit around the peak (Cobby & Le Du, 1978). Estimates of the parameters of each of the models were obtained for each individual lactation curve. For each model were calculated the typical characteristics of the lactation curve, peak day, peak milk yield and total milk yield. Cluster analysis was used to investigate the nature of the lactation curves in each model. Analysis of variance was performed for the comparisons of the parameter estimates between seasons and number of lactations. Based on information theory, several methods have been developed for comparing models, determining which model is more likely to be correct for describing the used data. The mean of mean square error (MMSE) was calculated as:

$$MMSE=(1/N)*(MSE) \qquad \textbf{(6)}$$

Where N is the number of animals and MSE is the mean square error.

Akaike information criterion (AIC) was calculated as

$$AIC=N\ln(RSS/N)+2K \qquad \textbf{(7)}$$

Where RSS is the residual sum of squares, N is the number of data points and k is the number of independent parameters of the model (Burnham & Anderson, 2002, Motulsky & Christopoulos 2003).

With data sets without a large number of data points (N) or for models containing more parameters the corrected AIC_C is more accurate:

$$AICc=AIC+2k(k+1)/N(N+1) \qquad \textbf{(8)}$$

Bayesian information criterion (BIC; Leonard & Hsu 2001) is a model order selection criterion and imposes a penalty on more complicated models for inclusion of additional parameters:

$$BIC = N*N \ln(RSS/N)+K*\ln(N) \qquad \textbf{(9)}$$

A small numerical value of MMSE, AIC, AICc, BIC indicates a better fit when comparing models.

Table 1. Number of lactations with the smallest information criteria for each model

	Wood	Cappio Borlino	Djikstra	Cobby & Le Du	Wilmink
Number of lactations with the smallest AIC	153	21	43	86	47
Number of lactations with the smallest BIC	186	25	22	97	20
Number of lactations with the smallest MSE	124	19	60	71	76

Table 2. Information criteria for each model

Model	MMSE	AIC	AIC_C	BIC	R^2	Convergence Percentage (C %)
Wood	347.4681	1,056.436	1,056.733	1,063.856	0.79	82.1
Cobby	457.9985	1,076.762	1,073.041	1,084.2278	0.78	77.3
Cappio	423.5469	1,076.931	1,073.2102	1,084.386	0.76	81.01
Wilmink	530.7866	1,087.444	1,082.9083	1,097.423	0.79	63.5
Djikstra	636.6438	1,076.621	1,077.117	1,086.582	0.59	53.5

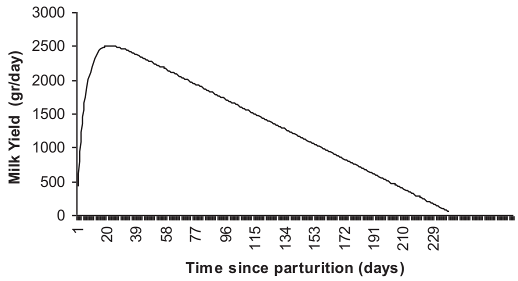

Fig.1. The plot of the average lactation curve for Cobby & Le Du Model.

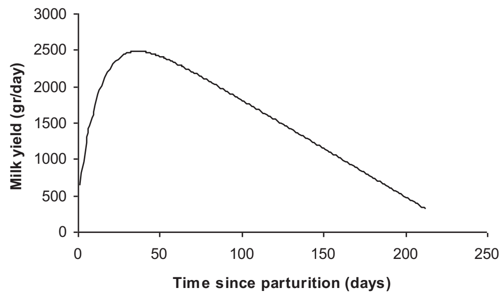

Fig.2. The plot of the average lactation curve for Wilmink Model.

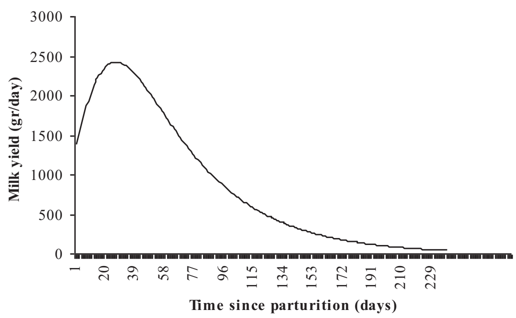

Fig.3. The plot of the average lactation curve for Djikstra Model.

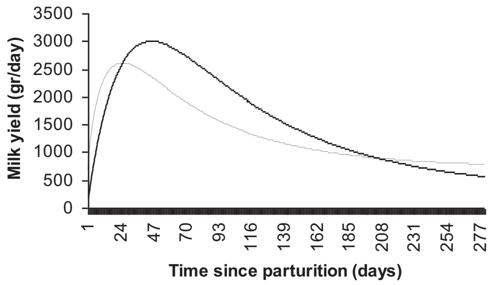

Fig.4. The plot of the average lactation curves of two clusters for Cappio Borlino Model (cluster 1 solid line, cluster 2 dashed line).

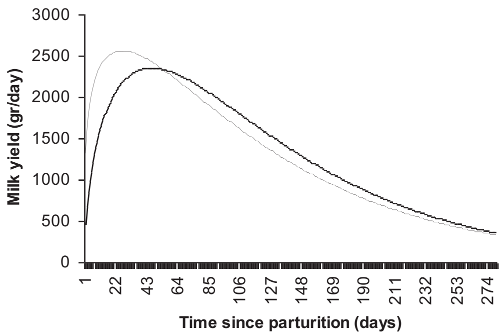

Fig.5. The plot of the average lactation curves of two clusters for Wood Model (cluster 1 solid line, cluster 2 dashed line).

Table 3. Cluster Analysis for Cobby & Le Du model

	a	b	c	Time of peak Yield
Cluster	Mean	Mean	Mean	Mean
1	2,830.8497	11.6251	0.1706	31

Table 4. Cluster Analysis for Wilmink model

	a	b	c	k	Time of peak yield
Cluster	Mean	Mean	Mean	Mean	Mean
1	3,145.3152	2,670.9527	13.3077	0.0746	38

Table 5. Cluster Analysis for Djikstra model

	m	m1	k	l	Time of peak yield
Cluster	Mean	Mean	Mean	Mean	Mean
1	1,301.6837	0.0805	0.0506	0.0131	40

3 Results

Some lactations were well-fitted and others poorly fitted by each of the models examined. Information criteria (MMSE, AIC, AICC, BIC) confirmed the comparison between models. Wood model was superior in fitting the Chios sheep lactation curves showing smaller MMSE, AIC, AIC_c, BIC (Table 2) based on the average values of information criteria. For more than half of the Chios sheep lactation curves BIC criterion values were lower than those of the rest of the models (Table 1). This indicates that the Wood model provided a better fit than the others for over the half of the lactation curves. It was considered not converged each lactation curve model that completed 100 iterations without reaching the reduction of the sum-of-squares-error (SSE) or whose parameters converged to unreal values. The percentage in each lactation curve model was calculated. Djikstra's model showed the worst convergence percentage for the used data. Wood's model had the higher convergence percentage and then follows the Cappio Borlino model. This was expected because Cappio Borlino's model is a non-linear modification of Wood's model. Problems of convergence have been previously reported for the models by Rook et al. (1993), (Perochon et al., 1996, Vargas et al., 2000) and Pollot (2000), Val-Arreola et al., (2004). The coefficient of determination (R^2) also showed a higher value for the Wood model and the Wilmink equation. This result revealed that the Wood model provided a better fit to lactation curves. Although the model by Wilmink presented a good coefficient of determination the values of MMSE, AIC, AIC_C, BIC were high and also showed a lower convergence percentage.

Having established that the fit of the Wood model is the best for the used data cluster analysis was performed in order to investigate the behavior of the lactation curves. For the models Cobby & Le Du, Wilmink, Djikstra cluster analysis detected no differences in the behavior of the lactation curves (Table 3, Table 4, Table 5). The results showed that in these three models the lactation curves showed similar behavior with mean parameter values as seen in Tables 3, 4, 5. The plots of the average lactation curves for the three above models are presented in figures 1, 2, 3. Cluster analysis for the models Cappio Borlino and Wood detected difference in the behavior of the lactation curves. The results are shown in Tables 6 and 7. The plots of the average lactation curves of the two clusters are presented in figures 4 and 5. At Cappio Borlino model the animals of the first cluster start with a lower initial milk yield and reach their peak 2-3 weeks later. The animals of the second cluster start with a higher initial milk yield reach their peak earlier and have a lower decreasing rate c. At Wood model the animals of the first cluster have lower initial milk yield reach their peak about three weeks later comparatively with the animals of the second cluster which have a higher initial milk yield and reach a higher peak milk yield. Peeters et al. (1992), Cappio Borlino et al. (1995) noted that ewes with high milk yield at the beginning of the lactation had a significant reduction of their production due to a genetic effect. Katsaounis and Zygogiannis (1984b) formulated that lactation curve is significantly influenced by the genotype of the ewes. It is very possible that the variation in the behavior of the lactation curves in the used data is due to the differences in the genotype of the animals.

Along with the comparison of information criteria values for all models it is necessary to examine the pattern of the residuals. Lactation data were combined to give a mean lactation curve for all data. Plots of residuals (resulting from comparing the fitted curves against the observed experimental values) are shown in Figures 6, 7, 8 and 9. The latter Figures clearly indicate a better fit by the Wood model than others demonstrating smaller and more randomly distributed residuals (Figs 6, 7, 8, 9).

Analysis of variance was performed for the comparisons of the parameter estimates, time of peak, peak milk yield and total milk yield between seasons and number of lactations for the Wood model which is the best model to describe our data. The data were ranked according to the lactation number, into first, second, third or greater and according to the season of lambing into winter (season 1), spring (season 2), summer (season 3) and autumn (season 4). Results are shown in Tables 8 and 9. The analysis of variance shows that season effects significantly the initial milk yield a ($P<0.01$) of the animal. The initial milk yield a for the animals of the two clusters has a greater value in winter. The animals of the second cluster start with a higher initial milk yield reach their peak two to three weeks earlier and have a higher total milk yield. Parameter b ($P<0.01$) is lower for the animals lambing in winter. The decreasing rate of milk yield c ($P<0.01$) is lower for the animal lambing in winter. A lower value of parameter c denotes a higher persistency in lactation. The number of lactation has significant influence in the parameters and in the typical characteristics of the lactation curves. Parameters a ($P<0.05$), b ($P<0.01$), peak milk yield ($P<0.01$), total milk yield ($P<0.01$) have the tendency to increase in second and decrease in the following lactations. Parameter c ($P<0.01$) has the tendency to increase with the number of lactations. The animals of the first lactation reach their peak later comparatively with later lactations.

Table 6. Cluster Analysis for Cappio Borlino model

		a	b	c	Time of peak yield
Cluster	N	Mean	Mean	Mean	Mean
1	162	212.4825	0.9079	0.0059	46
2	124	705.5924	0.5514	0.0123	27

Table 7. Cluster Analysis for Wood model

		a	b	c	Time of peak yield
Cluster	N	Mean	Mean	Mean	Mean
1	143	469.9499	0.5713	0.0125	46
2	147	1,330.144	0.2868	0.0108	26

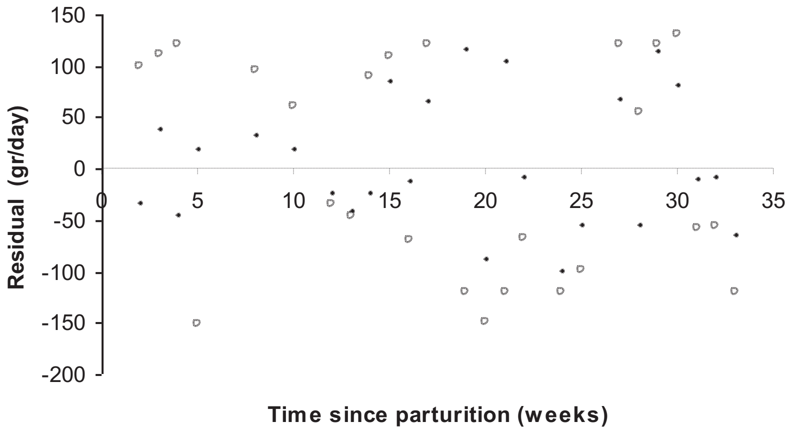

Fig.6. The residual plot for: Wood model (•), Cobby and Le Du model (◦).

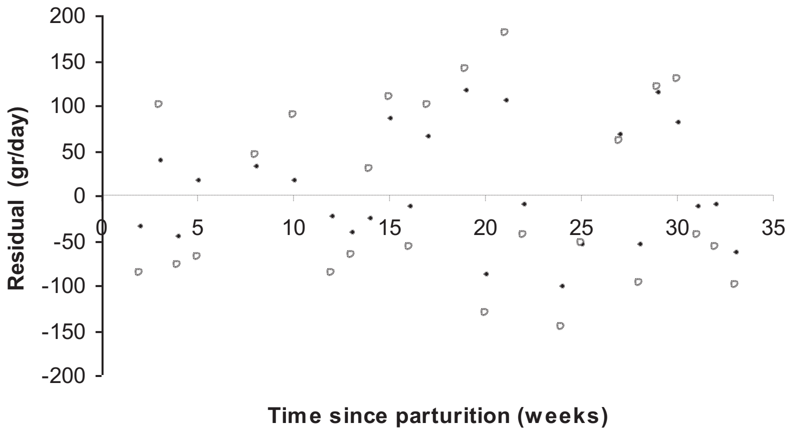

Fig.7. The residual plot for: Wood model (•), Cappio Borlino model (◦).

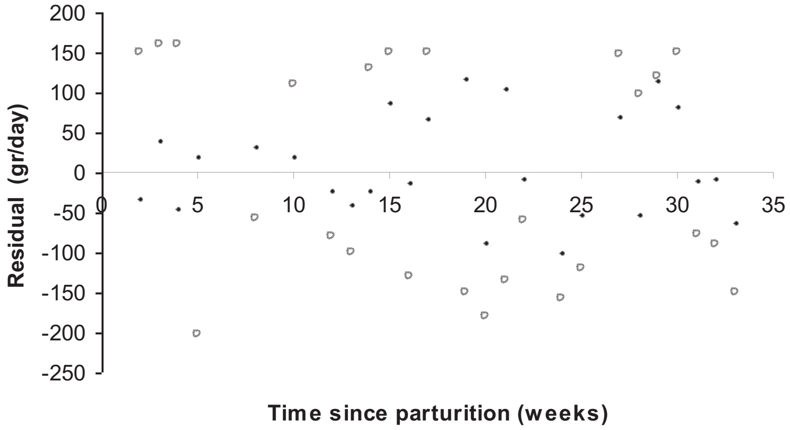

Fig.8. The residual plot for: Wood model (•), Wilmink model (◦).

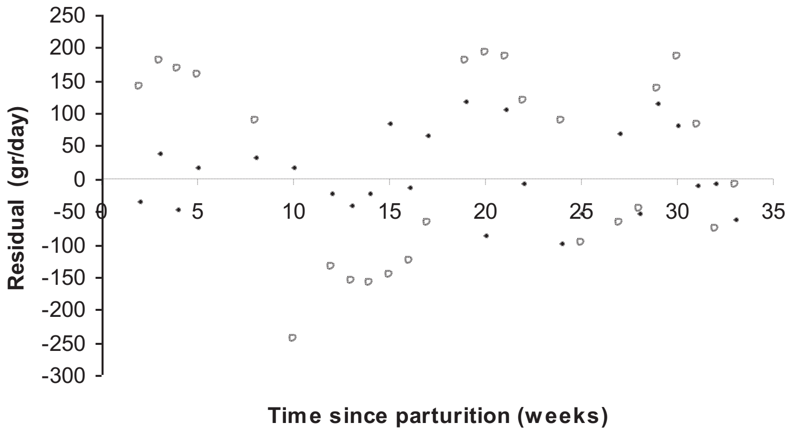

Fig.9. The residual plot for: Wood model (•), Djikstra model (◦).

Table 8. Parameters and estimates of the Wood model (Cluster 1) for the data

Wood (1967) Cluster 1	a	b	c	Pday	PY	TY
Season 1	581.71297 (48.2602)	0.4802 (0.0426)	0.0108 (0.0007)	44 (2)	2,007.909 (117.9499)	291,941.1877 (17,418.0397)
Season 2	396.6664 (30.6201)	0.611 (0.027)	0.0116 (0.00045)	53 (1)	2,156.6187 (74.8368)	318,768.4752 (11,051.388)
Season 3	516.0028 (30.0631)	0.5633 (0.02658)	0.01344 (0.00044)	42 (1)	2,278.521 (73.4754)	307,230.3048 (10,850.3495)
Season 4	478.213 (38.8608)	0.5895 (0.0343)	0.0142 (0.0005722)	41 (2)	2,337.3908 (94.9774)	309,210.5243 (14,025.6112)
No lactation 1	460.3654 (30.6854)	0.5473 (0.0271)	0.0107 (0.0004)	50 (1)	2,001.1615 (74.9963)	299,531.051 (11,074.9456)
No lactation 2	526.5262 (41.7315)	0.5753 (0.0369)	0.0134 (0.00061)	43 (2)	2,396.3517 (101.9935)	325,904.06829 (15,061.7088)
No lactation 3	492.5548 (25.2103)	0.5604 (0.0222)	0.0134 (0.00037)	41 (1)	2,187.8165 (61.6149)	294,927.7498 (9,098.8792)

[1] Values in parenthesis = standard deviation.

a, b, c, = parameters of the Wood model, PY = peak milk yield , Pday = Peak day, TY = total milk yield

Table 9. Parameters and estimates of the Wood model (Cluster 2) for the data

Wood (1967) Cluster 2	a	b	c	Pday	PY	TY
Season 1	1,474.2059 (63.6863)	0.2303 (0.018)	0.0089 (0.0005)	26 (1)	2,448.8119 (73.4418)	340,085.1043 (11,090.9179)
Season 2	1,028.6415 (99.4689)	0.3436 (0.0282)	0.0108 (0.00082)	31 (2)	2,429.6752 (114.7056)	332,038.5337 (17,322.4357)
Season 3	1,362.07084 (72.4404)	0.2733 (0.0205)	0.01162 (0.0006)	23 (1)	2,450.0601 (83.5369)	304,214.8992 (10,085.2688)
Season 4	1,267.6736 (74.7357)	0.2867 (0.0212)	0.01079 (0.0006)	26 (1)	2,460.165 (86.1837)	319,155.1797 (13,015.1623)
No lactation 1	1,375.2912 (96.7763)	0.2106 (0.02745)	0.009 (0.0008)	23 (2)	2,168.12461 (111.6005)	292,155.2798 (16,853.5172)
No lactation 2	1,434.8362 (73.6961)	0.3324 (0.0209)	0.0109 (0.00061)	30 (1)	2,628.4687 (84.9849)	353,573.3822 (12,834.1276)
No lactation 3	1,285.3165 (46.7921)	0.3074 (0.0132)	0.01158 (0.00038)	26 (1)	2,544.941 (53.9598)	325,891.6257 (8,148.8196)

[1] Values in parenthesis = standard deviation.

a, b, c, = parameters of the Wood model, PY = peak milk yield , Pday = Peak day, TY = total milk yield

4 Discussion

Over the years, Wood's equation has been the standard model to describe the lactation curve of animals. Wood in 1977 tried to integrate the rate parameters of this empirical model with the processes of proliferation and death of mammary gland cells. The Wood (1967) model was generally found to be of statistically better fit than other's equations. The animals of the second cluster have a lower value of parameter c. This means that persistency is higher. Animals with a more persistent lactation curve may be less stressed, have better feed utilization efficiency and less nutrition related diseases than animals with a less persistent lactation curve. Also, differences in persistency between animals of two clusters may exist because of genetic selection (Shanks et al., 1981).

In most mammals there is a tendency for the amount of milk produced to increase with successive lactations up to a certain age and thereafter to decline. This is also observed to our data. Those who have studied the effect of age on milk yield in sheep have demonstrated a similar pattern, for example, Bonsma (1939) and Barnicoat et al. (1949). In dairy sheep, Montanaro (1940) found that in Sicilian sheep milk production increased in succeeding lactations to reach a maximum in the fifth and subsequently declined. A similar trend is observed for the peak milk yield. In literature have been reported similar trends (Ramirez-Valverde et al., 1998; Rekik et al., 2003; Magana-Sevilla). Casoli et al. (1989), Hatziminaoglou et al. (1990) and Ubertalle et al. (1990) observed increasing milk yields with the progress of lactation periods. Hatziminaogloy et al. (1990) in their study for the sheep Karagouniko reported that lactation period influences significantly the milk yield. Ewes reach maturity at second lactation period. Similar results have been found by Bencini and Purvis (1990), Kremer et al. (1996), Maurogenis (1996), El Saied et al. (1996). According to Gootwine και Goot (1996) at first lactation period is observed the lowest milk yield. Gradiz et al. (2009) reported that milk yield is usually low in first parity cows because the animal is not fully developed yet and they partition more resources to maintenance and growth at the expense of milk production. The high milk yield in later lactations could also be attributed to selection since animals with low milk yields are normally culled as part of the herd management practices leaving only high producers in the herd.

The influence of season of parturition has been studied very early mostly in dairy cows. Danell (1982) reported that in countries where the grazing season is short and cows are foddered indoors for most of the year, the highest lactation yield is given by cows calving during the autumn and early winter (eg. Johansson & Hansson, 1940, Syrstad, 1965). Effect of month calving can vary in different years, herds and regions (the weather conditions may be one reason), though the general pattern seems to be the same overall (Wunder & McGilliard, 1971, Danell, 1976). Similar reports have been demonstrated (Durhes, M. C., and J. F. Keown. 1991, Freeman. A. E. 1973, D. Norman, R. Meinert, M. Schutz, 1995, Tekerli et al., 2000). A same trend is shown in our results. A highest lactation yield is given by ewes lambing during the autumn or/and winter. It is generally known that climatic conditions influence milk yield in different ways. One way is by changing the animal's metabolism as a result of high temperature and indirectly determining the season of forage and feed utilization (Collier et al., 1982; Jonsson et al., 1999). Gradiz et al. (2009) reported that there was a tendency of cows that calved in the rainy season to have lactations with higher milk production levels than those that calved during the dry seasons. Hatziminaoglou et al. (1990) reported that the important climatic differences and the resulting grazing availability between consecutive production periods are probably responsible for the differences in the effect of the month of lambing and the level of feeding on milk yields.

The model by Wood (1967) has a greater advantage of producing a good fit measurement with only three parameters. This model has been widely used in several types of studies, such as for new models assessments (Cobby Le Du, 1978), genetic breeding (Ferris et al., 1985) milk production simulation systems (Rotz et al., 1999) and nutrition (Fox et al., 2003), because of its recognized capability allied to its simplicity. In our study it is also apparent that the Wood (1967) model still remains a good choice with a great suppleness for describing lactation curves with different behavior.

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