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The application of a mechanistic model to analyze the factors that affect the lactation curve parameters of dairy sheep in Mexico

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Abstract

Pollott´s mechanistic model has been designed to describe lactation curve parameters based on the known biology of milk production and can be useful for analyzing the factors that affect this process. A total of 556 lactations (10,008 weekly test-day records) of crossbred dairy sheep from four commercial farms located in Mexico, were analyzed to investigate environmental factors that influenced lactation curve parameters, using Pollott's 5-parameter additive model. This model was fitted to each lactation using an iterative nonlinear procedure. The estimated parameters were maximum milk secretion potential (MSmax), relative rate of increase in cell differentiation (GR), maximum secretion loss (MSLmax), relative rate of decline in cell numbers (DR) and the proportion of parenchyma cells dead at parturition. A general linear model procedure was used to determine the effect of type of lambing, lambing number, flock and lambing season on total lactation milk yield (TMY) and estimated total milk yield (eTMY). Ewes had an average milk yield of 72 kg with an average lactation length of 140 days. Flock had a significant ($P < 0.05$) effect on most of the analyzed traits, which can be explained by the different farms´ management practices. The TMY were significantly ($P = 0.005$) higher for twin-lambing than single-lambing lactations. Sheep in their first lambing had lower TMY than those in their fourth lambing ($P = 0.01$), possibly explained by the lower values of MSmax (2.85 *vs,* 5.3 kg) and the decrease in DR throughout life ($P = 0.03$). However, the relative GR was greatest ($P = 0.04$) during first lambing and then decreased as lambing number increased. Both lambing number and type of lambing also affected milk yield. The parameters of the Pollott model can be useful to explain, with a biological approximation, the dynamics of differentiation, secretion and death of mammary cells in dairy sheep.

Keywords: dairy sheep; lactation curve; biological factors; mechanistic models of lactation curve

Introduction

Dairy sheep production is an important livestock and economic activity in Mediterranean countries. Recently Latin American countries have developed a dairy sheep industry with the aim of improving farm incomes and providing consumers with high quality dairy sheep products. In order to achieve adequate milk yields that provide financial support to dairy sheep producers, several improvements have been carried out by both genetic and non-genetic means. In Mexico recently there has been a rise in the number of dairy sheep flocks with the introduction of specialized dairy breeds. However, there is no available information about milk production levels and the characteristics of lactation curves that allow evaluation of the production performance and subsequent implementation of improvement strategies.

The lactation curve is a graphical representation of milk production over time and provides useful information for breeding programs and management practices (Dag et al., 2005). Lactation curves can be analyzed using mathematical models. There are several types of mathematical models applied to animal science according to a) their randomness approximation (deterministic and stochastic), b) a temporal approach (dynamic and static) and 3) the depth understanding of biological process (empirical and mechanistic). Mechanistic models of lactation curves have deeper theoretical assumptions about the complex physiological mechanisms that underlie the milk secretion process (Pollott, 2000; Vetharaniam et al., 2003)

Milk production and the shape of the lactation curve are determined by the number of active epithelial cells, their secretory activity and the gradual reduction in number of secretory cell as a result of apoptosis (Svennersten-Sjaunja and Olsson, 2005). Several mechanistic models have been developed based on a biological approach to the lactation curve (Dijkstra et al., 1997; Neal and Thornley, 1983; Pollott, 2000; Vetharaniam et al., 2003). In the majority of these models the number and efficiency of mammary cells are the basis of the mechanistic approach to modeling the mammary gland (Dimauro et al., 2011).

The Pollott model has been specifically designed to describe milk production patterns based on studies (Knight et al., 1998; Knight and Wilde, 1993; Wilde et al., 1997) which focused on the dynamics of the mammary cell population (Albarrán-Portillo and Pollott, 2008). This mechanistic model mimics three processes that occur during pregnancy and lactation: differentiation of mammary secretory cells, programmed secretory cell death (apoptosis) and milk secretion cell per cell (Pollott, 2000). Pollott's model has been compared to empirical and mechanistic models of lactation curve fitting (Angeles-Hernandez et al., 2013; Elvira et al., 2013a; Pollott and Gootwine, 2000) and this model have been found to be the best-fit method using sheep's milk yield records; also, it has the advantage that it provides parameters which can have biological interpretation.

Milk production is a complex biological process and the definition of strategies to improve milk yield requires an understanding of several factors that affect it, including genetics, animal health, seasonal effects, management techniques, udder morphology and nutrition (Pulina et al., 2007). Hence, the use of an appropriate mathematical model to fit lactation curves is needed in order to study the biological factors that affect milk production (Pollott and Gootwine, 2000). The aim of this study was to identify the biological parameters of a lactation mechanistic model that are able to detect the factors that could be managed to enhance productivity of dairy sheep in Mexico.

Material and methods

A total of 553 lactations comprising 9,956 weekly test-day records (TDR) of crossbred sheep, from 4 commercial dairy farms located in the central region of Mexico (Table 1), were analyzed to investigate the factors that influenced the lactation curve parameters of dairy sheep using a 5-parameter Pollott mechanistic model (Pollott, 2000). The crossbred ewes were progeny of East Friesian (sire line) by Suffolk, Pelibuey, Black Belly and Hampshire (maternal line).

Ewes were milked mechanically and milk yields were recorded once per week. Only lactations with the following information were considered for the analysis: ewe identity, lambing date, lambing number and type of lambing. Lactations averaged 18.3 weekly TDR with a minimum of five and maximum of 35 TDR and lactation length ranged between 94 and 166 days post-lambing. The lactation was considered to be finished when the ewe produced less than 0.1 L. Lactations with at least five TDR were analyzed with the five parameter reduced version of the Pollott model; also, only lactations that had their first TDR before day 60 post-lambing were analyzed to allow identification of the peak lactation.

The 5-parameter reduced additive model described by Pollott (2000) was fitted to each lactation using an iterative non-linear procedure (NLIN, SAS Institute, 2002):

$$MY = (MSmax/(1 + (Z*\exp(-GR\,(n-150))))) - (MSLmax/(1 + ((1 - NOD)/NOD)*\exp(-DR*n))) \quad (1)$$

Where: MY = milk yield (L/day) on day n of lactation, MSmax = maximum milk secretion potential of the lactation, Z = ((1-0.999999)/0.999999), GR = relative proliferation rate of secretory cell number during early lactation, MSLmax = maximum secretion loss, DR = relative decline rate in cell number, NOD = proportion of parenchyma cells dead at parturition. For each lactation, the convergence criterion was reached when the difference between the error sum of squares of two successive iterations was lower than 10^{-6}.

Total lactation milk yield (TMY) was computed using the so-called Fleischmann method (Sargent et al., 1968):

$$TMY = y_1 t_1 + \Sigma_{i=2}^{k}((y_i + y_{i+1})/2) * D_i) + y_{k+1} * 7 \quad (2)$$

Where TMY = total milk yield (L); y_1 is yield at first milk recording; t_1 is the interval, in days, between lambing and first milk recording; y_i is the yield at recording *i* and D_i is the interval between the record *i* and record (*i* + 1)(*i* = 1,…k), and 7 is the interval in days, between the last recording and the dry-off.

The biological parameters of the Pollott model were used to estimate total milk yield (eTMY); calculated by summation of the daily milk yields estimated by the Pollott model. The general linear model procedure GLM (SAS Institute, 2002) was used to determine the effect of lambing type (single or twin), lambing number (1^{st}, $2^{nd,}$ 3^{rd} and 4^{th}), farm (1, 2, 3 and 4) and season of lambing (spring, summer, autumn and winter), on dependent variables: TMY, and the parameters of the Pollott model (MSmax, MLSmax, DR, GR and NOD). The assumption of normality of the dependent variables were tested. We defined $P < 0.05$ as significant and P value between 0.05 and 0.1 as a trend. The first order interactions of independent variables were tested, which were found to be not significant in almost all dependent variables; therefore, the final model used was:

$$y_{ijklm} = \mu + Flock_i + Type_j + Number_k + Season_l + e_{ijklm} \quad (3)$$

y_{ijklm} = TMY (L), MSmax (L), MLSmax (L), DR, GR or NOD, respectively.

μ = the overall mean

$Flock_i$ = the effect of *i* level of flock (*i* = 1, 2, 3, 4)

$Type_j$ = the effect of *j* level of lambing type (*j* = single, twin),

$Number_k$ = the effect of *k* level number of lambing (*k* = 1st, 2nd, 3rd, 4th),

$Season_l$ = the effect *l* level of season of lambing (*l* = spring, summer, autumn, winter),

e_{ijklm} = the random residual error

The goodness of fit of the Pollott model was evaluated using the mean square of prediction error (MSPE) using the formula;

$$MSPE = \sum_{i=1}^{n}(O_i - P_I))^2/n - Q \quad (4)$$

Where *n* is the number of TDR's, O_i and P_i are the observed and predicted values of milk yield and *Q* is the number of parameters in the model. The Pearson correlation (r) between TMY and eTMY was calculated to quantify the degree of association between actual and estimated values. Also, Pearson correlations between the lactation traits and parameters of the Pollott model were calculated. Both correlation analyses were performed using the *corrplot* routine from the *corrplot v. 0.77* package (Wei and Viliam, 2016) of R software v. 3.2.2. (R Core Team, 2016)

Results

The Pollott model showed an adequate mean goodness of fit (MSPE = 0.013 L^2, and r = 0.92). Lactations had an average milk yield of 74.4 L during a mean lactation length of 140 days. The mean of parameter values from fitting the Pollott model and tests of significance of the analyzed effects are shown in Table 2. Flock had a significant ($P < 0.05$) affect on most of analyzed traits (Table 3); only MSmax, MSLmax and NOD were found to be non-significant ($P > 0.05$).

Figures 1 and 2 show graphically the effect of lambing number on MSmax, GR, DR and TMY (LSmeans and standard error). Lambing number significantly affected ($P < 0.05$) TMY, MSmax, GR and DR (Table 2). Ewes at first lambing showed the lowest TMY (68.1 L); this increased in the second (72.2 L) lambing and reached the peak in the third lambing (95.9 L), and then declined at fourth lambing (75.0 L) (Fig. 1). The MSmax was lowest in the first lactation (2.8 L) and, increased with lambing number until the fourth lambing, which showed the highest value (5.3 L). The GR and DR were greatest ($P < 0.05$) during the first lambing and then decreased as the number of lambing increased, except for DR at the fourth lambing (Fig. 2).

Lambing season did not affect milk yield or the biological parameters of the Pollott model ($P > 0.05$). Litter size significantly influenced ($P < 0.01$) TMY, in both traits; twin-lambing ewes produced more milk than single-lambing ewes. There was a trend in MSmax ($P < 0.1$) in relation to litter size, showing the same pattern as found for TMY, higher values in ewes carrying multiple foetuses (Table 4). Figure 3 shows Pearson coefficients between TMY and parameters of the Pollott model. Traits TMY and eTMY had the largest correlation (r = 0.92); also, the relationship between LL and TMY was considerable (r = 0.71). The significant (P < 0.05) correlation coefficients that involved parameters of Pollott models showed values of low to moderate (r = -0.12 to 0.52).

Discussion

The milk yields found in the current study are lower than those reported in specialized dairy breeds (Elvira et al., 2013b; Gootwine and Goot, 1994; Pollott and Gootwine, 2004). However, they are similar to previous literature reports of TMY in meat breeds (Ochoa-Cordero et al., 2002; Sakul and Boylan, 1992) and crossbred ewes (Kremer et al., 2010; Mioč et al., 2009). The significant flock effect on milk production and parameters of the Pollott model can be explained by the different farms' management practices, mainly the feeding and weaning management. The experimental flocks had differences in feed management but they all used a moderate to high level of feed supplementation (Table 1). This was likely to reduce the effect of agro-climatic conditions and variation due to the seasons, and could explain the lack of difference in milk production, and lactation curve parameters, in relation to lambing season.

The parameters DR and MSmax could help to explain the differences in TMY between flocks. Flock 1 had the highest TMY, lowest DR (0.12, P = 0.03) and a trend to have the highest level of MSmax (3.43 L, P =

0.08). Hence, higher milk yields are associated with higher MSmax and lower rate of decreasing number of mammary cell due to apoptosis (DR) (Elvira et al., 2013a); fortunately, these parameters were negatively correlated (r = -0.35). MSmax is highly correlated with the peak yield (r = 0.99) (Pollott and Gootwine, 2004). Rekik et al., (2003) suggested that animals with the highest peak yield produce the highest TMY. Largest peak yield (~MSmax) can be associated with a higher genetic potential (Pollott and Gootwine, 2001) and major availability and quality of nutrients (Pollott, 2004). Flock 1 had the longest lactations (166.1 d), which means that the rate of daily milk yield decrease was lower (more persistent lactations), because these sheep had the capacity to maintain daily milk yield above 0.1 L for more days compared with the other flocks. This is in agreement with Pollott and Gootwine, (2001) who suggested that the genes for high yields are linked with a low rate of cell loss (DR), a characteristic of better persistency.

Previous studies have reported higher milk yields of sheep carrying twins in comparison to singles (Afolayan et al., 2002; Gootwine and Pollott, 2000). Higher MSmax values of ewes bearing twins could explain, although showing only a trend (P = 0.09), the observed differences in milk production between single and twin-bearing ewes. This is in agreement with Gootwine and Pollott (2000) who analyzed the effect of type of lambing on Awassi sheep. They mentioned that higher values of milk production and MSmax of twin-bearing ewes was due to a greater number of secretory cells, a higher secretion rate or a combination of both. In this model MSmax (N x S_a) is defined as the product of total of mammary epithelial secretory cells (N) produced and, differentiated through lactation by maximum secretion rate (S_a, kg/cell/d). *In vivo* experiments support our findings of Pollott parameters, where ewes giving birth to multiple lambs had greater mammary growth and development, with higher total mammary DNA and RNA contents as indicators of number of epithelial cells and their synthetic activity, respectively (Manalu et al., 2000; Manalu and Sumaryadi, 1998; Rattray et al., 1974).

Previous research has shown that differences in the dynamics of mammary cell renewal have a strong influence on the shape of the lactation curve and productivity (Castañares et al., 2013; Colitti and Farinacci, 2009; Manalu and Sumaryadi, 1998). The findings in the current work suggest that differences in secretory cell dynamics, which is orchestrated by elegant and specific hormonal control, are associated with the effect of litter size. Ewes bearing multiple foetuses have more *corpora lutea* and heavier placental mass (Pulina et al., 2007); therefore the higher MSmax and TMY values in twin lambing ewes can be due to an increase in progesterone and placental lactogen (PL), secreted by the corpus luteum and placenta, respectively (Gootwine, 2004). PL has a prolactin-like and growth hormone biological effects, that enhance the preparation of the mammary gland for lactation, stimulation of steroidogenesis, foetal growth and alteration of the maternal metabolism (Akers, 2002). Also, a positive relationship between litter size and PL levels with milk yield has been reported previously (Lérias et al., 2014). The role of progesterone is not only at the onset of lactation because, as has been reported, ewes with higher progesterone concentrations maintain more cells and higher synthetic activity at the end of lactation (Manalu and Sumaryadi, 1998).

Milk production depends on both the ewes' milk production potential and the net energy available for lactation (Dimauro et al., 2011). There is evidence that high-yielding ewes do not reach their potential milk production due to their inability to satisfy their nutritional requirements during early lactation, even under *ad libitum* feeding. The use of body reserves is a key practice in order to achieve adequate milk yields, mainly in the first phase of lactation. The lower TMY of primiparous in comparison to multiparous ewes has been previously reported (Pulina et al., 2007; Ruiz et al., 2000) and it could be in part associated with the lower provision of nutrients to the mammary gland to synthesize milk components, as primiparous animals have to use their nutrients not only for lactation, but also for their own growth (Lérias et al., 2014).

Additionally, younger ewes have lower body weight, body condition score and body reserves (González-García et al., 2015) than older ewes; a factor that must be taken into account here is the age at first lambing (AFL). Hernandez et al., (2011) found that ewes with extremely early AFL had lower TMY, as a consequence of their less developed bodies at first lambing. On the other hand, the same authors found that ewes lambing at ages older than 510 d showed lower milk production per lifetime, fewer productive lactations and numbers of lactations/ewe per year of productive life and higher lambing intervals. Hence, AFL has important effects not only on milk production performance but also on reproduction and longevity parameters; therefore, the AFL should be managed to optimize the whole production system, including mammary development. However, none of the flocks analyzed had available data about AFL despite the important effect of this factor on milk production; therefore, recording of AFL must be added to the registered variables at flock level.

As the lambing performance increases with age there is an improvement in the efficiency of homeorhetic dynamics involved in the partition of nutrients to the developing mammary gland and milk synthesis (González-García et al., 2015). Our results show an increase of TMY with lambing number, as previously (Angeles-Hernandez et al., 2013; González-García et al., 2015). The substantial difference of parameters that define the patterns of lactation curve and milk yield between lactation numbers are probably related to the biology of the mammary gland.. By interpreting the biological parameters from Pollott´s model, it can be established that the maximum TMY reached in third lambing is associated with lower decline in the udder cells (DR). This disagrees with the results from the Awassi (Pollott and Gootwine, 2004) and Lacaune sheep (Elvira et al., 2013a), both studies showed that milk yield declined as the ewes aged. Also DR increased and MS declined as lambing number increased. However, our results and both studies are in agreement about the positive correlation between eTMY with MSmax and lactation length (LL) (r = 0.17 and r = 0.68, respectively) and the negative relationship of LL with DR (r = -0.18) (Fig. 3). Although, the correlation between eTMY and MSmax was lower than the value reported by Pollott and Gootwine, (2004)(r = 0.72), this discrepancy in the level of association between studies can be associated with the differences in management practices and genetic potential of the sheep analyzed in each study.

According to Pollott (2000), the GR describes the speed at which active cell numbers increase during pregnancy and early lactation. In the current work, the GR decreased with lactation number in contrast to milk production that increased with age. There is evidence that in small ruminants alveoli and secretory structures development from the previous lactation do not disappear entirely during involution, but are added to those which grow in the following lactation, increasing the udder volume, especially the secretory parenchyma tissue (Lérias et al., 2014). This possibly explains the higher TMY and MSmax in multiparous ewes despite of their lower GR values.

Biological parameters of the Pollott model help us to explain the characteristics of lactation, predict appropriate milk yields and detect the systematic changes in yield caused by biological factors; this is in agreement with previous work in crossbred sheep (Angeles-Hernandez et al., 2013) and pure breeds like Awasssi (Pollott and Gootwine, 2000, 2004) and Lacaune (Elvira et al., 2013a, 2013b).

At farm level, the biological interpretation of parameters of the Pollott model can contribute to the improvement of dairy sheep performance. The estimation and interpretation of MSmax and the selection of animal with better values, according to our findings, can help to raise milk yields in sheep flocks of studied region; supported by the results of previous works that found heritability to be moderately high (h^2 = 0.28) for this parameter (Albarrán-Portillo and Pollott, 2008). The management of factors to decrease apoptosis rate (e.i. avoid stressor, increase milking frequency) may enhance lactation persistence, since the results of current work showed that as DR decreases there was an increase of milk production (Pulina et al., 2007).

Conclusion

Flock, lambing number and lambing type effects were the main factors that affected milk production in crossbreed sheep. Also, the parameters of the Pollott model can help to explain, with a biological approximation, the dynamics of differentiation, secretion and death of mammary cells in dairy ewes. The information that provides the fit of the Pollott model may be translated into management strategies (nutritional, breeding, milking technique, etc.) to enhance the dynamic cell of the mammary gland and improve milk production of dairy sheep.

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Figure captions

Figure 1. Lambing number effects on total milk yield (L) and maximum secretion potential (MSmax) of dairy sheep (LSmeans + S.E.[1]).

MSmax, maximum milk secretion potential of the lactation.

[a, b, A, B] Means without a common superscript differ significantly ($p<0.05$) by Tukey´s post hoc test.

[1] LSmeans = least square means; S.E. = standard error of the mean.

Figure 2. Lambing number effects on total milk yield, relative growth rate (GR) and death rate in cell differentiation (DR) of dairy sheep (LSmeans + S.E.[1]).

GR, relative proliferation rate of secretory cell number during early lactation; DR, relative decline rate in cell number.

[a, b, c, d, A, B] Means without a common superscript differ significantly ($p<0.05$) by Tukey´s post hoc test.

[1] LSmeans = least square means; S.E. = standard error of the mean.

Figure 3. Pearson correlation coefficients between total milk yield and parameters of the reduced additive Pollott model.

$^{*}P< 0.05$, $^{**}P<0.01$.

TMY, total milk yield; eTMY, estimated total milk yield; LL, lactation length; MSmax, maximum milk secretion potential of the lactation; MSLmax, maximum secretion loss; GR, relative proliferation rate of secretory cell number during early lactation; DR, relative decline rate in cell number; NOD, proportion of parenchyma cells dead at parturition.

Table 1. Management and database characteristics of four flocks analyzed.

	Flock			
Traits	1	2	3	4
Feeding management[a]	Grazing[1] + S1	Grazing[1] + S2	TMR feedlot[2]	TMR feedlot[3]
Weaning management[b]	DY1	MIX	DY15	MIX
Reproductive management	Natural breeding	AI	AI	Natural breeding
Lactation length (days)	166.1	127.5	100.2	94.1
Day at first TDR	9.5	45	20.2	38.2
Number of TDR	23.4	10.4	11.9	9
Daily milk yield (L/day)	0.52	0.64	0.56	0.75

[1]Alfalfa and ryegrass; S1, alfalfa hay (0.5 kg/ewe/day) and corn grain (0.5 kg/ewe/day) provided at milking time; S2, concentrate commercial (1.2 kg/ewe/day) provided at milking time.

[2]Sorghum grain 28.4%, corn grain 17%, soybean meal 12%, oat hay 10%, cottonseed 10%, canola meal 9%, bran wheat 7%, mineral premix 3.5%, calcium carbonate 1.6% and protected rumen fat 1.5%.

[3]Comercial concentrate 74.14 %, oat hay 17.69 %, alfalfa hay 3.63 %, corn silage 2.54 %, and mineral premix 2 %.

[b] DY1, ewes were weaned from their lambs at 24 h postpartum and then were milked once daily, and their lambs raised artificially; MIX, ewes were milked once daily from day 31 after lambs were removed during the evening only, and milked twice daily after lambs were weaned at 60 days old; DY15, ewes reared to their lambs until the day 15, hence ewes were weaned and milked twice daily.

IA, artificial insemination; TDR, test day record.

Table 2. The influence of the analyzed effects on total milk yield, estimated total milk yield, lactation length and estimated parameters of the Pollott model.

Traits	Mean	SD[1]	Effect probability			
			Flock	Lambing season	Lambing number	Litter size
TMY (L)	74.4	53.9	0.001	0.9	0.01	0.005
LL (days)	140	65.5	0.002	0.33	0.3	0.16
MSmax (L)	3.12	2.6	0.08	0.6	0.04	0.09
GR	0.049	0.06	0.004	0.54	0.04	0.83
DR	0.164	0.32	0.03	0.47	0.03	0.24
MSLmax (L)	2.98	2.8	0.1	0.52	0.28	0.34
NOD	0.21	0.16	0.69	0.26	0.78	0.22

[1] SD = standard deviation

TMY, total milk yield; LL, lactation length; MSmax, maximum milk secretion potential of the lactation; MSLmax, maximum secretion loss; GR, relative proliferation rate of secretory cell number during early lactation; DR, relative decline rate in cell number; NOD, proportion of parenchyma cells dead at parturition.

Table 3. Flock effect on milk production and parameters of the reduced additive Pollott model (LSmeans[1]).

Traits	Flock				S.E.[1]
	1	2	3	4	
TMY (L)	89.8[a]	81.7[a]	40.1[b]	70.2[ab]	8.20
LL (days)	166.1[a]	127.5[b]	100.2[b]	92.1[b]	9.55
MSmax (L)	3.43	3.19	2.67	2.06	0.42
GR	0.035[b]	0.096[a]	0.047[b]	0.086[ab]	0.01
DR	0.12[a]	0.29[b]	0.17[b]	0.28[b]	0.04
MSLmax (L)	3.40	2.38	1.83	1.51	0.44
NOD	0.24	0.10	0.21	0.21	0.05

TMY, total milk yield; LL, lactation length; MSmax, maximum milk secretion potential of the lactation; MSLmax, maximum secretion loss; GR, relative proliferation rate of secretory cell number during early lactation; DR, relative decline rate in cell number; NOD, proportion of parenchyma cells dead at parturition.

[a, b] within a row, means followed by a common superscript do not differ significantly ($P < 0.05$)

[1] S.E. = standard error of the mean, LSmeans = least square means.

Table 4. Litter size effect on milk production and parameters of the reduced additive Pollott model (LSmeans[1]).

Traits	Single	Twin	S.E.[1]
TMY (L)	75.3[b]	107.5[a]	3.28
LL (days)	153	147	4.06
MSmax (L)	2.98	3.54	0.16
GR	0.05	0.048	0.005
DR	0.17	0.12	0.019
MSLmax (L)	2.82	3.49	2.92
NOD	0.22	0.22	0.16

TMY, total milk yield; LL, lactation length; MSmax, maximum milk secretion potential of the lactation; MSLmax, maximum secretion loss; GR, relative proliferation rate of secretory cell number during early lactation; DR, relative decline rate in cell number; NOD, proportion of parenchyma cells dead at parturition.

[a, b] within a row, means followed by a common superscript do not differ significantly (*P* < 0.05)

[1] S.E. = standard error of the mean, LSmeans = least square means.