UNIVERSITÀ DEGLI STUDI DI SASSARI

SCUOLA DI DOTTORATO

SCIENZE DEI SISTEMI AGRARI E FORESTALI E DELLE PRODUZIONI ALIMENTARI

XXII CICLO

Indirizzo

Scienze e Tecnologie Zootecniche

The mathematical description of the lactation curve of Ruminants: issues and perspectives

Direttore della Scuola: Prof. Pietro Deidda
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Tutor: Dr. Corrado Dimauro   **Dr. Roberto Steri**

Anno Accademico 2008-2009

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TABLE OF CONTENTS

CHAPTER IV

LACTATION CURVES OF MASSESE EWES

CHAPTER V

CHAPTER VI

<center>**CHAPTER I**</center>

INTRODUCTION

Milk Production

Milk production is a complex physiological process of great importance in mammals representing the way for providing food for the offspring in early stages of life.

From an economic standpoint, milk obtained from ruminants species (and, to a lesser extent, from camels and horses) represents one of the main food sources for a large part of the World population (table 1).

Table 1. World milk production (Mt) for cattle, buffaloes, goat and sheep (FAO, 2009)

	Buffaloes	Cattle	Goat	Sheep	Total by continent
Europe	0.2	208.6	2.6	3.0	214.4
Asia	84.1	144.4	8.8	4.2	241.5
Americas	-	162.1	0.7	0.04	162.8
Africa	2.3	26.6	3.1	1.8	33.8
Oceania	-	25.1	0.00004	-	25.1
Total by species	86.6	566.9	15.1	9.0	677.6

The phenomenon of milk production, or lactation, starts at parturition and continues until the dry-off of the lactating female. Its evolution over time is characterised by a peculiar pattern, common to several species of mammals, generally known as lactation curve. The standard shape of the lactation curve is characterised by an initial increasing phase, from parturition till a maximum, followed by a declining phase that ends at the dry-off. Such a pattern can be considered the result of two main components. The first one is regular and continuous and can be ascribed to a general pattern of the phenomenon. The second one is random and unpredictable and refers to individual

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives"   - 1 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

deviation from the general pattern. Actually, this is a common feature of several biological phenomena that are the result of the interaction between a deterministic component, that refers mainly to genetic and systematic factors affecting the phenomenon under study and a stochastic component, peculiar to each individual and, therefore, largely unpredictable. (Cappio-Borlino et al., 2004).

The first component of the lactation curve shape is a direct consequence of the physiological processes that occur in the mammary gland during milk production. Milk compounds are either synthesized and secreted by specialised epithelial cells of the mammary gland or filtered from the blood stream. The basic mammary secretive structure is represented by the alveoli, a spherical aggregate of cells with a central lumen where the milk is secreted. Such a structure is not fixed but it is subjected to modification during the evolution of lactation. During pregnancy there is a phase of rapid cellular activation which diminishes gradually in early lactation. Then a cellular regression occurs and continues, at varying rates, till the cessation of lactation (Hurley, 1989). Considering that the quantity of milk produced by the mammary gland in each particular phase of lactation strongly depends on the number of active secretory cells and on the efficiency in synthesising of each cell, the above mentioned mechanism of evolution of the mammary gland explains the standard shape of the lactation curve (Figure 1). In this figure, the basic traits of the lactation curve shape can be observed: a rapid increase in milk production until the maximum or peak production (ym), the time at which peak occurs (tm); the rate of decrease of milk yield in the second part of lactation, whose inverse represents the persistency of lactation, i.e. the ability of the lactating animal to maintain a more or less constant yield in the declining phase of lactation.

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives"
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

- 2 -
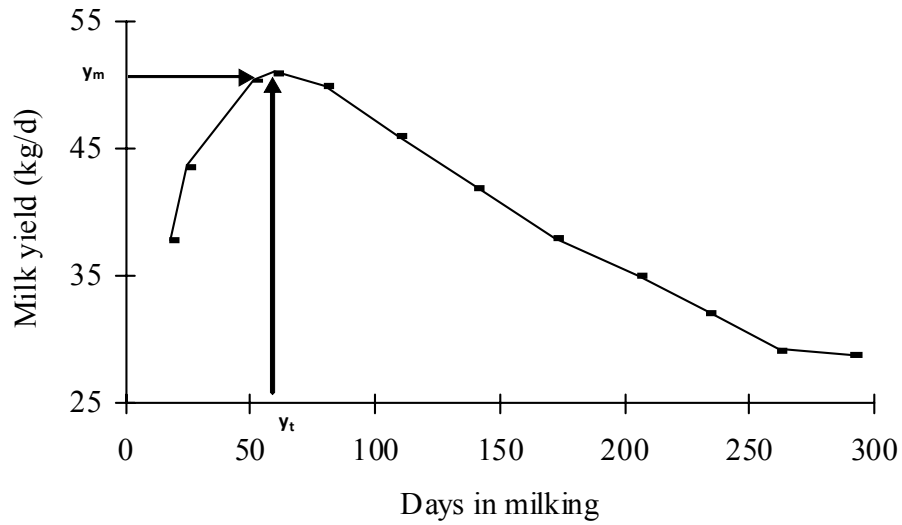
Figure 1. The standard lactation curve of dairy cattle.

This pattern is rather common in different species of ruminants. Figures 2 a, b, c, and d report lactation patterns of cattle, buffaloes, goats and sheep, respectively.

It can be clearly observed that, in spite of different quantitative levels of production, the trend of production over time shows the same tendency, with an initial growing phase up to a maximum, followed by a more or less slow decline.

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives"
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

- 3 -
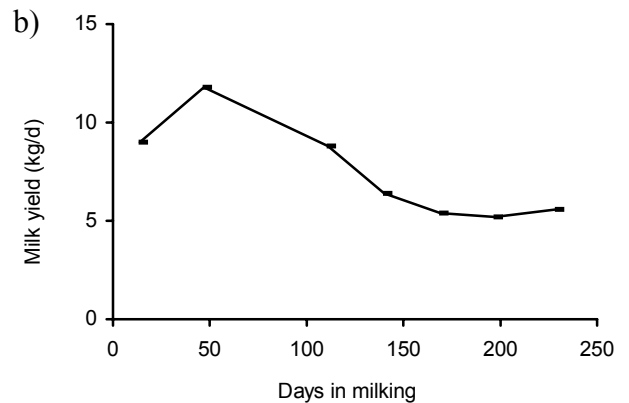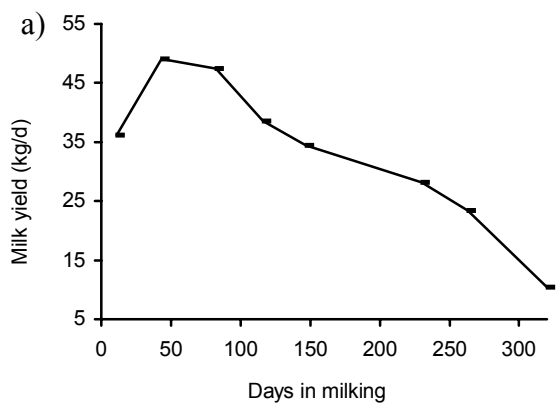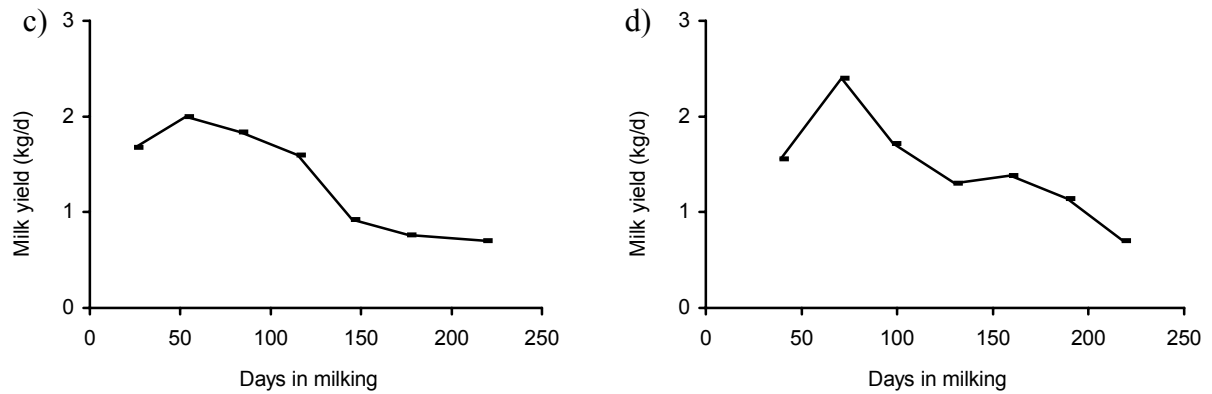
Figures 2. *Evolution of daily milk yield along the lactation period in dairy cattle a), buffaloes b), goat c) and sheep d).*

In wild ruminants, including those closely related to domestic ruminants, milk production by the mother covers just the suckling period of the newborn, usually three or four months (Pulina et al., 2001a). Thus, offspring starts autonomous feeding and the mammary gland of the mother is restored for a further pregnancy. Longer lactation lengths enlarge the period of parental care, make search for feeding more problematic, increase the danger of attack by predators, and lower reproductive efficiency of animals. On the other hand, selection performed on domesticated ruminants for over 10,000 years results in a marked modification of the lactation curve shape. In particular, the rate of decline of milk production after the lactation peak has been deeply modified. Actually, the selection has affected mainly the mechanism that regulates the cellular regression process occurring in the second half of lactation. As a result, species and breeds selected for milk production are characterised by a reduced rate of decay of secretive cells and, therefore, a reduced slope of milk yield after lactation peak. So, persistency of lactation is one of the traits of lactation curve that mainly characterises dairy animals. As an example, figure 3 reports the lactation curves of meat and dairy ewes.

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives"
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche
- 4 -
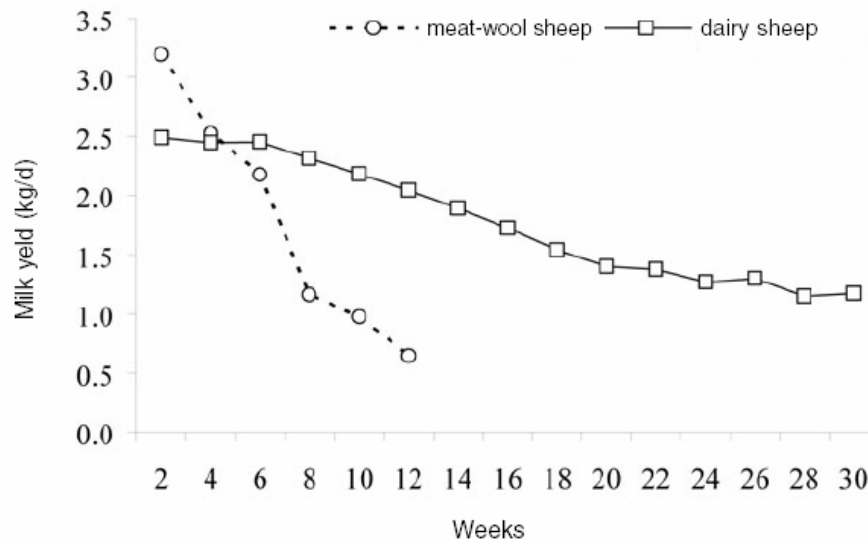
Figure 3*. Lactation curves of meat (circle) and dairy (square) ewes (from Snowder and Glimp, 1991 and Cappio-Borlino et al., 1997, reported by Pulina et al., 2007).*

Sheep selected for milk production show a lower raise to the peak, higher persistency and longer lactation length in comparison with meat animals.

The second component of the milk production pattern is represented by individual deviations from the regular pattern and can be ascribed to several factors of variation such as the genetic background, feeding, farming system, environmental conditions and health status of the animal (Macciotta et al., 2008). As an example of deviations from the standard shape, figure 4 reports some individual lactation curves of dairy cattle. Compared to the standard shape (curve S), the pattern P is characterised by a reduced rate of increase in the first phase, a lower peak yield with later occurrence and a greater persistency. The curve WPD lacks of the peak yield: such kind of curves are called atypical and have been observed in cattle (Congleton and Everett, 1981; Shanks et al., 1981; Olori et al., 1999; Rekik and Ben Gara, 2004), sheep (Cappio-Borlino et al., 1997; Franci et al., 1999; Portolano et al., 1996), goats (Macciotta et al., 2008) and buffaloes (Macciotta et al., 2006). The occurrence of atypical curves, that in dairy sheep

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives"   - 5 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

has been estimated in around 20-30% (Cappio-Borlino et al., 1997), can been ascribed to the biological variation between animals, the structure of the data analysed and to the mathematical structure of the model used (Macciotta et al., 2005). Finally, curve WPC does not show a defined trend.
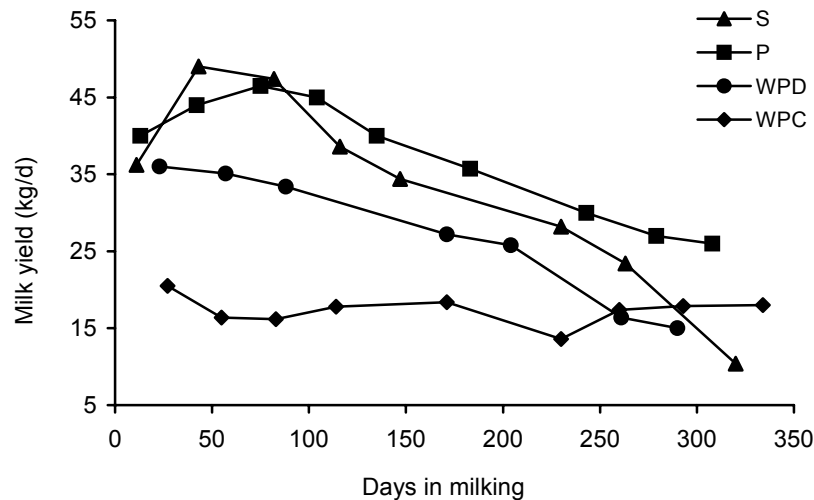
Figure 4*. Example of different shapes of lactation patterns in cattle: standard (triangle), persistent (square), without peak and decreasing (circle) and without peak and constant yield (rhombus).*

Another typical pattern of animal farmed on pasture-based system is characterised by the occurrence of a double lactation peak. Such a feature has been observed in sheep and cattle (Garcia and Holmes, 2001). Figure 5 reports a double peak curve of dairy sheep. The first peak corresponds to the physiological lactation maximum whereas the second occurs in spring, when there is the highest availability of pastures, that represent the main feeding source for sheep farmed in semi-extensive systems of the Mediterranean area.

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" – 6 –
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche
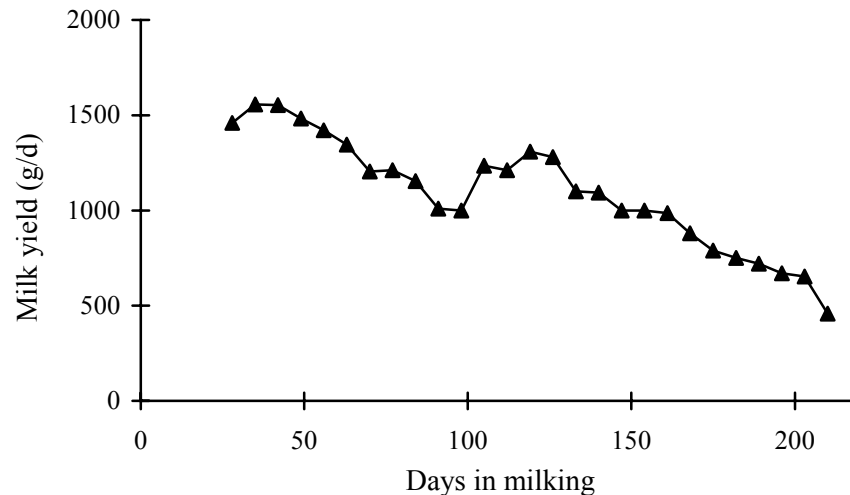
Figure 5. Lactation curve of a dairy sheep with two peaks.

Why to model lactation curve?

The mathematical description of the temporal evolution of milk production in ruminant species farmed for milk production represents one of the most important applications of mathematical models in animal science (Pulina et al., 2001b; France and Thornley, 1984). Several reasons can be found for the need of a mathematical modelling of the lactation pattern. Mathematical models of the lactation curve and, in general, of the mammary gland represent a valuable tool for basic research studies aimed at increasing the scientific knowledge of complex physiological mechanisms that underlie the milk secretion process (Dimauro et. al 2007). Lactation curves may be used by physiologists, nutritionists and other researches to mimic the lactation process and to study the relationships existing between secretory cells, hormones, energy supply and environmental effects affecting the milk production process.

On a dairy farm scale, the pattern of milk yield across the year depicts the trend of the main farm income. Moreover, it is strongly correlated with evolution of the nutritive requirements of the animals and, consequently with feeding costs, that

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 7 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

represent one of the most important expenses in dairy farming. Thus a mathematical tool able to accurately describe the pattern of milk yield during the year and to forecast future yield supplies useful pieces of information to assist the farmer and the agricultural extension workers in several management decisions. Such information is of aid in the programs of genetic improvement, herd management, feeding, health monitoring and profits evaluation, besides the construction and validation of bioeconomic models and software for livestock species (Freeze and Richards, 1992; Pulina et al., 1995; Boe et al., 2005). Actually, several softwares commonly used in farm feeding management as the Cornell CNPCPS model for dairy cattle (Fox et al., 2004) incorporate in their routines the model of lactation curve to estimate the daily requirements of lactating animals.

At animal level, the knowledge of main traits of lactation pattern provides important elements for predicting future yields thus enabling an anticipate choice of animals that have to be culled, or that are affected by some disease but that do not show clinical signs, or that have some special dietary needs (Gipson and Grossman, 1989).

Another important field of application of lactation curve modelling is the genetic improvement of milk production traits. Since the 90's, the estimation of the genetic merit of cattle was performed by analysing the cumulated lactation yield for a standardised lactation length of 305 days with BLUP animal models. In this approach, lactation curve functions were useful, for example, for the projection of the lactation in progress of daughters of young bulls running progeny test in order to anticipate their first crop evaluation. When the estimation of the genetic merit based on daily test for milk yield and constituents was proposed, with the so-called test day models (Ptak and Schaeffer, 1993), it became obvious that the genetic models should have to include a function able to account for the effect of the lactation stage at which the measure was

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives"
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche
- 8 -

taken, i.e. the effect of the lactation curve. In the most updated version of the test day model, the random regression model, individual curves of animals are modelled with mathematical functions and random coefficients for each animal are calculated (Jamrozik et al, 1997). Finally, the knowledge of genetic basis of main traits of lactation curve, as peak yield and persistency, may supply interesting indication for modifying the lactation shape in an economically desirable direction.

From all the above mentioned considerations, it is clear that lactation curve modelling has to address two main issues. The first is the reconstruction of the regular and continuous component of the lactation pattern. This requirement is particularly evident for applications in management decision but also in research studies. The other issue is represented by the need for fitting individual deviations that have a greater interest for the estimation of the genetic merit of the animals via random regression test day models. These two basic requirements and their relative importance have markedly affected the evolution of the mathematical modelling of the lactation curve over the years.

LACTATION CURVE MODELLING

Lactation curve modelling means to express main features of the lactation shape in few terms with biological and technical meaning. Under a statistical standpoint, the variable to be modelled, i.e. daily milk yield at different time distance from parturition, represents a case of repeated measures along a trajectory of time. Basic traits of the curve can be defined those that determine the succession of points of inflection and of curvatures along the lactation trajectory: rate of increase of yield from parturition to the peak; days in milk at which peak yield occurs (time at peak); milk

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 9 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

yield at lactation peak (peak yield); rate of decrease of milk production after the peak, the inverse of which is called persistency of lactation and represents the ability of the animal to maintain a constant yield after the peak.

According to the theoretical approach used to describe the main components of the lactation pattern, mathematical models suggested for studying the lactation curve can be divided into two main classes: empirical models and mechanistic models.

Empirical mathematical models are essentially aimed at disentangling the regular and continuous component from the stochastic one regardless possible biological interpretation of the parameters of the function used and the mechanisms that underlie the process itself. Actually empirical models are those that found large application in different fields of animals science, basically due to their limited mathematical complexity.

Mechanistic models are essentially aimed at translating in mathematical terms a hypothesis about biological and biochemical processes that regulate the phenomenon of interest (Neal and Thornley, 1983). Such an approach, even if of great interest for research and also for practical implementations, has been little developed in animal sciences. This was due to the high theoretical complexity of mechanistic models, to the large number of input variables involved and to the high computation requirements (Macciotta et al., 2008).

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives"
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche
- 10 -

The functional approach

Several empirical mathematical functions have been proposed to describe the lactation curve of dairy cattle (Beever et al., 1991; Grossmann and Koops, 1999; Sherchand et al., 1995), differing in mathematical properties, in the number of parameters and in their degree of relationships with the main features of a typical lactation pattern, such as peak yield, time at peak and persistency.

The most common approach is to fit the milk yield at time t with a continuous function of time

$$y = f(t) + e$$

where $f(t)$ is a continuous and differentiable function of the time that corresponds to the lactation length, and e is the random residual.

A first attempt to synthesize the temporal variation of milk yield with a functional relationship was proposed by Brody et al. (1923) which used an exponential function to describe the declining phase of lactation in dairy cattle as following:

$$Y_t = ae^{-ct} \qquad [1a]$$

where:

y_t = daily milk yield at time t

a = function parameter representing the approximate initial milk yield at the beginning of lactation

c = declining slope parameter.

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 11 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

Such a function generates a monotonically decreasing curve. Therefore it is not able to fit the initial raise to the lactation peak. To overcome this limitation, the authors presented an improved version of this model by incorporating an inclining rising phase (Brody et al., 1924):

$$Y_t = ae^{-bt} - ae^{-ct} \qquad [1b]$$

where:

   b = inclining slope parameter up to peak yield.

Cobby and Le Du. (1978) observed that model [1b] overestimated milk yield around peak and during late lactation and underestimated it in mid-lactation.

Sikka (1950) proposed a parabolic exponential function for modelling the lactation curve:

$$Y_t = ae^{(bt - ct^2)} \qquad [2]$$

where:

   b = Inclining slope parameter up to peak yield

   c = declining slope parameter.

Model [2] gave good fit for curves of first parity cows, but it was less efficient for older parities, being symmetric around the lactation peak (Gahlot et al., 1988).

An inverse polynomial model was suggested by Nelder (1966) :

$$Y_t = t /(a + bt + ct^2) \qquad [3]$$

where:

   a = approximate initial milk yield after calving

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives"   - 12 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

b = Inclining slope parameter up to peak yield

c = declining slope parameter.

The combination of the parameters of model [3] allow for the calculation of some basic traits of the lactation curve. Thus peak milk yield is calculated as

$$y_m=(2/(ac)+b)^{-1}$$

and time at peak as

$$t_m=\sqrt{(a/c)}$$

Compared to model [2], Nelder's Inverse polynomial yields better fits. In a study carried out on individual lactation curves of Holsteins, Olori et al. (1999) showed that model [3] under-predicts the milk yield around the peak and over-predicts it immediately afterwards.

The model that follows is probably the most popular and widely used empirical model of the lactation curve, the modified gamma function proposed by Wood (1967):

$$Y_t = at^b e^{-ct} \qquad [4]$$

where:

Y_t, a, b and c have the same meaning of model [3].

Wood function is a multiplicative model consisting of two main components regulating yield increase and decrease respectively (figure 6).

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives"   - 13 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche
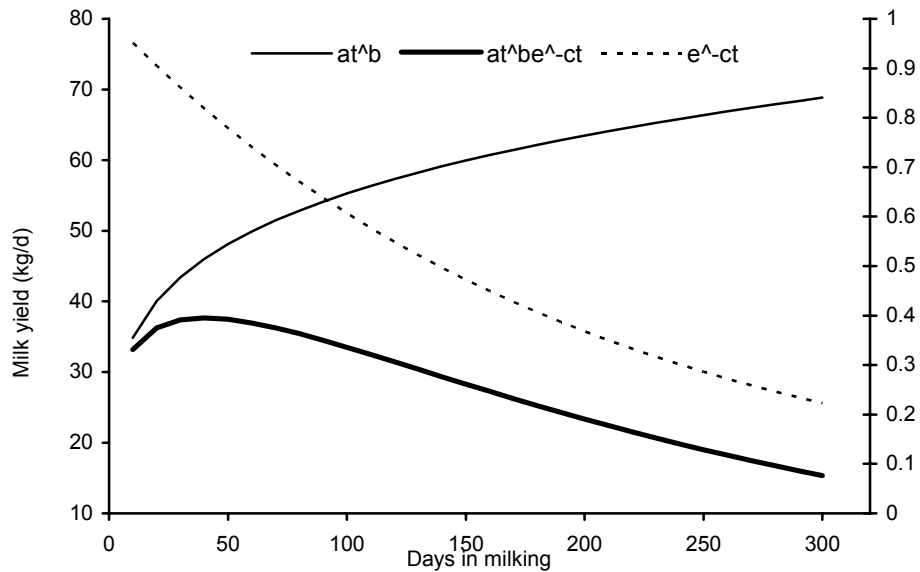
Figure 6. *Decomposition of Wood function (modified from Pulina, 2009)*

Reasons for the great popularity of the Wood model can be found in the immediate and easy understanding of relationships between its parameters and main curvatures of the lactation pattern. Such features has led, for example, Varona et al. (1998) to use the Wood model for a Bayesian approach to model lactation curve in cattle. Moreover, although the original formulation of the Wood function is non linear, it can be easy linearised by a log transformation:

$$Log(y_t) = loga + blogt + ct$$

Model [4] is also able to represent several patterns of curves, depending on sign of its parameters (Macciotta et al., 2005). A relative maximum (or minimum) in the Wood function can be found at $t = -\dfrac{b}{c}$, that is the time at which the first derivative is equal to zero. As a consequence, being t positive, accepted solutions are

$b>0$ and $c<0$ or

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives"   - 14 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

b<0 and *c*>0.

The study of the second derivative gives useful information about the shape of the lactation curve to respect the sign of the parameters. Therefore, the solution with b>0 and c<0 corresponds to the standard form of the lactation curve. On the contrary, the solution *b*<0 and *c*>0 relates to a reversed shape, characterised by a first decreasing phase till a minimum, followed by an increase. This pattern corresponds to the lactation curve of milk main components as fat and protein. Finally, the combination of *b*>0 and *c*>0 represents a continuously increasing curve, whereas *b*<0 and *c*<0 describes a continuously decreasing curve, i.e., the so called atypical curve for milk yield (Congleton and Everett, 1980). A synthesis of all possible curve shapes that can be described by the Wood model is reported in table 2.

Table 2. *Theoretical curve shapes that can be fitted by Wood function (the parameter a is always greater than 0) (adapted from Macciotta et al., 2005).*

Parameter		Curve shape
b	c	
+	-	Standard curve
-	-	Continuously decreasing (atypical) curve
-	+	Reversed standard
+	+	Continuously increasing

Finally, function parameters can be easy combined to calculate some lactation curve characteristics:

Time at peak yield	$tm = b/c$
Peak milk yield	$y_m = a(b/c)^b e^{-b}$
Persistency	$S = -(b+1)\ln(c) + \Gamma(b+1)$

Total milk yield at time n

$$y_n = a \int_0^n n^2 \exp(-b)$$

In this formulation, lactation persistency is a non dimensional measure of the time interval during which the milk yield has a value that is closer to the peak yield. Subsequently, Wood proposed a simplified measure of persistency in log form (Wood, 1970):

$$S = -(b+1) \ln c$$

Table 3 reports some examples of Wood function coefficients estimated in four dairy ruminant species. The trend of values across parities highlight the relationship of parameters with main features of lactation curve. Values of a, i.e. the scale parameter that expresses the general level of production, tends to increase with parity. On the other hand, the coefficient c that is related to the rate of decline after the peak, tends to increase in absolute value (it has the negative sign) with parity, indicating a decrease of persistency.

Table 3. *Estimated parameters of the Wood's model in different breeds of cattle, buffaloes, goats and sheep.*

Species/breed	Parity	a	b	c	Reference
Cattle					
Holstein	1	13.89	0.25	0.0036	Rekik and Ben Gara (2004)
	2	17.46	0.24	0.0046	
	3	19.56	0.23	0.0058	
Holstein	1	13.46	0.22	0.0041	Tekerli et al. (2000)
	2	15.79	0.21	0.0046	
	3	15.96	0.21	0.0045	
Reggiana	1	20.26	0.19	0.026	Sabbioni et al. (2003)
	2	25.50	0.23	0.037	
	3	26.47	0.22	0.034	
Simmental	-	18.43	0.05	0.06	Cilek and Keskin (2008)
Water Buffaloes.	-	7.27	0.17	0.0054	Unpublished data
Goat					
Derivata di Siria		1.338	0.16	0.005	Giaccone et al. (1995)
Sarda		1.007	0.18	0.007	Macciotta et al. (2007)
Sheep					
Awassi	2	0.42	0.33	0.012	Dag et al. (2005)

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 16 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

	3	0.37	0.42	0.016	
	4	0.45	0.38	0.014	
Sarda		1.05	0.19	0.041	Cappio-Borlino et al. (1987)

In table 4 are reported some of technical parameters of the lactation curve of the four

ruminant dairy species obtained from the estimated coefficients of Wood function.

Table 4. *Time at peak yield (Tm), Peak milk yield (Ym) and lactation persistency (S) calculated from parameters estimated by Wood's mode in different breeds of cattle, buffaloes, goats and sheep.*

Species/breed	Parity	Tm (days)	Ym (kg)	S	Reference
Cattle					
Holstein	1	69.4[b]	26.5	7.15	Rekik and Ben Gara
	2	52.2[b]	30.8	6.76	(2004)
	3	39.7[b]	33.3	6.65	
Holstein	1	53.7[b]	26.6	6.85	Tekerli et al. (2000)
	2	45.7[b]	30.3	6.63	
	3	46.7[b]	30.5	6.62	
Reggiana	1	44.5[b]	22.2	4.37[b]	Sabbioni et al. (2003)
	2	37.8[b]	26.8	4.07[b]	
	3	36.5[b]	27.2	4.14[b]	
Water Buffaloes	1	42	9.61		Catillo et al. (2002)
	2	35	10.96		
	3	35	12.32		
	-	33	10.90		Dimauro et al. (2005)
Goat					
Saanen	1	64.4	3.22	7.04	Groenewald and
	2	54.4	4.21	6.84	Viljoen. (2003)
	3	58.8	4.53	7.02	
Sarda	1	32	1.35	6.07	Macciotta et al.
	2	31	1.57	6.04	(2007)
	3	38	1.53	6.01	
Sheep					
Awassi	2[a]	27.6	0.91		Dag et al. (2005)
	3[a]	26.8	0.96		
	4[a]	26.1	1.06		
Sarda	-	32,4[b]	1.16[b]	6.54[b]	Cappio-Borlino et al. (1989)

[a] Years of age.
[b] Calculated using Wood parameter values reported by the authors.

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 17 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

Also main drawbacks of the Wood model are widely known. First of all, function parameters are highly correlated due to the multiplicative nature of the function. Moreover, model [4] tends to overestimate milk yield in early and late lactation and to under predict in the middle of lactation (Cobby and Le Du, 1978; Grossman and Koops 1988). Several modifications of Wood's model have been proposed in literature to overcome specific problems.

Dhanoa (1981) reparameterised the incomplete gamma function proposed by Wood with the purpose of reducing correlations among parameters:

$$Y_t = at^{mc}e^{-ct} \qquad [5]$$

where m is the time until peak milk yield is reached.

Goodall (1983) proposed the inclusion in lactation model of a categorical variable D equal to 0 in the period from October to March and to 1 from April to September (in the northern hemisphere) as following:

$$Y_t = at^{b}e^{-ct+dD} \qquad [6]$$

where d estimates the seasonality factor.

Cappio-Borlino et al. (1989a) proposed the inclusion of an additional parameter (W_i) able to correct the deviation of the theoretical curve from real data when lactation curves of dairy sheep farmed in extensive and semi-extensive system are modelled:

$$Y_t = W_i \, at^{b}e^{-ct} \qquad [7]$$

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives"   - 18 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

Another modification of the Wood's model was proposed by Cappio-Borlino et al. (1995) in the following form:

$$Y_t = at^{b\exp(-ct)} \qquad [8]$$

this function, gave lower fitting performances in comparison with the original model [4], but it was more effective in describing a rapid increase in the first phase of lactation. Such a property was confirmed by the work of Franci et al. (1999), where model [8] was successfully used to fit lactation curves of Massese sheep characterized by a rapid increase of milk yield to lactation peak.

Fuller (1969) and Gipson et al. (1987) used Grafted polynomials, which are piecewise polynomials continuous over the range of the data and have continuous first derivatives (Gipson and Grossman, 1990), to model lactation curves of dairy goats:

$$Y_t = a_0 + a_1t + a_2t^2 + a_3r_1{}^2 + a_4r_2{}^2 \qquad [9]$$

where r_1 has value t - 52 when t > 52 day and 0 otherwise and r_2 has value t - 85 when t > 85 days and 0 otherwise.

A third-order polynomial function of time was also used to fit lactation curves in dairy sheep (Cappio-Borlino et al. 1989b):

$$Y_t = a_0 + a_1t + a_2t^2 + a_3t^3 \qquad [10]$$

The model was effective in describing lactation patterns characterised by a delayed lactation peak.

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 19 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

The use of polynomials allows a good flexibility but the estimated parameters usually do not possess a clear meaning in terms of relationships with basic features of lactation curve shape, especially for high-order polynomials (Cappio-Borlino et al., 2004).

A polynomial regression model that has been widely used for dairy cattle is the one proposed by Ali and Schaeffer (1987)

$$Y_t = a_0 + a_1 X + a_2 X^2 + a_3 \log (1/X) + a_4 (\log(1/X))^2 \qquad [11]$$

where $X = t$/lactation length; $a_0, a_1, a_2, a_3,$ and $a_4,$ are parameters to be estimated.

Wilmink (1987) proposed two lactation models. The first is a combination of an exponential and a linear term with the following form:

$$y_t = a + be^{kt} + ct \qquad [12]$$

where a is a scaling factor; b controls the rate of variation of milk yield in the first part of the curve; c, that measures the slope of the straight line ct, is mainly related to the rate of decline in the second part of lactation, i.e., the lactation persistency. A graphical meaning of the terms of model [12] can be clearly observed form figure 7.

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 20 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche
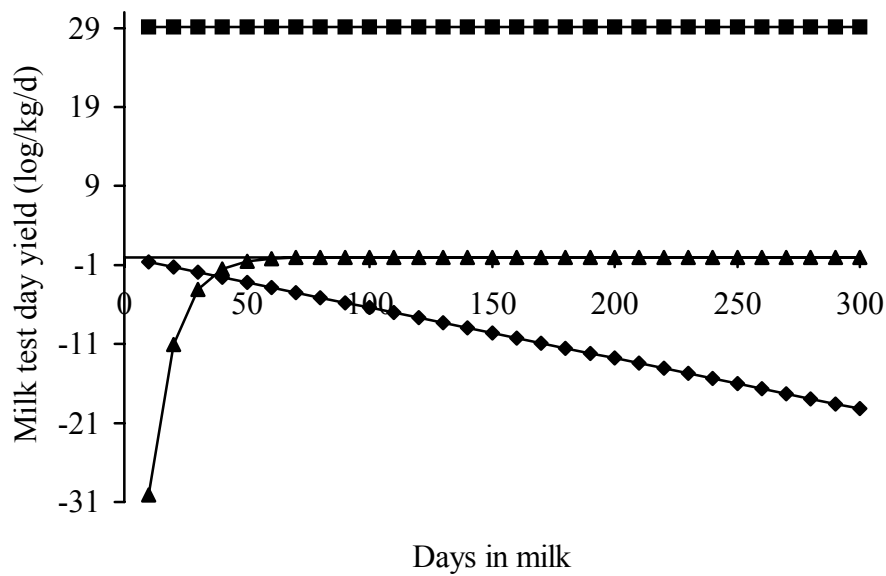
Figure 7. *Decomposition of Wilmink function [12] (■ = a; ▲ = b^{-kt}; ♦ = ct). From Macciotta et al. (2005)*

Model [12] can be reduced to a three parameter by setting the k exponent to a suitable fixed value. In this way, the function becomes linear and an ordinary linear regression can be used to fit data. Wilmink in the original paper proposed a value of -0.05 for Dutch-Friesians dairy cattle, which corresponds approximately to 50 days postpartum. Olori et al. (1999) estimated a value k = 0,61 for UK Holstein-Friesian. Catillo et al. (2002) used 0.70 for modelling average lactation curves of Italian river Buffaloes. However, for each experiment, the k parameter could be estimated by fitting the Wilmink function to the whole data in its original form [12] using a non linear regression.

In the second model a quadratic term was added:

$$y_t = a + be^{kt} + ct + dt^2 \qquad\qquad [13]$$

Such a modification resulted in a function more flexible than [12] although together with an increase of the number of parameters.

A different approach was introduced by Grossman and Koops (1988) with multiphasic logistic function. The general idea is that lactation pattern is partitioned into different phases, each fitted with a specific logistic function, and therefore total milk yield can be regarded as the sum of the yield of each phase. The general form of the model is:

$$y_t = \sum_{i=1}^{n} \left[a_1 b_1 \left[1 - \tanh^2 (b_1 (t - c_i)) \right] \right]$$

[14]

where:

n is the number of lactation phases considered

$tanh$ is the hyperbolic tangent.

Model [14] has three parameters for each phase. For example, if the lactation curve is partitioned into two phases, i.e. for a diphasic curve, the parameters will be six a_1, a_2, b_1, b_2, c_1 and c_2. Some lactation curve traits can be calculated for each phase using the parameters of the equation [14]. Peak yield is equal to $a_i b_i$ and occurs at time c_i, the duration of each phase is related to $2/b_i$ that represents the time necessary to reach 75% of asymptotic total yield during that phase.

A further development of the multiphasic approach is represented by the lactation persistency model (Grossman et al., 1999). The authors described the lactation curve as the result of three intersecting lines: the first represents the initial rise in yield to peak, the second line has a slope of zero and represents the peak yield over the period for

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 22 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

which it is maintained, whereas the third line fits the subsequent decline after peak. As a result, two models were suggested:

The first is the full lactation persistency model:

$$y_t = y_p + b_1(t - t') - a_1 b_1 \ln\left[\frac{e^{\left(\frac{t}{a^1}\right)} + e^{\left(\frac{t'}{a^1}\right)}}{1 + e^{\left(\frac{t'}{a^1}\right)}}\right] + a_2 b_3 \ln\left[\frac{e^{\left(\frac{t}{a^2}\right)} + e^{\left(\frac{(t'+p)}{a^2}\right)}}{1 + e^{\left(\frac{(t'+P)}{a^2}\right)}}\right] \qquad [15]$$

where:

y_p is the level of constant yield during the peak phase

b_1 is the slope of the line during the initial inclining phase

b_2 is the slope of the line during the final declining phase

t' is the transition time from the slope of the first line to the slope of the second line

a_1 and a_2 are the durations of transition from the slopes of the first to the second, and from the second to the third line

P is the number of days during which the level of constant yield of the peak phase is maintained

The second is the reduced lactation persistency model :

$$y_t = \frac{y_p}{t'} t - \frac{y_p}{t'} \ln\left[\frac{e^t + e^{t'}}{1 + e^{t'}}\right] + b_3 \ln\left[\frac{e^t + e^{t'+P}}{1 + e^{t'+P}}\right] \qquad [16]$$

where parameter interpretations are the same in the lactation persistency model above.

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 23 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

The number of days during which the level of constant yield is maintained is the new measure of persistency and can be calculated as $P = t_2 - t_1$. This measure of persistency is different from the other because is expressed not in terms of production but in terms of time of duration.

Multiphasic functions were used to model lactation curves of dairy cattle (Grossman and Koops, 1988; De Boero et al., 1989) and of dairy goats (Gipson and Grossman, 1988; Gipson and Grossman, 1989). Both the diphasic and a triphasic function were tested, the latter showing a better fit, smaller and less correlated residuals. As expected the fitting performances, usually measured by the coefficient of determination adjusted for the number of parameters (adjusted R^2), tend to improve when the number of parameters of the function increases. However, a constraint to the increase of the number of parameters is represented by the number of data to be fitted. When average lactation curves are modelled a large number of records is available. On the other hand, individual curves are characterized by a small number of test available (on average 8 in cattle and 5 in sheep and goat). Thus the use of functions characterised by an high number of parameters, as multiphasic of high order, becomes problematic in this cases.

Another peculiarity of individual lactation curve modelling is represented by the different balancing between the two components of milk production pattern. In individual curves, as depicted in figure 4, deviations from the regular component can be relevant. Thus the use of models specifically conceived to fit the standard shape of the lactation pattern could be not a good option. In this context, flexibility of the model and numerical properties are key elements for improving modelling efficiency. For this reason, in several genetic studies where lactation curve functions are used to model individual curves, more general functions are used. An example are the Random

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 24 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

Regression test day models where individual lactation curves are fitted using the Legendre orthogonal polynomials and Splines functions (Kirkpatrick and Heckman, 1989; Kirkpatrick et al., 1990; White et al., 1999, Meyer, 2005; Bohmanova et al., 2008; Silvestre et al., 2006; Druet et al., 2003).

The Legendre orthogonal polynomials can be written as:

$$\mathbf{y_t} = \sum_{i=1}^{n} \alpha_i P_j \qquad [17]$$

where:

α_i is the coefficients to be estimated

P_j is the function of time

n is the degree of polynomial.

Legendre Orthogonal Polynomials have been used to fit individual curves of dairy cattle (Macciotta et al., 2005; Silvestre et al., 2006). In comparison with three parameter models specifically conceived to fit lactation curves, they show better fitting performances due to their high flexibility.

Splines are a type of segmented regression in which the curve is divided into different segments of the dependent variable, joined at points named knots, each fitted with different polynomials (Guo and White, 2005).The general model of a spline regression can be written as:

$$Yt = \sum_{i=0}^{n} \beta_{0i} \cdot t^{i-1} + \sum_{j=1}^{m} \beta_j \cdot \left(t - t_j\right)^{n} \qquad [18]$$

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives"
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche
- 25 -

where:

β are function parameters

n is the degree of spline

m is the number of knots

t_j is the knot point.

Splines have been used by Silvestre et al. (2006) to fit individual lactations of dairy cattle.

Test Day Model

A main limitation of lactation curve modelling with continuous function of time is that environmental effects that influence milk yield are implicitly assumed to average effect over lactation, whereas there are some factors as variation in feed quantity and quality, climate, health status that may specifically affect only some part of lactation (Stanton et al., 1992). To address such an issue, the use of mixed linear models, called Test Day Model (TDM), has been proposed. Besides other factors of variation, test day models include a days in milk factor (DIM), whose least squares solution allows to reconstruct the lactation curve corrected for environmental effects included in the model. The general form of a test day model is the following:

$$Y = \mu + F + DIM + L + e \qquad [19]$$

where Y is the test day milk yield, μ is an overall mean , F are the fixed factors included in the model (i.e. herd, year of production, litter size), DIM is the fixed effect of days in milking, L is the random effect associated with each individual lactation and

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives"   - 26 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

e is the random residual. Lactation curves of homogeneous groups of animals can be estimated by the least square means of DIM effect nested within the level of environmental factors (Cappio-Borlino et al., 2004). Figure 9 shows the lactation curve of Sarda dairy ewes farmed at different levels of altitude (Macciotta et al., 1999) estimated with a test day model. The effect of altitude of location of flocks, that is a sum of environmental, management and genetic effects, is clearly evident and is different in the various stages of lactation.
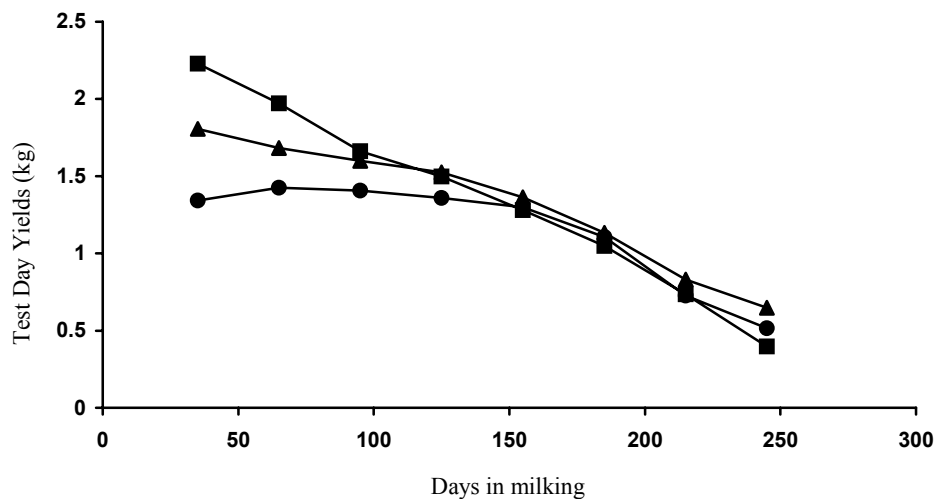
Figure 9. *Average lactation curve for milk yield of Sarda dairy ewes famed in flocks located at different levels of altitude (■ = plain; ▲ = hill; ♦ = mountain). (From Macciotta et al., 1999).*

Other empirical approaches have been proposed to address specific issue in the analysis of milk production: time series analysis (Deluyker et al., 1990; Macciotta et al., 2000; Macciotta et al., 2002), partial least squares regression (Macciotta et al., 2006), neural networks

(Fernandez et al., 2006), principal component analysis (Van Arendok and Fimland, 1983; Olori et al., 1999; Macciotta et al., 2006;) and multivariate factor analysis (Macciotta et al., 2004; Macciotta et al., 2006; Wilmink 1987).

MECHANISTIC MODELS

The construction of a mechanistic model generally starts from a strong theoretical hypothesis on the biology of the phenomenon considered based on the achieved knowledge on underlying physiological and biochemical processes. In the case of the evolution of milk production along the lactation, a common starting point for developing a mechanistic model is the assumption on the direct proportionality between milk produced in the mammary gland (*MY*) at time *t* and the number of active secretory cells (*nC*) and the synthesis efficiency of each cell (*h*)

$$MY = h \; nC$$

Once the core of the system is built, the system can be enlarged by further considering other related physiological processes and exogenous inputs. Thus, starting from a simplified system, the model is progressively complicated by adding several sub-models that are connected by regulatory mechanisms.

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives"   - 28 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

Neal and Thornley (1983) developed one of the most famous mechanistic models of the lactation curve for dairy cattle, based on a multi-compartmental representation of the mammary gland. In this model (figure 10), the mammary gland is represented by compartments of undifferentiated cells (Cu), differentiated cells (Cs) produced by cell division from Cu, and the compartment (C) that consists of alveoli, ducts, and gland cistern containing the produced milk (M).

The number of secretory cells Cs increases for cell differentiation at a rate V that depends on the level of a generic hormone H and decreases for cell death. The level of hormone H varies over time with an exponential trend according to the following relation: $H = H_0 \exp(-k_h t)$, whereas cell death varies at rate L_S that depends on a specific rate k_s and on milk present in the compartment C.

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Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 29 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche
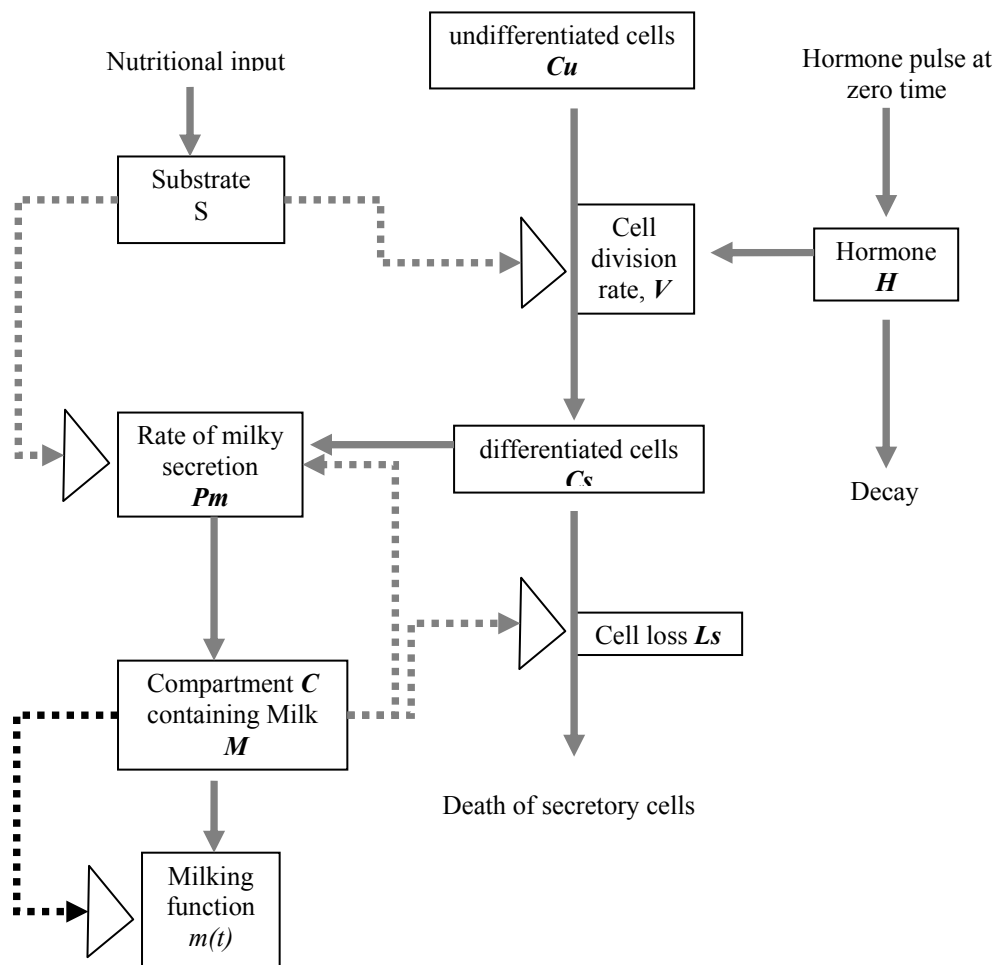
In such system the quantity of produced milk M depends on the rate of milk secretion (P_m) and from the milk removal (R_m) with milking. P_m is proportional to the number of differentiated cells Cs but is inhibited when the amount of M is close to maximum capacity of C.

Neal and Thornley's model is able to efficiently represent the mammary system, giving accurate predictions when fitted to actual data. However it is still remarkably complex and its use in practice is constrained by the required inputs, generally not available (Cappio-Borlino et al., 1989; Dijkstra et al., 1997).

A simplified version of Neal and Thornley's model was proposed for dairy cattle by Ferguson and Boston (1993), and subsequently adapted to dairy sheep by Cappio-Borlino et al. (1997). The mammary gland is represented as a bi-compartmental system. The first is the compartment of the undifferentiated cells (q_1), the second the compartment of the differentiated cells (q_2). Milk secretion rate is assumed to be constant for all cells and for all the lactations. Thus milk production at time t is due to the number (q_2) of active cells in the mammary gland that is regulated by the passage with a rate k_1 from compartment one to compartment two, and by the rate (k_2) of cell apoptosis (Figure 11).

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 30 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche
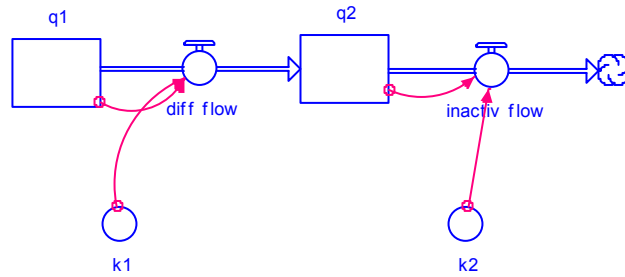
Figure 11. *A schematic representation of bi-compartmental model; q_1 = number of inactivated cells at time of lambing; q_2 = number of activated cells at time of lambing; k_1 = cell activation rate; k_2 = cell inactivation rate. (from Cappio-Borlino et al., 1997)*

From the mathematical point of view, the phenomenon can be described by the following system of linear equations:

$$\frac{dq_1}{dt} = -k_1 q_1 \qquad [20]$$

$$\frac{dq_2}{dt} = k_1 q_1 - k_2 q_2$$

The system has an analytical solution:

$$q_2(t) = \frac{k_1 Q_1}{k2 - k1} e^{-k_1 t} + \left(Q_2 - \frac{k_1 Q_1}{k2 - k1} \right) e^{-k_2 t} \qquad [21]$$

where Q_1 is the initial number of inactive cells in the first compartment and Q_2 is the initial number of active cells in the second compartment (Cappio-Borlino et al., 1997). The bi-compartmental model has been found to be sufficiently flexible to adapt to the great variety in the shapes of lactation curves of sheep while maintaining a connection with the biological mechanisms underlying milk production (Pulina et al., 2001). As an

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 31 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

example, figures 12a and 12b represent the fitting of model [20] to a standard (a) and to an atypical lactation curve of Sarda dairy sheep.
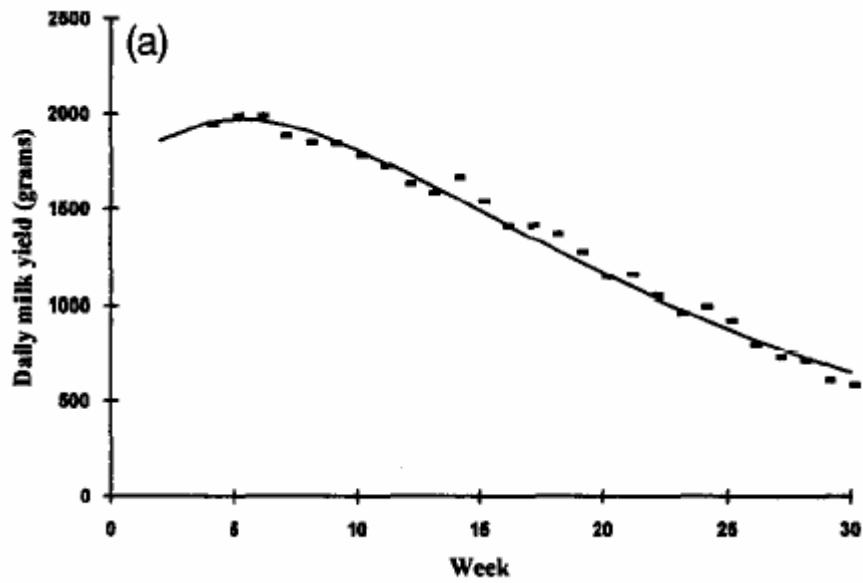
Figure 12a. *Fitting of the bi-compartmental model to regular lactation curve (*
- actual data, —— predicted data). (From Cappio-Borlino et al., 1997).
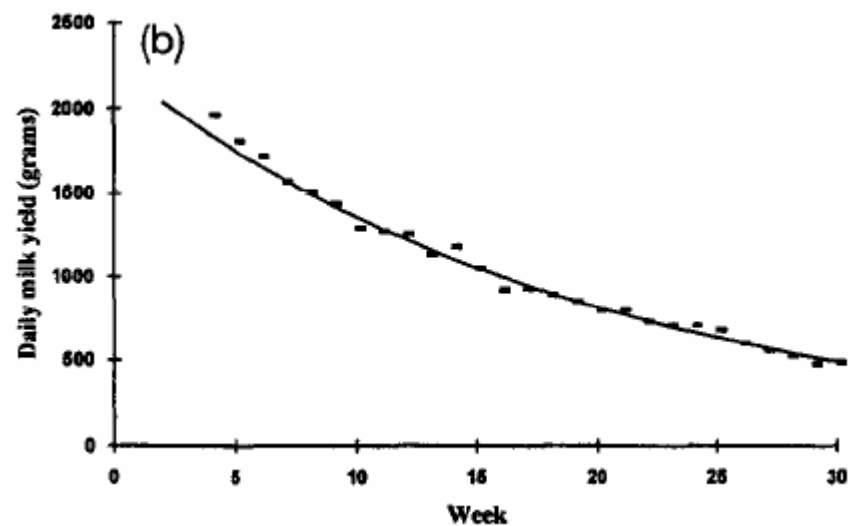
Figure 12b. *Fitting of the bi-compartmental model to an atypicallactation curve (- actual data, —— predicted data). (From Cappio-Borlino et al., 1997).*

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives"   - 32 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

In the development of his mechanistic models of the mammary gland, Dijkstra et al. (1997) started from the hypothesis that cell division in the mammary gland has an exponential trend in several species, including goats. This phenomenon starts during pregnancy and continues in the first weeks of lactation.

Dijkstra's model is based on a set of differential equations representing cell proliferation and cell death in the mammary gland that have been summarized into a function with four parameters:

$$y_t = ae^{\left[\frac{b(1-e^{-ct})}{c-dt}\right]}$$

[22]

where:

y_t is the cell population of mammary tissue (y in milligrams of DNA), or the parenchymal volume (milliliters), or the number of secretory cells (directly proportional to the produced milk)

a is cell population at parturition, or the theoretical initial milk production (in kg/d)

b is specific rate of cell proliferation

c is a decay parameter

d is specific rate of cell death.

This model is able to efficiently fit growth patterns of mammary gland throughout pregnancy and lactation, both in terms of number of mammary cells (expressed in DNA contents), volume of parenchymal tissue and milk yield.

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 33 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

A modified version of model [22] was presented by VanRaden et al. (2006), with the aim of modelling lactations exceeding 305 days of length (extended lactations). The model has the following form:

$$y = b_0 + b_1 \exp\left[\frac{b_2(1 - \exp(-b_3 t))}{b_3} - b_4 t \right] \qquad [23]$$

in this form model parameters loose their biological significance, but this formula properly fits extended lactations (VanRaden et al., 2006), and is currently used in evaluation of productive life traits for US Holsteins (Dematatewa et al., 2007).

Model [22] has been subsequently adapted by Hanigan et al. (2007) to describe the variation of the active cells (Q_{Cells}) and the level of the enzymes (V_m) involved in the synthesis milk process as following:

$$Q_{Cells} = Q_{Cells(T_O)} e^{\left[Sign \frac{\mu_{Division(TO)}}{k_{Decay}} \left[1 - e^{\left(-k_{Decay}|t| \right)} \right] - k_{Apoptosis}|t| \right]} \qquad [24a]$$

where:

Q_{Cells} is the total number of mammary cells at time t

T_0 is the time of parturition ($t = 0$)

sign assumed a value of −1 for $t < 0$ and 1 for $t \geq 0$

$\mu_{Division(T0)}$ is the cell division rate at T_0

$K_{Apoptosis}$ is the rate of cell death

K_{Decay} is the rate of decay in μ with respect to t

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives"   - 34 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

$$V_m = V_{m(T_O)} e^{\left[\frac{k_{Vm,Syn}}{k_{Vm,Decay}}\left[1-e^{\left(k_{Vm,Decay}*t\right)}\right]-k_{Vm,Deg}*t\right]}$$ [24b]

where:

V_m is the maximum speed for milk lactose synthesis

$V_{m(T0)}$ is the Vm at parturition

$k_{Vm,Syn}$, $k_{Vm,Decay}$, and $k_{Vm,Deg}$ are initially set to 0.005, 0.03, and 0.0005 and subsequently derived.

Pollott,. (1999; 2000) described the lactation curves in biological terms with two logistic curves. The first describes cell differentiation as following:

$$NDPC = \frac{N}{\left(1+\frac{1-P_0}{P_0}e^{-Gt}\right)}$$ [25a]

where:

$NDPC$ is the number of differentiated parenchyma cells

N is total number of parenchyma cells which become active during early lactation

P_0 is proportion of N present at the start of lactation

G is the relative growth rate in active cell numbers $(0 < G < 1)$

t is day of lactation.

The second logistic curve describes the decline in cell numbers (cell death) as:

$$NDCD = \frac{L}{\left(1+\frac{1-Q_0}{Q_0}e^{-Dt}\right)}$$ [25b]

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 35 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

where:

NDCD is the number of death cells due to apoptosis

L is total number of parenchyma cells dying off

Q_0 is proportion of *L* dead at start of lactation

D is the relative death rate of cells ($0 < D < 1$).

Assuming that daily milk production (M in kg/d) can be expressed as the product of the number of active parenchyma cells and their secretion rate (S) throughout lactation, the models [25a] and [25b] can be combined in the following formulation:

$$M_t = \left(s_a - \left(1 - e^{s_b t}\right)\right)\left(\frac{N}{1 + \frac{1 - P_0}{P_0} e^{-Gt}}\right) - \left(\frac{L}{1 + \frac{1 - Q_0}{Q_0} e^{-Dt}}\right) \qquad [26]$$

where:

N, P_0, G, L, Q_0, and *D* are same as defined above

M_t is milk yield at time *t*

S_a is the maximum secretion rate (in kg/cell per day)

S_b is the relative rate of change in secretion rate (with $S_b > 0$)

Model [26] cannot be used for practical purposes because is not possible to determine the parameters *N, L*, S_a and S_b). Thus authors proposed the followings models:

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives"   - 36 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

$$y_t = \left(\frac{MS_{max}}{1 + \frac{1-NO}{NO}e^{-GRt}} \right) - \left(\frac{MSL_{max}}{1 + \frac{1-NOD}{NOD}e^{-DRt}} \right) \qquad [27a]$$

$$y_t = \left(\frac{MS_{max}}{1 + \frac{1-NO}{NO}e^{-GRt}} \right) \left(\frac{MSL_{max}}{1 + \frac{1-NOD}{NOD}e^{-DRt}} \right) \qquad [27b]$$

where:

MSmax is the maximum potential milk secretion

MSLmax is the loss in total milk secretion due to apoptosis

NO=Proportion of final number of secretory cells present at the start of lactation,

GR=a factor associated with the growth rate in cell numbers,

NOD=Proportion of the secretory cells dead at start of lactation,

DR=a factor associated with death rate in cell numbers

This two forms, called additive and multiplicative respectively, have been used to describe the complete lactation of Awassi and Assaf dairy ewes farmed in intensive management (Pollott and Gootwine, 2000; 2004). They gave good results for modelling average lactation curves whereas the fitting of individual patterns was inferior. Albarran-Portillo and Pollott, (2008) using a two parameter multiplicative model, in alternative to the original seven parameter multiplicative model (Pollott, 2000), found an heritability of 0.27 for maximum secretion potential and of 0.08 for relative cell death rate in dairy cattle.

Grossman and Koops (2003) described the biological basis for Multiphasic lactation model. In this model, the ascending phase of milk yield is described as a linear

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 37 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

logistic function associated with the increase of both the number of mammary gland cells and the yield per cell. The decreasing phases after the peak is modelled by a sum of three functions: a quadratic logistic function that describes a first stage of apoptosis; a linear logistic function that fits the decrease in yield per cell due to pregnancy; finally a quadratic logistic function that describes a second stage of apoptosis. The final model is the following:

$$y_t = \frac{a}{1 - e^{-\frac{(t-c_1)}{b_1}}} - \frac{p_2 a}{1 + \left(0.5e^{-\frac{(t-c_{max2})}{b_2}}\right)^2} - \frac{p_3 a}{1 + e^{-\frac{(t-c_3)}{b_3}}} - \frac{p_4 a}{1 + \left(0.5e^{-\frac{(t-c_{max4})}{b_4}}\right)^2} \qquad [28]$$

where:

a is upper asymptotic level of milk yield (kg)

c_1 is time of maximum increase (d)

b_1 is proportional to duration of the increasing phase (d)

p_2 is the decrease proportional to a

b_2 is proportional to duration (d)

c_{max2} is time of maximum decrease (d)

p_3 is the decrease proportional to a

b_3 is proportional to duration (d)

c_3 is time of maximum decrease (d)

p_4 is the decrease proportional to a1

b_4 is proportional to duration (d)

c_{max4} is time of maximum decrease (d)

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives"   - 38 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

Model [28] was used to fit data of Holstein cows with standard and extended lactations, with a very good fitting (R^2 about 0.99), low residual standard errors (0.14 to 0.52) and lack of first order autocorrelation among residuals. The parameters estimated did not change as lactation length increase, except for c_3, b_4 and c_{max4}.

A part from the great theoretical complexity, the use of mechanistic models is characterised also by relevant mathematical problems. Simpler models are usually defined by linear equations that have an analytical solution. However, when models are enlarged and specific sub-models are developed, it is necessary to use systems of non-linear differential equations that cannot be solved analytically but only by numerical integration. Thus resultant models lose their mathematical rigour, because numerical integration necessarily leads to approximations (Dimauro et al., 2007). Some advances in computer technology offer new tools for developing complex mechanistic models. In particular, the so-called computer-aided design allows the representation of a complex system in terms of discrete, recognisable entities called objects that incorporate both data structure and system behaviour (Simonovic et al., 1997).

Dimauro et al. (2007), used a computer-aided design technique based on object-oriented methodology to develop a mechanistic model of the mammary gland in dairy sheep, based on the model proposed by Vetharaniam et al. (2003) for dairy cattle. The system is represented by stocks and flows which are the building blocks (objects) and simulate, respectively, the state variables and the relative rates of change.

The model proposed by Dimauro et al. (2007) is divided into three sub-models: alveolar, milk and energy. The alveolar sub-model (figure 13) contains three compartments: *A* active alveoli, *P* progenitor alveoli and *Q* quiescent alveoli. Flows between compartments are regulated by valves and connectors: for example the number

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 39 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

of alveoli that pass from *P* to *A* (r_{pa}) depends on a specific rate (k_1) and on number of alveoli present in *P* and it is calculated as $r_{pa} = P * k_1$. The energy sub-model provides the energy balance all over the lactation, whereas the milk sub-model simulates the milk harvest.
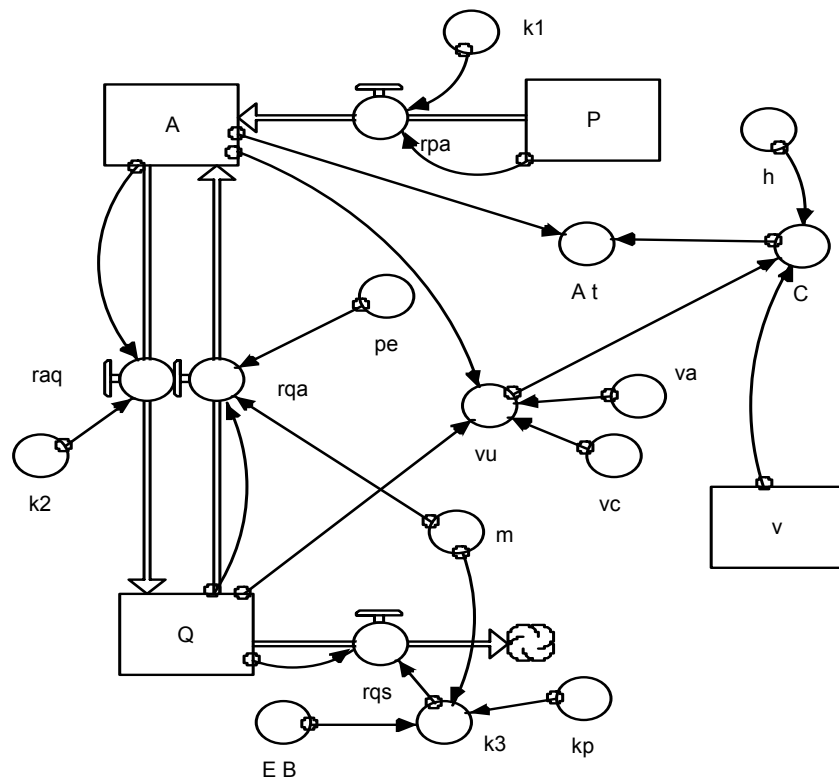
Figure 13*. The alveolar sub-model (From Dimauro et al., 2007)*

The principal output of the model is the pattern of milk production and of the alveolar turnover according with milking (or suckling) frequency (*m*). Simulations developed with the model can be useful to increase the knowledge on the physiological mechanisms of the synthesis, secretion, ejection and removal milk in ruminants, but can also result profit to mimic stress factors such as reduction in milking frequency or negative energy balance.

As an example, figure 14 shows results of a simulation of a energy stress caused by reduction in feed intake. Predicted milk yield show regular pattern when energy

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 40 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

intake is 100% (triangle) whereas when energy intake is 50% for 10 days (circle) or 50% for 30 days (square) the yield decreases for returning to normal levels when the stress ends. The simulation results are consistent with the experimental data obtained by Pulina et al. (2005) and able to explain, better of the empirical models, some anomalous patterns.
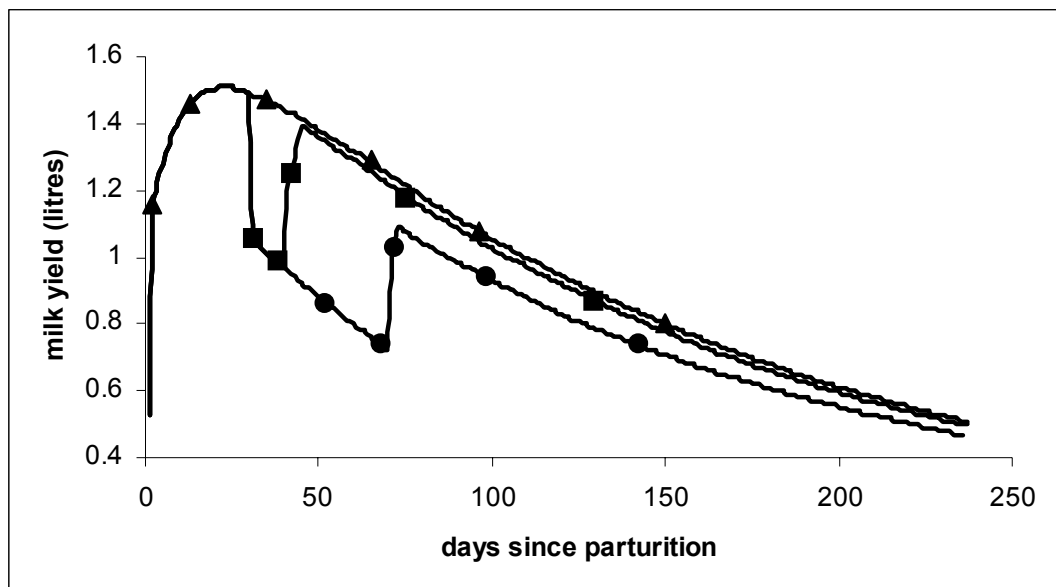
Figure 14*. Predicted daily milk production during lactation under energy stress caused by reduction in feed intake (▲ = 100% energy intake; ■ = 10 day at 50% energy intake; ● = 30 day at 50% energy intake). (From Dimauro et al., 2007).*

The critical review of different methods used to mathematically describe the lactation curve of ruminants has highlighted the relevant differences among approaches and their suitability to fit specific problems that can be found in lactation curve modelling. It is clearly evident that there is not a perfect model but the choice has to be done thinking about the specific issue that has to be addressed. In the section of experimental contribution some researches carried out on applications of mathematical modelling of lactation curve for different species and productive scenarios.

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 41 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

ISSUES IN MODELLING EXTENDED LACTATIONS IN ITALIAN HOLSTEIN COWS

Introduction

A rather common event that has occurred in the dairy industry of several countries is the increase of the number of high producing cows having lactations that exceed the standard 305 day length (Vargas et al., 2000). VanRaden et al. (2006) reported that more than 55% of US Holstein have lactations longer than 305 days. Vargas et al. (2000) stated that more than 25% of cows in Costa Rica are dried off after 330 d of lactation. For the last decade, an increase of 30 d per year for dairy cow lactation length has been estimated by Gonzales-Recio et al. (2004).

Extended lactations are often due to failures to conceive in early lactation because of a negative relationships between level of production in this stage and reproductive efficiency in intensively managed herds (Lucy, 2001). Actually, with the traditional calving system that aims at obtaining calving intervals of approximately one year, the cow has to be inseminated at around two months from parturition, i.e. when the lactation peak occurs. Considering that this stage a cow may produce more than 40 kg./day and that this increase has not being accompanied by a comparable increase of feed intake (Veerkamp et al., 1995), the cow suffers from a negative energy balance due to body reserves mobilisation with a subsequent marked decrease in conception rate (Bertilsson et al., 1997).

On the other hand, the choice to extend the calving interval from about 12-13 to 18-19 months in cows that are able to maintain a relevant level production for long time represents also a management choice. Actually, the possibility of increasing lactation

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 42 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

length has been considered as an alternative to the common strategy of maximizing lactation peaks and minimizing calving intervals (Grossman and Koops, 2003). It is generally assessed that breeding for increased yield has resulted in a major concentration of health problems around the period between calving and lactation peak. It is in fact estimated that some 60% of health disorders occurs during the first 40 days of lactation (Erb et al., 1984). Several authors have reported a number of positive effects of an increase of the waiting period between two matings (Knigt, 2005). First of all, cows with extended lactations could produce the same amount of milk with reduced risks of difficult calvings and of post partum metabolic diseases (Cole et al., 2009). Moreover, a reduction of insemination costs and of the number of days dry within the cow's lifetime is expected. Finally, the intensively managed dairy cow typically achieves three lactations in her lifetime and it is thus exposed to three of these "peak risk" periods. The immediate benefit of extended lactation would be to reduce this exposure to two cycles. Moreover, Knigt (2005) demonstrated that the milk yield in three years in 18 (extended lactation) and in 12 months (conventional lactation) lactation cycle is the same if the persistency is improved of the 1% in extended lactation.

A knowledge of main features of long lactations could therefore represent a key element for planning rational management and genetic strategies. In tables 1 and 2 are reported some of the characteristics of extended lactations of cows farmed in the United States and in Australia. It can be observed that US Holstein cows with extended lactations (longer than 800 days in milk) show higher peak yields and at later occurrence compared with standard lengths (table 1).

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 43 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

Table 1. *Peak yield and peak occurrence for US Holsteins of different parities and lactation length (from Dematatewa et al., 2007).*

Parity	Lactation length (days)	Peak yield (kg/d)	Time at peak (days)
First	305	26.4	94
Third or greater	999	25.4	98
First	305	38.0	51
Third or greater	999	35.2	70

These features can be observed also in figures 1 and 2 that report examples of individual curves for standard and extended length, in first (figure 1) and third (figure 2) parity cows.

Figure 1. *Example of individual milk yield lactation patterns in first parity cows classified in different classes of lactation length.*

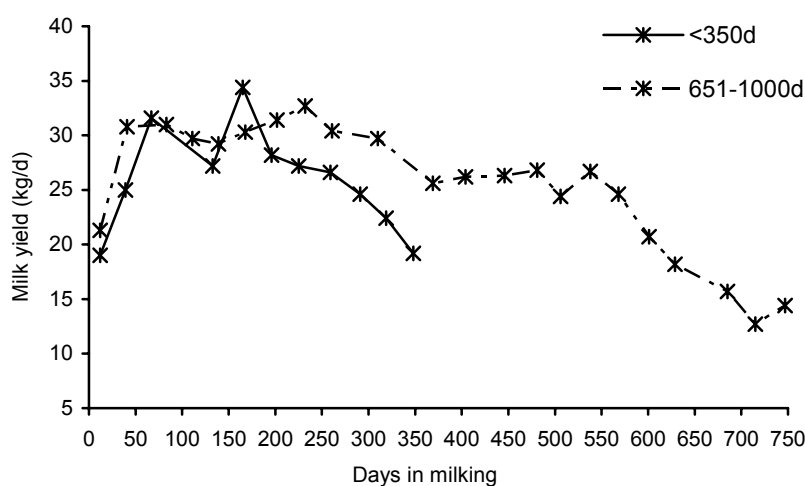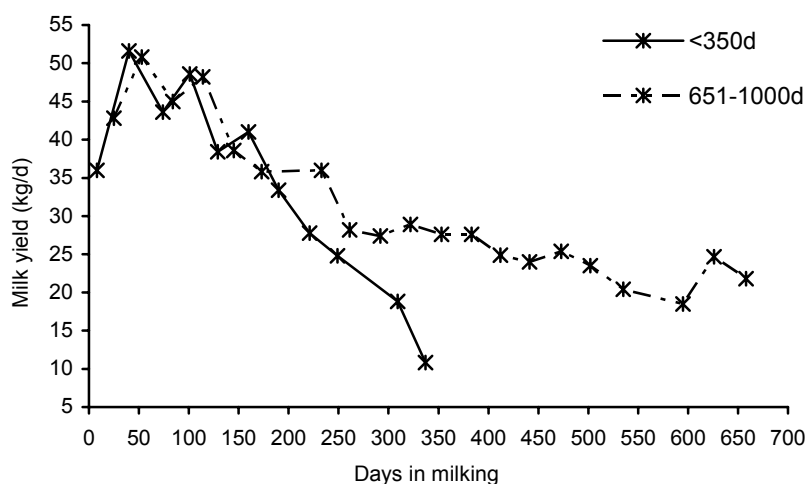**Figure 2.** *Example of individual milk yield lactation patterns in third parity cows classified in different classes of lactation length.*

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 44 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

As far as the distribution of milk production across the different lactation stages is concerned, it is of interest to notice that average daily yield between 301 and 600 days in milk in Holstein and Jerseys cows farmed in Australia is about 18% and 27% lower than yield in the first three hundred days, both in first and second parity cows (Haile-Mariam and Goddard, 2008).

Table2. *Average daily milk yield in the first 300 days and in the second 300 days of lactation in cows of different breed and parity farmed in Australia (From Haile-Mariam and Gooddard, 2008)*

Breed	Parity	Milk yield first 300 days (kg/d)	Milk yield second 300 days (kg/d)
Holstein	First	22.1	17.9
Jersey	First	15.2	12.4
Holstein	Second	25.9	18.0
Jersey	Second	17.0	12.6

Actually since the 90's, mathematical modelling of the lactation curve has paid little attention to milk yields recorded after 305 d from parturition.

Vargas et al (2000), working on extended lactation curves of cows of Costa Rica, tested nine models selected from the literature. They found that the Diphasic Model of Grossman and Koops (1988) was the most adequate to fit both standard and extended lactations, showing most favourable values of determination coefficient and residual autocorrelation. However, estimated parameters showed a great range of variation for different lactation lengths and calving to conception intervals. Moreover they found that the length of calving to conception interval has a negative effect on milk yield in standard lactations but not in extended ones. Finally, they estimated that cows with a lactation length of 16 months produced on averge 2200 kg, i.e. about 26% of the total yield per lactation.

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 45 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

Grossman and Koops (2003), suggested a multiphasic model to fit extended lactations. It can be considered somewhat between an empirical and a mechanistic model. Authors based the development of their model on the physiology of the mammary gland during lactation, that is characterised by a succession of phenomena of growth and regression, as the result of cellular proliferation and apoptosis. The model is able to describe the initial phase of increase and a series of decreasing phases of milk yield (for details see the paragraph "Mechanistic models" in the introduction section). The model resulted effective in modelling both standard and extended lactations.

An evaluation of nine different models for their ability to fit US Holstein extended lactations was carried out by Dematawewa et al. (2007). Functions used were Wood, Wilmink, Rook, Dijkstra, Pollot, Monophasic, Diphasic Multiphasic and Lactation persistency model (see the introduction section). The overall fitting performance was rather poor, with adjusted R-squared of about 0.21 and 0.37 for extended lactations of first and greater parities, respectively. Authors concluded that simple three or four parameter models as the Wood or the Rook functions could be more efficient in fitting long lactations than complicated mechanistic models with 6 parameters or more.

Some authors argue that models conceived for lactations of standard length may not be suitable for extended lactations and that specific functions should be developed (Grossman and Koops, 2003). Such consideration is probably correct for models characterised by a scarce flexibility, with a small number of parameters, but may be questionable if flexible and more general models are used. On the other hand, functions with a high number of parameters may have computational problems. VanRaden et al. (2006), in a paper dealing with the estimation of productive life for US Holsteins,

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 46 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

started from the assessed poor fitting performances of lactation curve functions in later lactation stages, particularly the underprediction of yields compared to measured data, and suggested a specific model to fit extended lactations. This function is a modification of the Dijkstra et al. (1997) model.

In this research the modified Dijkstra function proposed by VanRaden (2006) is compared to other mathematical models commonly used to fit standard 305 d curves to evaluate their efficiency in describing extended lactations of Italian Holsteins.

Materials and methods

Data

Data were supplied by the Italian Association of Holstein Breeders (ANAFI) and consists of 726,739 test day records of milk yield belonging to 68,899 lactations of 45,132 Italian Holstein cows, recorded in the period from 2002 to 2006 in Northern Italy. Lactation records were discarded if the first test occurred after 70 d from parturition or if the last test date occurred after 1000 d of lactation.

Lactations were grouped according to parity (first second and third) and to lactation length (class1 <305 d; class2 = from 351 to 450 d; class3 =from 451 to 650 d; class4= from 651 to 1000 d). The distribution among parity classes is reported in table 3. It can be observed that almost a half of records are of first parity cows. Moreover, it is of great interest to notice that the younger cows show the highest length of lactation (around 360 d). These figures are in agreement with previous findings in US Holsteins, for which an average lactation length of 360 days (sd 100 days) was reported (Dematawewa et al., 2007)

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 47 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

Table 3. Means and standard deviations (days) of lactation length for three parity.classes

Parity	n. of lactations	Relative frequency	Average length	Sd
First	31,461	46 %	360	96
Second	22,739	33 %	347	85
Third	14,699	21 %	344	82
All	68,899	100 %	352	90

Moreover the proportion of first parity in the class length tends to increase with lactation length, ranging from 43% in 350d class to 63.1% in 650-1000d class (figure 3), due to the known problems of fertility of younger animals.
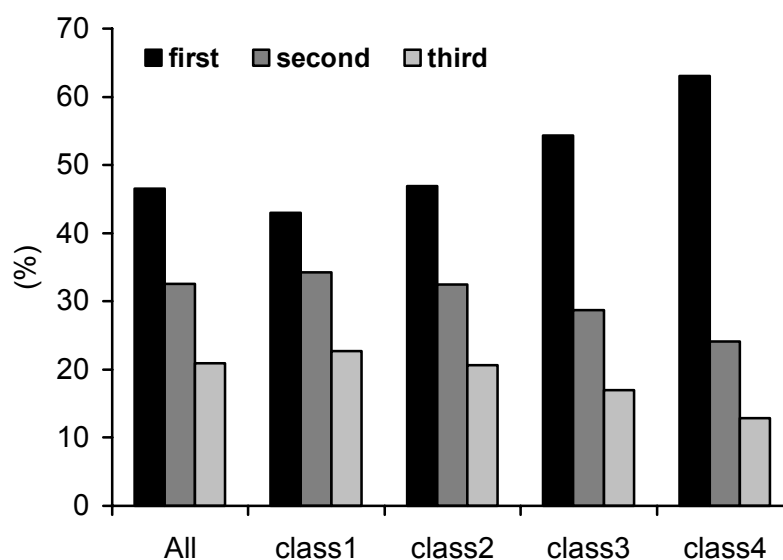
Figure 3. *Frequency (%) for all cows and for parity (first, second and third) in the classes of lactation length (class1 <350 d; class2 = from 351 to 450 d; class3 =from 451 to 650 d; class4= from 651 to 1000 d)*

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives"
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche
- 48 -

The distribution of records (either lactations or test day measures) across class of lactation length is reported in table 4. Approximately 40% of lactations have a length higher than 350d, whereas only 1.2 % of cows have lactations longer then 650 d. These results are different from those reported for U.S. cattle where more than 55% of the cows have lactations longer than 305 days (Dematawewa et al., 2007).

Table 4. *Percentage of lactations and test day available for each class length.*

	Percentage	
Length of lactation	Lactations	Test Day
<350	59	51
351 to 450	28	30
451 to 650	12	17
651 to 1000	1.2	2.3

Finally, table 5 reports average value of peak yield and peak occurrence for different parities and lactation lengths.

Also in the case of data analysed in this work, longer lactations tend to have higher peak yields and later peak occurrence than standard lactations, in agreement with what observed in US Holstens (Table 1) (Dematatewa et al., 2007).

Table 5. *Peak milk yields (kg/d) and peak occurrence (d) for first, second and third parities within lactation length class.*

Lactation length	Parity	Peak yield	Peak time
<350	1	30.75	56
	2	38.77	38
	3	40.13	55
351 to 450	1	31.33	88
	2	40.57	34
	3	41.48	39
451 to 650	1	32.66	67
	2	40.37	34

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 49 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

	3	42.08	34
651 to 1000	1	34.03	51
	2	42.81	39
	3	51.26	42

Model selection

The basic model used in this paper was the modified version of Dijkstra function (DF) of lactation curve that was specifically proposed by VanRaden et al. (2006) to fit extended lactations:

$$y = b_0 + b_1 \exp\left[\frac{b_2\left(1 - \exp(b_3 t)\right)}{b_3} - b_4 t \right]$$

where y is the milk at time t in days after parturition, whereas b_0, b_1, b_2, b_3, and b_4, are parameters to be estimated. Some technical information may be calculated from the combination of the parameters of the model. The solution of the first derivative of the function is a maximum point that represents the time at peak production (T_p):

$$Tp = -\frac{1}{b_3} \log\left(\frac{b_4}{b_2} \right)$$

It can be easily demonstrated that DF has an horizontal asymptote for time $\rightarrow \infty$. The value of the asymptote is b_0, that can be interpreted as the value of milk yield in the final phase of lactation. Information on final production level obtained in advance may be useful in management decisions as well as in genetic evaluations. VanRaden et al. (2006) calculated a baseline that corresponds to a level of production above which the

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives"
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche - 50 -

income of production exceeds the cost and therefore the cow can produce a profit. Such a threshold was estimated in 13.6 kg/day for US Holsteins.

Finally, the study of the second derivative gives as result an inflection point (T_f) that indicates the time at which the function representing the lactation pattern changes the curvature. In extended lactations, the inflection point may represent an important technical parameter to be estimated. An early T_f, in fact, may results in an asymptotic value of milk production sufficient to justify the maintenance of the lactation for a long period. The following equation allows the estimation of T_f:

$$T_f = \frac{1}{b_3}\left[\ln\left(\frac{\sqrt{b_3(b_3+4b_4)}+b_3+2b_4}{2}\right)+\ln(b_2)-2\ln b_4\right]$$

The modified Dijkstra function was compared with an empirical model chosen among those more frequently used to fit standard lactation curves. In particular, were tested two three-parameter functions selected among models with a limited number of parameters and four polynomials with five parameters.

For all models Y_t *represents test day milk yield (kg) recorded at time* t *(days);* a_0, a_1, a_2, a_3, a_4, b *and* c *are function parameters.*

The six models are:

The incomplete gamma function of Wood (1967) (WD):

$$Y_t = at^b e^{-ct}$$

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 51 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

that is the most popular and commonly used model of lactation curve, recommended also to fit extended lactations (Dematawewa et al., 2007).

The combined exponential and linear model (WIL) (Wilmink, 1987):

$$Y_t = a + be^{kt} + ct$$

fitted in the linear form by setting the parameter k to fixed value of 0.05 as suggested by Wilmink in his original paper. In this form, WIL is considered the best model with three parameters for dairy cattle (Olori et al., 1999) and it is also used in random regression test day models (Reinhardt et al., 2002).

The five-parameter polynomial regression of Ali and Schaeffer (AS) (1987):

$$Y_t = a_0 + a_1 x + a_2 x^2 + a_3 \log (1/x) + a_4 (\log(1/x))^2$$

where: x = t/lactation length.

A fourth-order Legendre orthogonal polynomial (LEG). It is commonly used in random regression model to model individual lactation curves:

$$Y_t = a_0 P_0 + a_1 P_1 + a_2 P_2 + a_3 P_3 + a_4 P_4$$

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 52 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

where: P_j is the function of time calculated using values published by Schaeffer, (2004).

A quadratic spline (QSPL) with three knots:

$$Y_t = a + b_1 t + b_2 t^2 + c(t - N_j)^2$$

A cubic spline functions (CSPL) with two knots:

$$Y_t = a + b_1 t + b_2 t^2 + b_3 t^3 + c(t - N_j)^3$$

where N_j is the position of the knot. Knots were placed at 50, 200 and 600 days.

Functions were fitted to individual curves. Linear regression was used for the WIL, AS, LEG QSPL and CSPL, whereas nonlinear regression with the Marquardt method (Marquardt, 1963) was used for the WD model. Goodness of fit was assessed using adjusted coefficient of determination (R^2_{adj}) calculated as:

$$R^2_{adj} = 1 - [(n - 1)/(n - p)] (1 - R^2)$$

where:

R^2 = multiple coefficient of determination (equal to 1-RSS/TSS);

n = number of observations;

p = number of parameters in the model.

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 53 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

Curves were classified according to five levels of R^2_{adj} (1<0.30, 2 = from 0.30 to 0.50, 3= from 0.50 to 0.70, 4= from 0.70 to 0.90, 5=>0.90).

Results and discussion of model selection

Table 6 shows the percentage of individual lactation curves within each class of adjusted R-squared obtained by fitting the different models for the four classes of lactation length. Figure 4 reports the percentages of individual curves having an adjusted R-squared higher than 0.70 for all models, within each lactation length class. It can be observed that best fits (represented by the percentage of lactations having an R^2_{adj} higher than 0.90) tend to decrease for increasing lactation lengths. As expected, functions characterised by an higher number of parameters show better fitting performances compared with three-parameter functions. In particular WD and WIL models have only the 55% of individual curves with a R^2_{adj} higher than 0.70 for the longest lactation class. Moreover, among models with five parameters, some differences can be observed due to the different flexibility: LEG and CSPL have the best fit in each length class with about 80% of curves showing an R^2_{adj} higher than 0.70 for lactations longer than 650 days. Nevertheless, AS and QSPL models have performances that does not differ considerably from LEG and CSPL.

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives"
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche
- 54 -

Table 6. *Distribution of fit for individual curves for milk yield ranked on five class of R^2_{adj} according to lactation length class, for Wood (WD), Wilmink (WIL), Ali and Schaeffer (AS), Legendre polynomials (LEG), quadratic splines (QSPL) and cubic splines (CSPL) models.*

Length class	R^2_{adj} class	Models					
		WD	WIL	AS	LEG	QSPL	CSPL
<350	<0.30	17.52	10.94	7.52	7.96	7.86	7.66
	0.30 - 0.50	12.93	9.21	6.17	5.55	6.25	6.17
	0.50 - 0.70	22.77	17.76	12.90	11.83	13.04	13.02
	0.70 - 0.90	36.13	39.27	35.21	32.07	35.39	35.50
	>0.90	10.65	22.82	38.20	42.59	37.46	37.66
351-450	<0.30	12.81	8.27	4.32	4.54	4.50	4.68
	0.30 - 0.50	12.24	8.00	4.90	4.60	5.02	4.62
	0.50 - 0.70	23.63	17.23	11.99	11.42	12.10	11.39
	0.70 - 0.90	39.58	41.87	39.24	37.01	39.70	37.60
	>0.90	11.75	24.63	39.55	42.43	38.68	41.71
451-650	<0.30	8.97	6.33	2.88	2.72	2.99	2.62
	0.30 - 0.50	11.50	7.63	4.43	3.88	4.90	3.97
	0.50 - 0.70	24.69	18.07	12.36	11.39	12.47	10.83
	0.70 - 0.90	43.09	45.45	43.15	42.08	43.61	42.01
	>0.90	11.75	22.50	37.18	39.92	36.03	40.57
651-1000	<0.30	7.24	6.66	3.27	2.01	3.77	2.76
	0.30 - 0.50	12.68	8.79	6.41	5.78	5.03	5.15
	0.50 - 0.70	24.95	21.23	14.70	12.44	13.57	11.81
	0.70 - 0.90	43.86	49.25	47.86	49.50	47.61	47.11
	>0.90	11.27	14.07	27.76	30.28	30.03	33.17

In the literature there are not data available on fitting individual extended lactation curves. However, results obtained in this study for lactations of standard length are similar to previous reports for dairy cattle (Olori et al., 1999; Silvestre et al., 2006; Macciotta et al., 2005), with a better fit for polynomials (AS, LEG and SPL) compared to models with three parameters, and better performances of WIL model compared to WD.

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 55 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche
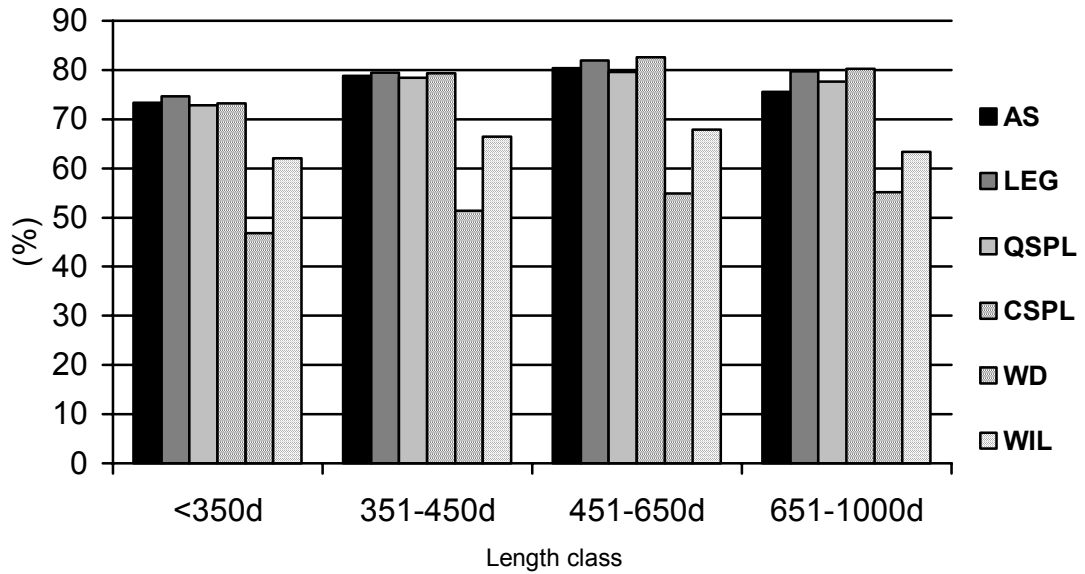
Figure 4. *Percentage of individual curves having an R^2_{adj} higher than 0.70 in the four length classes for Ali and Schaeffer (AS), Legendre polynomials (LEG), quadratic splines (QSPL), cubic splines (CSPL), Wood (WD) and Wilmink (WIL) models.*

Although Legendre polynomials and Spline functions gave better fitting performances compared with the AS model, the latter was chosen. This is because a) AS has the same number of parameters of the modified Dijkstra, b) as for DF, main features of lactation curves can be calculated from the estimated values of the parameters of the model.

From the first derivative of the AS model, the time at which peak yield occurs (Tp) can be obtained by solving the following equation:

$$a_1 X + 2a_2 X^2 = a_3 + 2a_4 \log(1/X)$$

the sum

$$a_0 + a_1 + a_2$$

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives"   - 56 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

gives the value of milk yield at the last test before the dry off. Finally the inflection point (T_f) can be calculated using the following equation:

$$a_3 + 2a_2 X_f^2 = -2a_4(1 + \log(1/X))$$

The DF and AS models were the used to fit average lactation curves for milk yield (MY), fat percentage (FP), protein percentage (PP) and somatic cell score (SCS) Curves were calculated by averaging all records taken on the same date, for each parity within each lactation length class. Linear regression was used for AS, whereas nonlinear regression, based on the Marquardt compromise, was used for DF model. Goodness of fit was assessed by using the multiple coefficient of determination (R^2) and the residual standard deviation (RSD). Moreover, the Durbin-Watson statistic (DW) was used to detect the presence of autocorrelation in the residuals from the regression analysis.

For MY average curve, time at which peak yield occurs (Tp), peak yield (Yp), time of the inflection point (T_f) were calculated. Cumulative milk production after 305d (P_{305}), at dry off (P_{tot}) and final test day production were also calculated.

Finally, to assess the capability of the two models to describe individual patterns, DF and the chosen model were fitted to individual curves. Curves were classified according to five levels of R^2 (1<0.30, 2 = from 0.30 to 0.50, 3= from 0.50 to 0.70, 4= from 0.70 to 0.90, 5=>0.90).

Results and discussion of the comparison between modified Dijkstra and Ali and Schaeffer model

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives"   - 57 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

Average curves

AS and DF models were fitted to the data using linear (for AS) and non linear (for DF) regression procedures, within class of lactation length and parity. Estimated regression parameters for milk are reported in table 4. Coefficients of other analysed traits are reported in appendix.

Table 7. Estimated parameters, for parity within lactation length class, Ali and Schaeffer (AS) and modified Dijkstra function (DF) models.

Model	Class of length	parity	Estimated parameters				
			a_0	a_1	a_2	A_3	a_4
AS	<350	1	36.25	-13.20	-3.67	-0.910	-0.468
		2	39.58	-22.02	-0.95	2.661	-1.130
		3	48.00	-35.93	4.48	-0.570	-0.790
	351-450	1	21.63	8.71	-13.93	7.333	-1.563
		2	32.29	-17.15	-0.73	7.187	-1.741
		3	38.90	-28.56	3.57	4.947	-1.521
	451-650	1	34.02	-21.78	1.92	1.437	-0.722
		2	41.61	-50.44	22.94	2.977	-1.103
		3	54.87	-75.54	35.35	-2.838	-0.419
	651-1000	1	30.82	-25.03	7.28	2.906	-0.821
		2	13.12	-10.08	10.08	15.331	-2.394
		3	7.61	-7.22	13.36	20.106	-3.129
			b_0	b_1	b_2	b_3	b_4
DF	<350	1	-955.6	979.6	0.00038	0.03188	0.00005
		2	-1111.9	1140.4	0.00069	0.05773	0.00006
		3	-1035.5	1064.0	0.00083	0.05750	0.00007
	351-450	1	-1233.4	1258.1	0.00026	0.03037	0.00003
		2	-379.2	405.0	0.00292	0.07687	0.00015
		3	-175.7	202.7	0.00547	0.06887	0.00033
	451-650	1	-924.5	946.9	0.00061	0.04892	0.00003
		2	2.8	25.3	0.02739	0.05686	0.00208
		3	5.4	24.6	0.02197	0.04202	0.00251
	651-1000	1	-14.5	37.0	0.01241	0.04717	0.00057
		2	9.5	17.9	0.03417	0.05919	0.00223
		3	10.9	16.2	0.04210	0.05540	0.00276

The parameters for DF in the longer lactations estimates in this study are similar, except for asymptotic yield, to values reported by VanRaden et al. (2006).

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 58 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

AS and DF models gave similar performances when average milk lactation curves (MY) were modelled showing an R^2 ranging, for both models, from 0.71 to 0.99 (table 5). The two functions were able to adequately fit milk composition (FP, PP and SCS) only for lactations shorter than 650 days (R^2 ranges from 0.65 to 0.92 for both models), whereas they gave poor results in the highest length class (>650d) with R^2 from 0.13 to 0.41 for FP and SCS. Better results were for PP with R^2 around 0.66. In general, goodness of fit tends to decrease as lactation length and parity increase. This behaviour is probably due to a reduced sample size in the longest lactations and in highest parity (tables 1 and 2),. Actually RSD increases markedly both with parity and classes of lactation length. However, for extended lactations (>650 days) it can be observed a substantial absence of autocorrelations among residuals (DW ~ 2.00) confirming the goodness of fit of the two models. Actually, previous studies comparing empirical and mechanistic models for their ability to describe the pattern of milk yield in long lactations (Vargas et al., 2000; Dematawewa et al., 2007) have found autocorrelation among residuals.

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 59 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

Table 8. *Goodness of fit for average curves for milk yield (MY), fat percentage (FP), protein percentage (PP) and somatic cell score (SCS) according to parity within lactation length class, for Ali and Schaeffer (AS) and modified Dijkstra function (DF) models.*

Model	Class of length	Parity	MY R^2	MY RSD	MY DW	FP R^2	FP RSD	FP DW	PP R^2	PP RSD	PP DW	SCS R^2	SCS RSD	SCS DW
AS	<350d	1	0.99	0.019	0.97	0.98	0.002	1.5	0.99	0.001	1.13	0.92	0.005	1.81
		2	0.99	0.026	1.22	0.96	0.003	1.55	0.99	0.001	1.1	0.97	0.005	1.92
		3	0.99	0.029	1.65	0.94	0.003	1.93	0.98	0.002	1.31	0.95	0.007	2.01
	351-450d	1	0.99	0.023	0.72	0.96	0.003	1.7	0.99	0.001	1.58	0.89	0.006	1.86
		2	0.99	0.031	1.57	0.94	0.003	1.77	0.99	0.002	1.72	0.93	0.008	1.84
		3	0.99	0.037	1.67	0.88	0.004	1.79	0.98	0.002	1.56	0.91	0.009	1.99
	451-650d	1	0.97	0.036	1.88	0.88	0.005	2.14	0.96	0.003	2.29	0.80	0.009	1.89
		2	0.97	0.055	1.88	0.71	0.007	2.09	0.91	0.004	2.22	0.69	0.015	1.93
		3	0.96	0.068	2.18	0.64	0.008	1.99	0.90	0.004	1.99	0.62	0.018	2.13
	651-1000d	1	0.82	0.084	2.00	0.37	0.012	2.14	0.73	0.006	2.15	0.41	0.023	2.08
		2	0.83	0.111	1.95	0.24	0.016	2.13	0.67	0.008	2.16	0.27	0.031	2.06
		3	0.71	0.182	1.99	0.14	0.021	1.81	0.59	0.009	1.97	0.16	0.046	2.04
DF	<350d	1	0.98	0.024	1.42	0.95	0.003	0.81	0.99	0.001	0.99	0.92	0.005	1.82
		2	0.99	0.026	1.24	0.95	0.003	1.13	0.99	0.002	0.84	0.97	0.005	1.84
		3	0.99	0.029	1.51	0.93	0.003	1.56	0.98	0.002	1.03	0.95	0.007	1.99
	351-450d	1	0.98	0.031	1.29	0.95	0.003	1.58	0.99	0.001	1.51	0.88	0.006	1.77
		2	0.99	0.029	1.43	0.94	0.003	1.69	0.99	0.002	1.73	0.92	0.008	1.76
		3	0.99	0.035	1.54	0.88	0.004	1.84	0.98	0.002	1.64	0.90	0.009	1.94
	451-650d	1	0.97	0.035	1.86	0.88	0.005	2.15	0.96	0.003	2.28	0.79	0.010	1.80
		2	0.97	0.056	1.93	0.70	0.007	1.99	0.91	0.004	2.10	0.69	0.016	1.92
		3	0.96	0.069	2.27	0.63	0.008	1.94	0.90	0.004	1.91	0.62	0.018	2.14
	651-1000d	1	0.82	0.084	1.99	0.37	0.012	2.16	0.73	0.006	2.15	0.40	0.022	2.05
		2	0.83	0.110	1.93	0.23	0.016	2.10	0.66	0.008	2.09	0.27	0.031	2.04
		3	0.72	0.181	1.98	0.13	0.020	1.80	0.59	0.009	1.96	0.15	0.046	2.01

Lactation curves estimated with AS and DF function for the different traits (MY, PP, FP and SCS) in the longer class of lactation (650-1000 days) for each parity class, are reported in figures 5, 6, 7 and 8. No sensible difference was found in the shape of the four traits between AS and DF models. As expected (figure 5), first parity cows showed an initial and peak milk yield lower than second and third parity cows but together with a greater persistency. This is expected because it is known for different species of ruminants that lactation curves of first parity are characterised by a lower peak production and a greater persistency (Stanton et al.,1992; Friggens et al., 1999; Dimauro et al., 2005; Macciotta et al., 2005; Portolano et al., 1997; Cappio.Borlino et

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 60 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

al., 1992). This is due to the fact that in first calving animals processes of body growth and maturation of mammary tissue are still active, thereby counterbalancing the decline in milk production of the second part of lactation (Pulina et al., 2005).

Actually the curve of first parity cows do not show the sudden decline at around 300 days that can be observed for older animals but tends to maintain a constant slope along the whole lactation. Thus after 300 days, the production level of second and third parity is lower than first parity and tend to an asymptotic value. Similar patterns were observed for US (Dematawewa et al., 2007) and Australian (Haile-Mariam et al., 2008) Holstein.

Milk components showed an opposite trend compared to MY (figures 6, 7 and 8). In particular, FP and PP (figures 6 and 7) did not show a significant variation among parities, whereas differences have been detected for SCS, with an higher level for the older cows. Moreover, FP and PP tended to reach a plateau around 500-600 days in milk whereas SCS showed a continuously increasing trend. Similar patterns were obtained also by Haile-Mariam et al. (2008). These results suggest to limit the number of older cows in herds with longer lactation especially if the milk is paid according to quality.

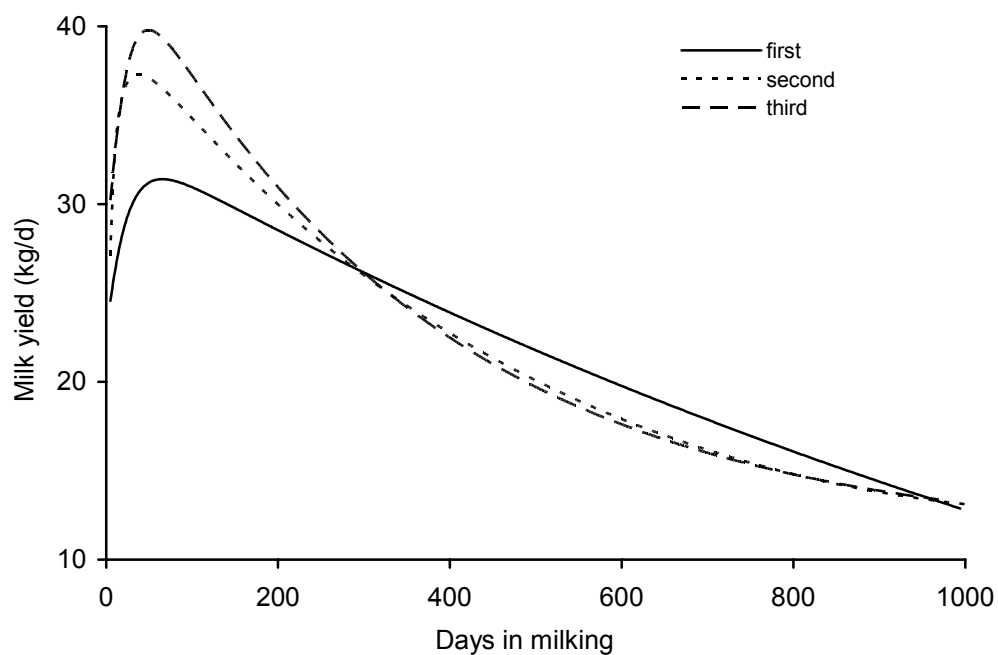*Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives"* - 61 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

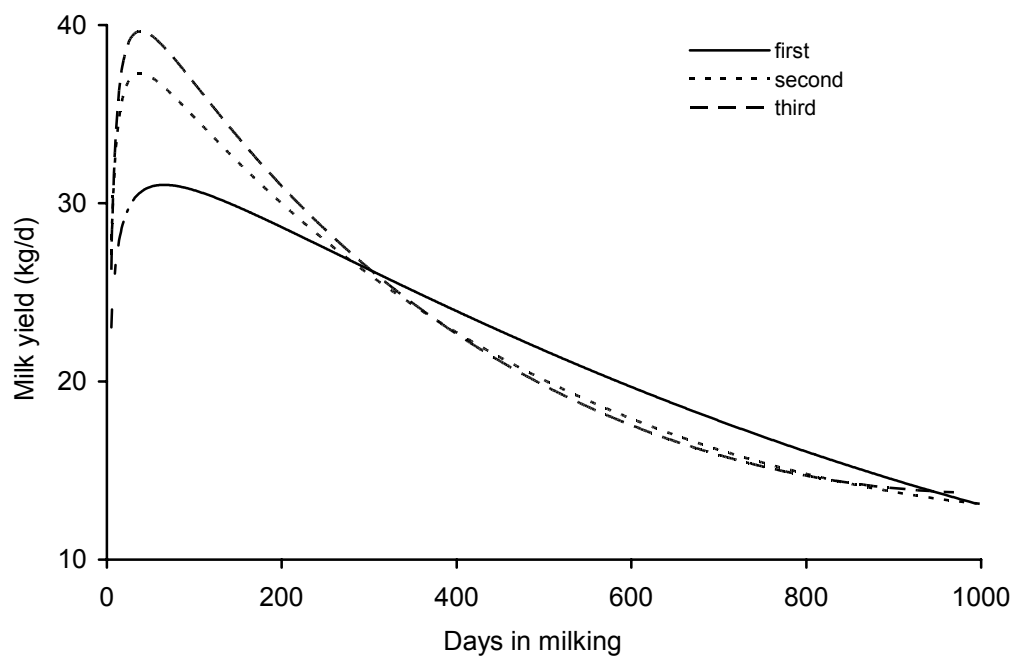**Figure 5.** *Estimated milk yield lactation curves for different parities by the AS a) and DF b) models for the 650-1000d lactation length class.*

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 62 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
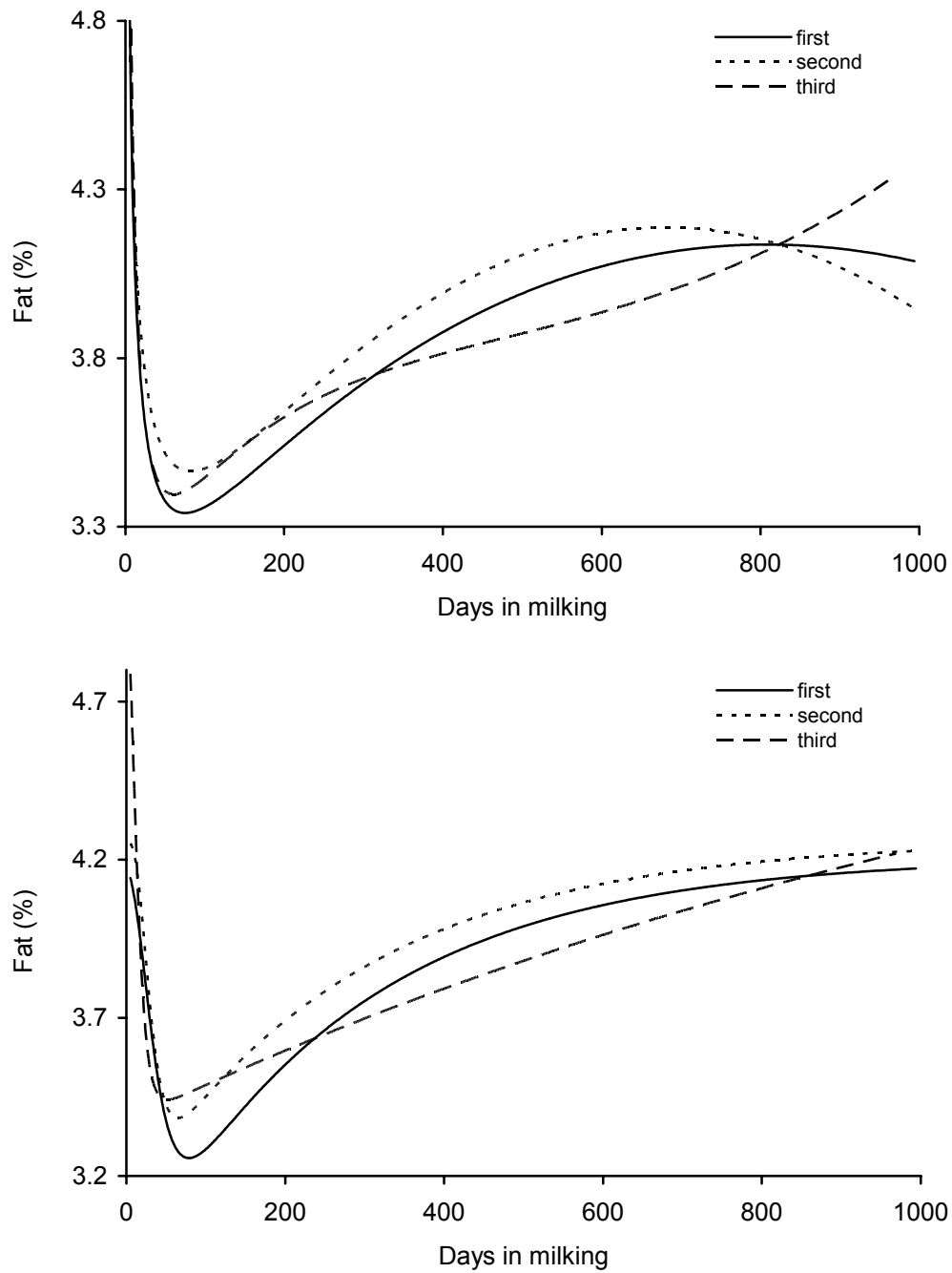*Indirizzo Scienze e Tecnologie Zootecniche*

Figure 6. *Estimated fat percentage lactation curves for different parities by the AS a) and DF b) models for the 650-1000d lactation length class.*

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 63 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
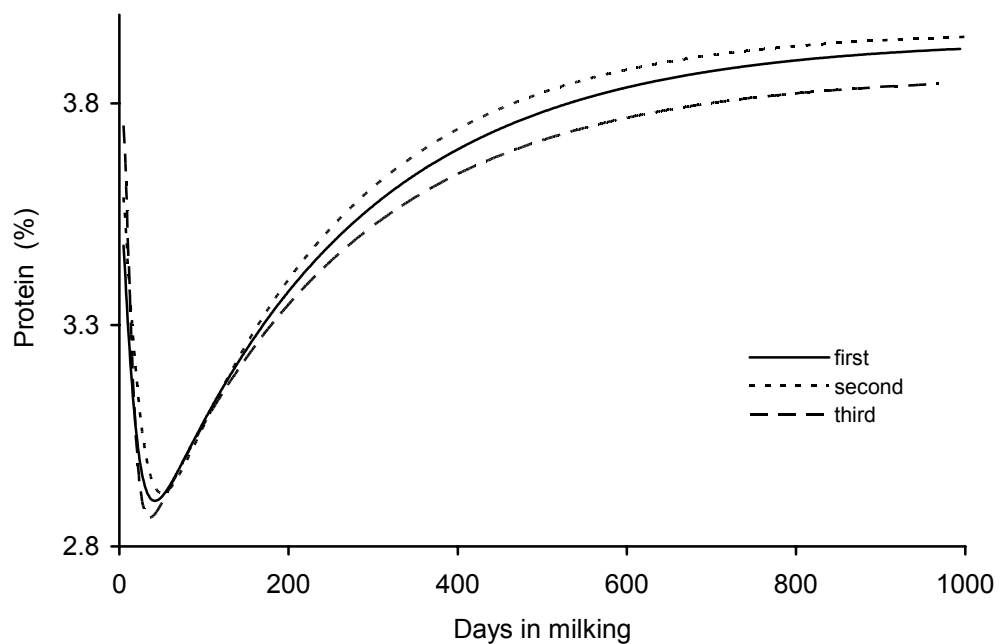*Indirizzo Scienze e Tecnologie Zootecniche*

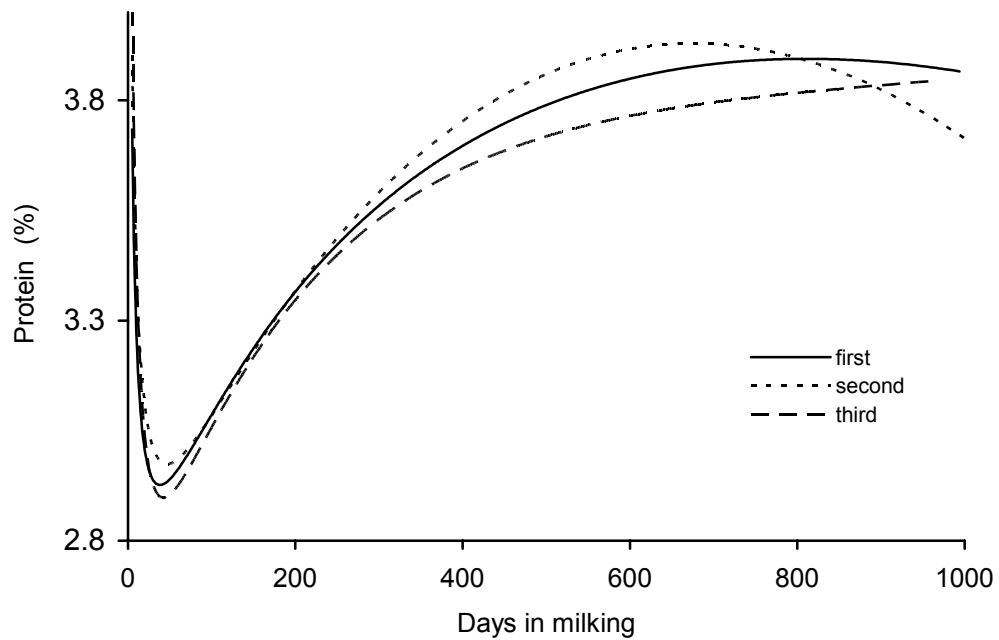**Figure 7.** *Estimated protein percentage lactation curves for different parities by the AS a) and DF b) models for the 650-1000d lactation length class.*

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 64 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
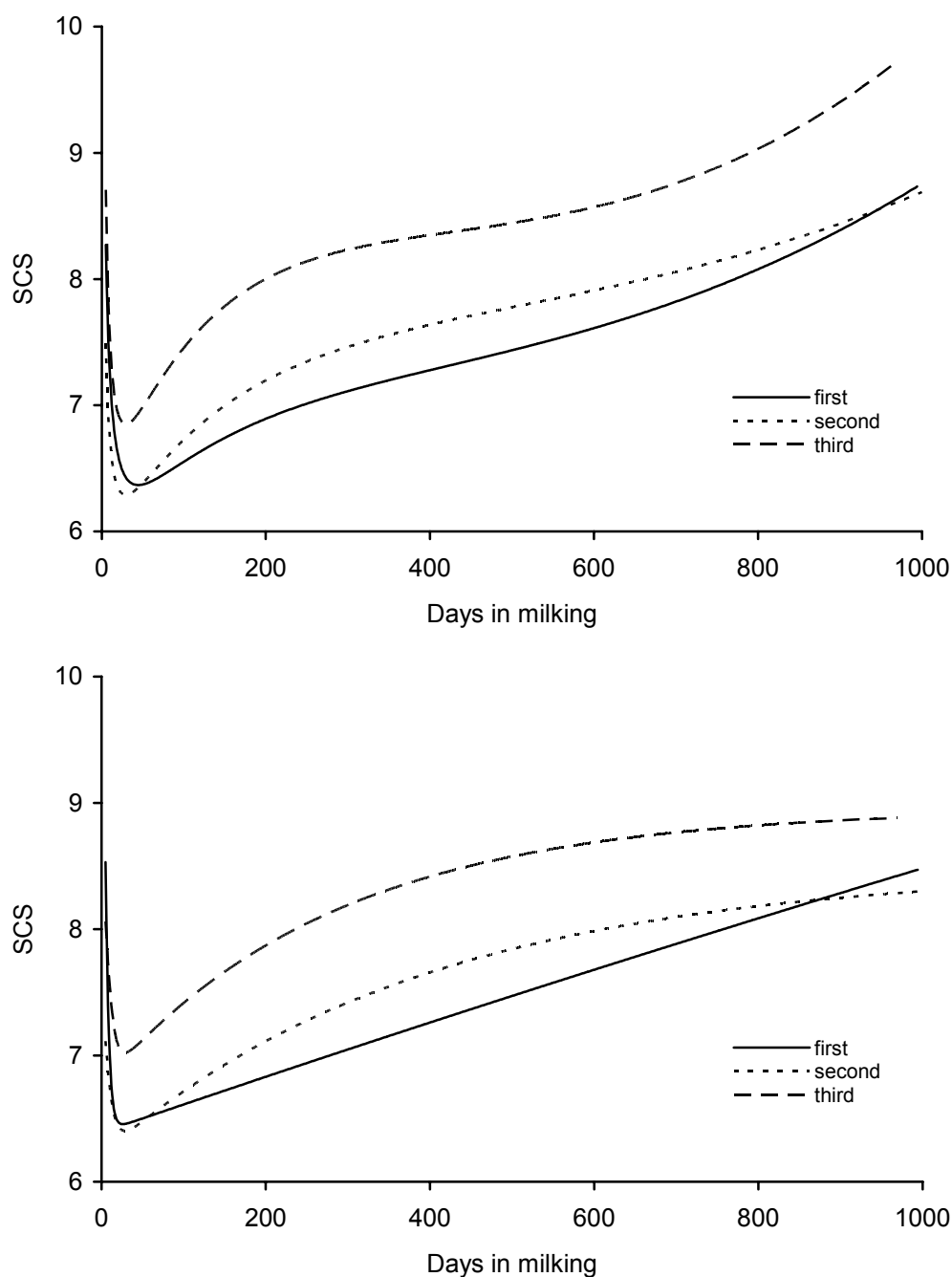*Indirizzo Scienze e Tecnologie Zootecniche*

Figure 8. *Estimated SCS lactation curves for different parities by the AS a) and DF b) models for the 650-1000d lactation length class.*

Main features of milk lactation curves estimated from the combination of AS and DF parameters, are reported in table 6.

In agreement with other researches on mathematical modelling of extended lactations in cattle (Dematawewa et al., 2007; VanRaden et al., 2006), also in the present research there is no difference in time at which peak occurs (T_p) for the different

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives"
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche
- 65 -

classes of lactation length. In general, the modified Dijkstra function systematically predicts T_p 5-8 days after compared to the Ali and Schaeffer function. Between each class, first parity cows show a later peak occurrence (about 60-65 days after parturition) in comparison with older parities (40-45 days in milk). This is a rather frequent event: in cattle and in other species has been observed a later occurrence of peak yield in primiparous animals compared to older ones (Tekerli et al., 2000; Gipson and Grossman, 1990).

Similarly, peak yield (y_p) did not show substantial differences among length classes, in agreement with Dematawewa et al. (2007) and VanRaden et al. (2006). These results confirm the conclusion that long lactation records are mainly caused by non genetic factors. First calving cows showed a predicted peak yield of 31 kg, whereas older animals, had higher peaks (about 37-39 kg) in all classes of lactation length.

As expected, milk yield during the first 305 days (P_{305}), showed an increasing trend with parity. A similar behaviour can be observed for total yield for the actual length (P_{tot}), a part from the class with the longest lactations (651-1000 days) where milk production decreases as parity increases (about 20600 kg, 19800 kg and 18400 kg for first, second and third parity respectively, for both models). Such a result may be at least partly explained with the higher persistency of younger cows. Estimated curves (Figures 5a and 5b) clearly show that the pattern of first calving cows is constantly higher than those of older parities in the interval between 300 and 1000 days in milk. The fact that first parity cows had higher daily milk yield after, approximately, 300 days compared to higher parities was also observed by Van Amburgh et al. (1997), Schutz et al. (1990) and VanRaden et al. (2006). These figures seem partly in disagreement with those reported by Haile-Mariam and Goddard for Australian Holstein farmed in pasture-based systems: they did not find substantial differences in the average daily milk yield

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives"   - 66 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

of first and second parity cows in the period between 300 and 600 days of lactation (Table. 2).

Table 9. *Time to the peak (Tp), production to the peak (Yp), production to the final test day (Ftd), cumulative production until 305 day (P_{305d}), cumulative production until the dry off (P_{tot}) and time et inflection point (T_f), for parity within lactation length classes.*

Model	Class of length	Parity	Tp	Yp	Ftd*	P_{305d}	P_{tot}	T_f
AS	<350d	1	61	30.8	19.37	8,307	9213	no
		2	38	37.5	16.61	9,125	9931	no
		3	40	39.0	16.56	9,377	10181	203
	351-450d	1	53	31.0	16.42	8,516	11437	no
		2	38	38.0	14.42	9,472	12152	no
		3	40	39.5	13.91	9,751	12389	171
	451-650d	1	61	31.3	14.16	8,670	15379	330
		2	42	38.3	14.12	9,744	16021	150
		3	47	39.2	14.68	9,991	16174	170
	651-1000d	1	65	31.0	13.08	8,740	20659	259
		2	38	37.3	13.12	9,599	19834	105
		3	39	39.6	13.75	9,668	18460	104
DF	<350d	1	66	31.2	-955.6	8,293	9235	266
		2	41	37.8	-1111.9	9,116	9942	161
		3	42	39.3	-1035.5	9,374	10185	160
	351-450d	1	69	31.4	-1233.4	8,501	11482	299
		2	39	38.2	-379.2	9,471	12141	120
		3	41	39.8	-175.7	9,749	12369	118
	451-650d	1	60	31.8	-924.5	8,665	15386	213
		2	45	38.9	2.8	9,719	15906	105
		3	52	39.8	5.4	9,956	16026	121
	651-1000d	1	65	31.4	-14.5	8,736	20576	159
		2	46	37.3	9.5	9,609	19855	103
		3	40	39.6	10.9	9,679	18403	105

*Ftd = (sum of coefficients a_0, a_1 and a_2 for AS model; b_0 for DF model).

The yield at the final test day available (Ftd) estimated by the AS model (table 6) tends to decrease for increasing lactation length, with value of about 13 kg in the 651-1000d class. This value is similar to the threshold yield for a milked cow to be profitable, estimated by VanRaden et al. (2006). On the other hand, the asymptotic level of production (Ftd) estimated with DF model has negative values for lactations of standard length and tends to increase in as lactation length increases, reaching positive value in lactations longer then 450 days for second and third parity, whereas for first parity is negative also in 651-1000d class. These values are obviously mathematical artefacts that can be explained looking at figures 9 and 10 that report milk yield lactation curves of third parity cows for different lactation length class, estimated with

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives"
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche   - 67 -

AS and DF models. For standard length (<350d) the phase beyond the lactation peak consists of a declining slope. Thus a production at final test date can be calculated but the asymptotic yield is obviously negative.
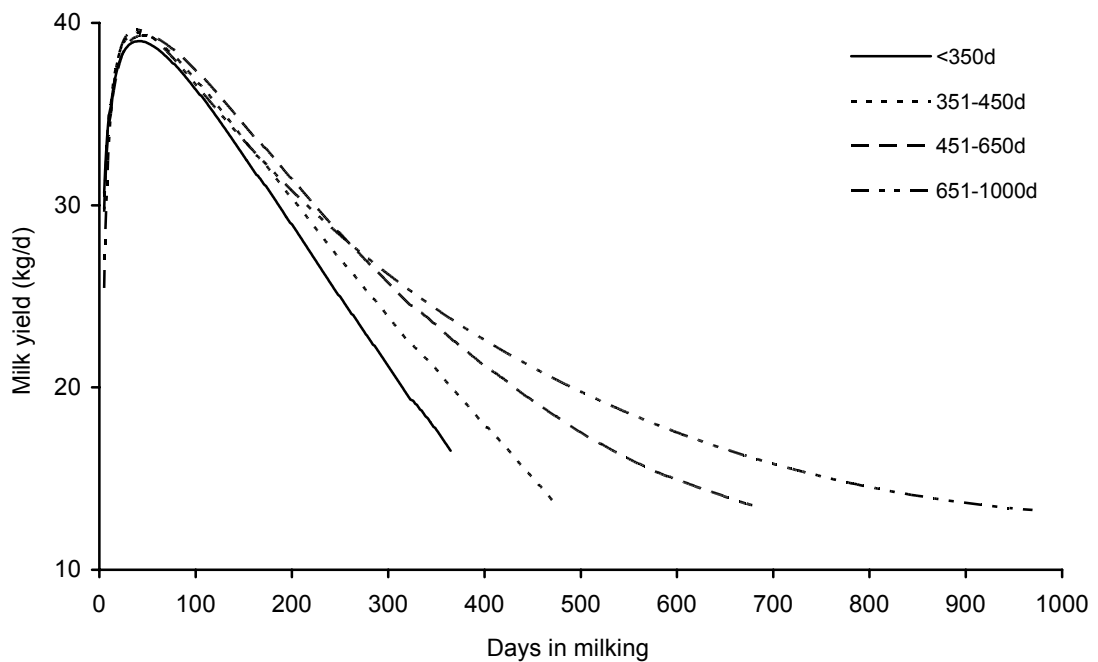
Figure 9. *Estimated milk yield lactation curves for third parity in different length classes by AS model.*

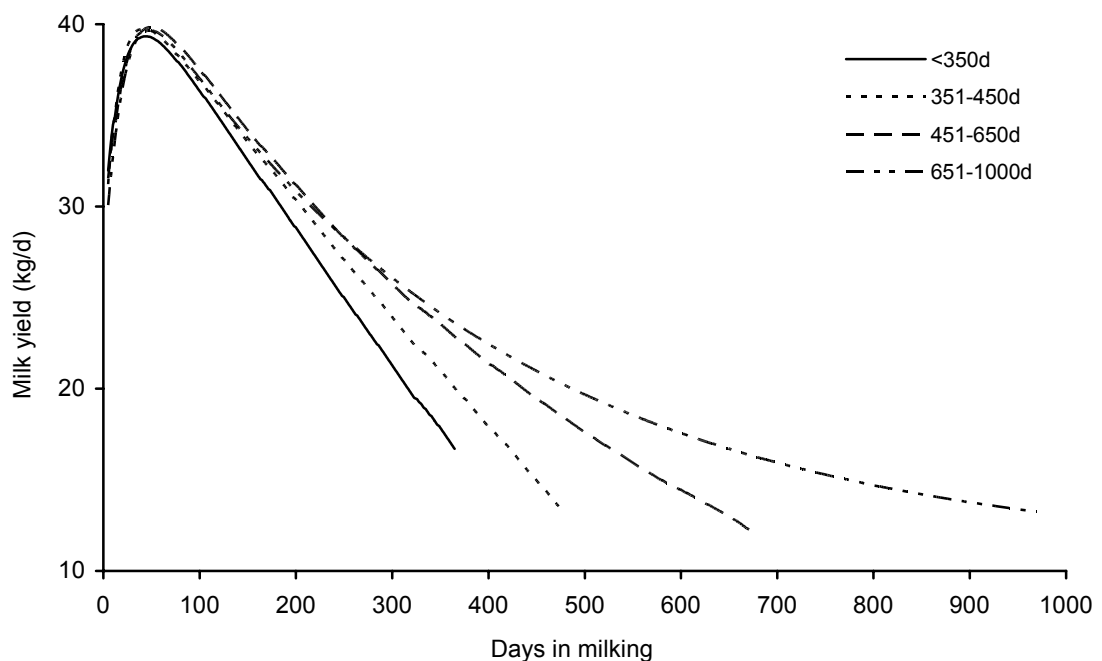**Figure 10.** *Estimated milk yield lactation curves for third parity in different length classes by DF model.*

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives"   - 68 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

Finally, DF model was able to detect the inflection point for all lactation length, whereas AS had not solution for first and second parity cows in first two classes lactation length. Generally, T_f has an earlier occurrence in older cows respect to first parity for all classes of lactation length, with value around 105 days for second and third parity and between 159 and 259 in first parity cows, respectively, for the longest lactation classes.

As previously reported, the knowledge of values at which production tends in later lactation is a key element for deciding whether it is profitable to keep milking a cow. From a technical standpoint, it would be very effective to be able to estimate such a value as soon as possible. Figure 11 shows values of parameter b_0 for DF model estimated for different days in milk at which the last test is available. It can be noticed that asymptotic production can be efficiently estimated with the last test test available at about 450 dim for second and third parity cows, whereas in first parity values tend to decline first. The trend seems to take a clear pattern in old animals, whereas it appears less defined in younger animals.
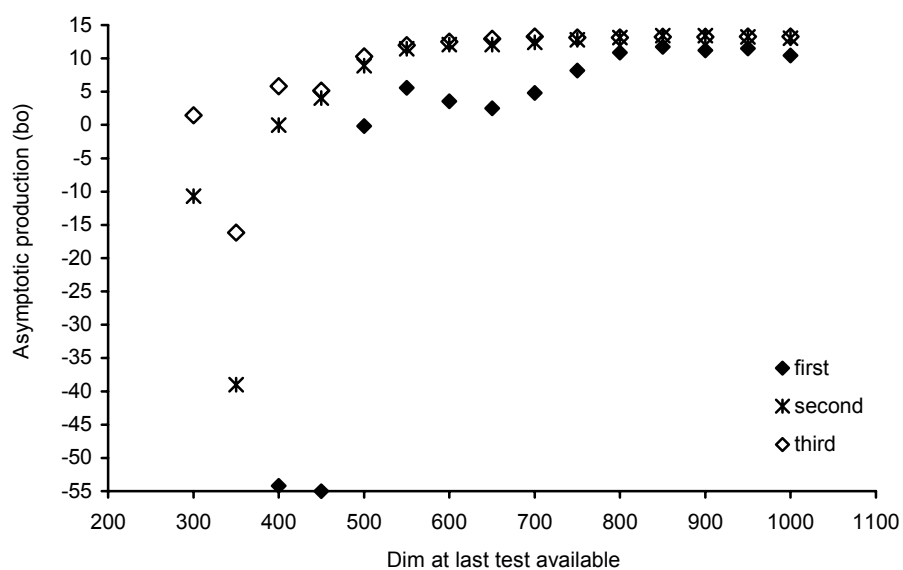
Figure 11. *Effect of the DIM et the last test available on the estimation of the asymptotic production.*

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 69 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

Individual curves

AS and DF models were fitted also to individual curves of the four traits (MY, PP, FP and SCS) and classified according to five levels of R^2 value (1<0.30, 2 = from 0.30 to 0.50, 3= from 0.50 to 0.70, 4= from 0.70 to 0.90, 5=>0.90) as reported in table 10. In general, goodness of fit is markedly lower compared to average curves, thus confirming the higher variability of individual patterns. As observed in average curves, fitting performances tend to decrease as the lactation length increases..

AS model fits adequately MY and PP, obtaining about 83% and 69% curves with R^2 higher than 0.7 for the two traits, respectively, in the 650-1000d length class. Also DF model shows a similar trend but its fitting performances are systematically lower than AS, with about 78 % and 62 % of individual curves for MY and PP, respectively. with an R^2 higher than 0.7 in the last class of lactation length. On the contrary for FP and SCS poor fitting performances were found, especially in longer lactation, with only 17.6% and 19.7% for AS and 13.6% and 12.3% for DF, for FP and SCS respectively, of individual curves having an R^2 higher than 0.7. Also in the case of this two traits, AS performed better than DF. Moreover, for DF model, convergence problems in the non linear procedure occurred in many cases.

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives"
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche
- 70 -

Table 10. *Distribution of R^2 for Ali and Schaeffer (AS) and modified Dijkstra function (DF) models estimates of individual lactation curves for milk yield (MY), fat percentage (FP), protein percentage (PP) and somatic cell score (SCS), according to lactation length classes.*

length	R^2 class[*]	MY AS	MY DF	PP AS	PP DF	FP AS	FP DF	SCS AS	SCS DF
<350	1	0.67	3.81	1.32	7.1	7.71	24.9	6.76	40.98
	2	2.31	4.31	3.65	6.76	14.31	16.51	13.4	13.50
	3	6.95	10.12	8.93	13.59	22.59	21.38	22.00	15.81
	4	28.83	35.23	32.23	37.64	36.31	27.21	36.08	20.15
	5	61.24	46.54	53.87	34.9	19.09	9.98	21.75	9.55
351-450	1	0.63	3.07	1.50	21.59	10.19	29.08	10.81	28.85
	2	2.25	4.04	2.83	4.92	18.27	17.87	17.95	17.92
	3	6.85	10.09	8.12	10.87	27.06	22.17	25.95	21.17
	4	31.91	36.95	35.71	33.36	34.75	25.34	33.88	23.96
	5	58.37	45.84	51.84	29.26	9.73	5.53	11.41	8.10
451-650	1	0.8	2.7	2.09	10.28	14.44	35.52	16.55	49.1
	2	2.13	3.67	3.61	5.68	22.34	21.87	22.18	15.4
	3	7.77	10.87	11.67	14.50	30.82	23.18	28.60	16.67
	4	38.08	41.57	44.60	45.22	28.49	17.49	27.91	15.56
	5	51.22	41.19	38.03	24.32	3.91	1.93	4.76	3.28
651-1000	1	1.88	3.52	2.89	7.88	22.11	34.47	24.62	53.2
	2	2.89	4.90	7.91	7.88	31.28	28.02	27.14	16.65
	3	11.93	13.94	20.35	22.42	29.02	23.84	28.52	17.82
	4	44.74	45.48	54.15	49.24	17.21	13.21	18.47	10.8
	5	38.57	32.16	14.70	12.58	0.38	0.46	1.26	1.53

[*] R^2 classes: 1<0.30, 2 = from 0.30 to 0.50, 3= from 0.50 to 0.70, 4= from 0.70 to 0.90, 5=>0.90

For genetic purposes, it may be of interest to have a first look at individual values of extended lactation features. Table 11 shows the median of technical parameters for MY, calculated with the estimated values of the parameters of AS and DF models for 651-1000d class length. The asymptotic level of production estimated with DJ was about -7, 11 and 8 kg for first, second and third parity respectively, whereas AS estimated the final production around 5, 8 and 5 kg for the same parity. The inflection point (T_f) was about 138 and 41 days for DJ and 596, 669 and 589 days for AS, for first, second and third parity respectively. Tm was found around 33, 60, and 50 days for DJ and 60, 45 and 46 days for AS.

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 71 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

Table 11. *Median of estimated technical parameters of individual lactation curves by AS and DF models for 651-1000d class length.*

Model	Parity	Ym	Tm	Ftd*	Tf
AS	1	33.76	49.54	5.51	596
	2	41.10	33.72	8.44	669
	3	42.25	41.00	5.53	589
DF	1	43.38	82.47	-7.25	138
	2	51.82	53.63	11.46	78
	3	54.04	52.94	8.51	41

*Ftd = (sum of coefficients a_0, a_1 and a_2 for AS model; b_0 for DF model).

Based on the general shape and on the average level of production, individual lactation curves can be grouped into three classes of shape. The first (Figure 12), that is rather frequent for first parity cows, is characterised by a decreasing phases after the peak yield with constant slope. The second and the third (figures 13 and 14) have the same pattern with a variation of the slope, approximately at around 300-500 days after calving, and a tendency to reach an asymptotic level of production. The main difference between these two groups is represented by the level of asymptotic yield.

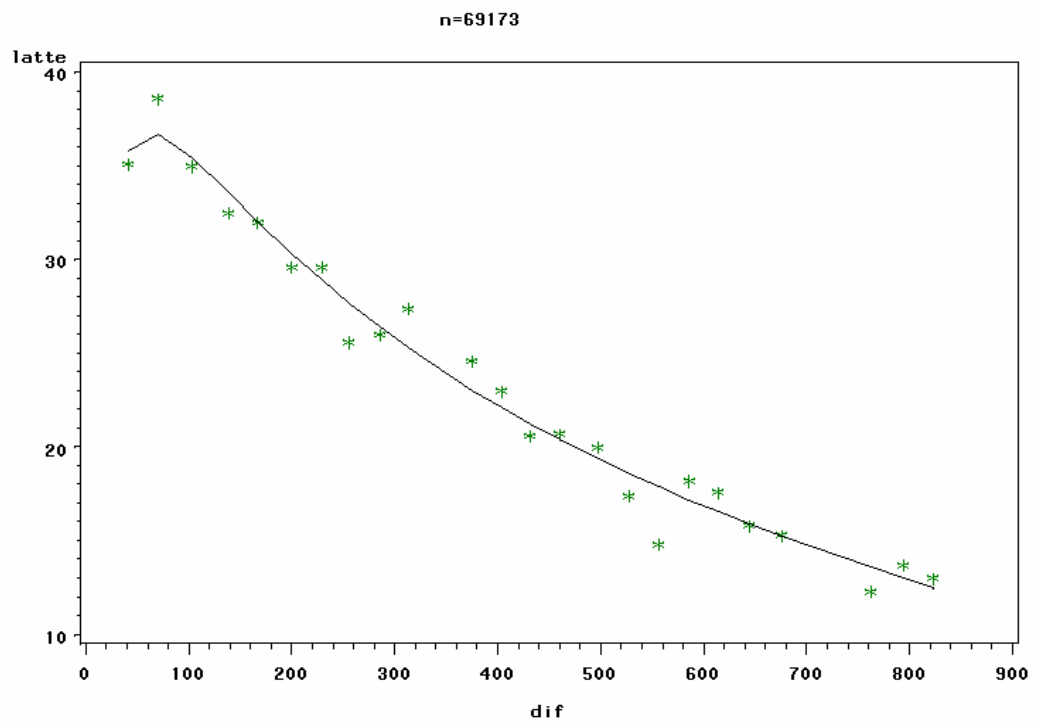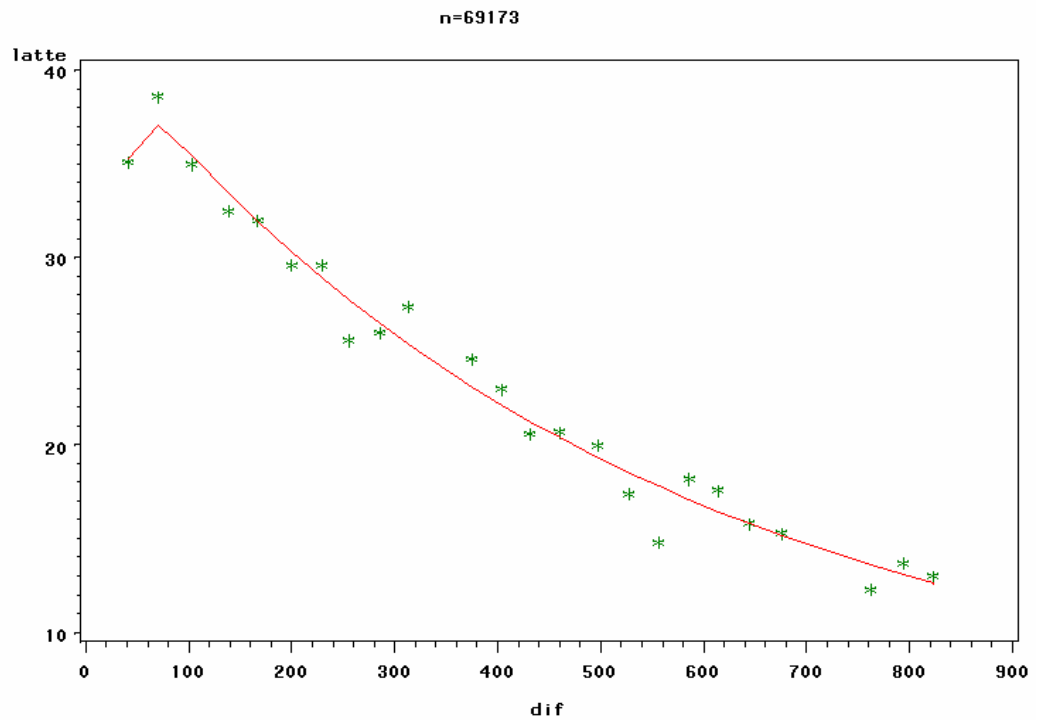*Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives"* - 72 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

Figure 12. *example of lactation curves with decreasing phases with constant slope*

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives"
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
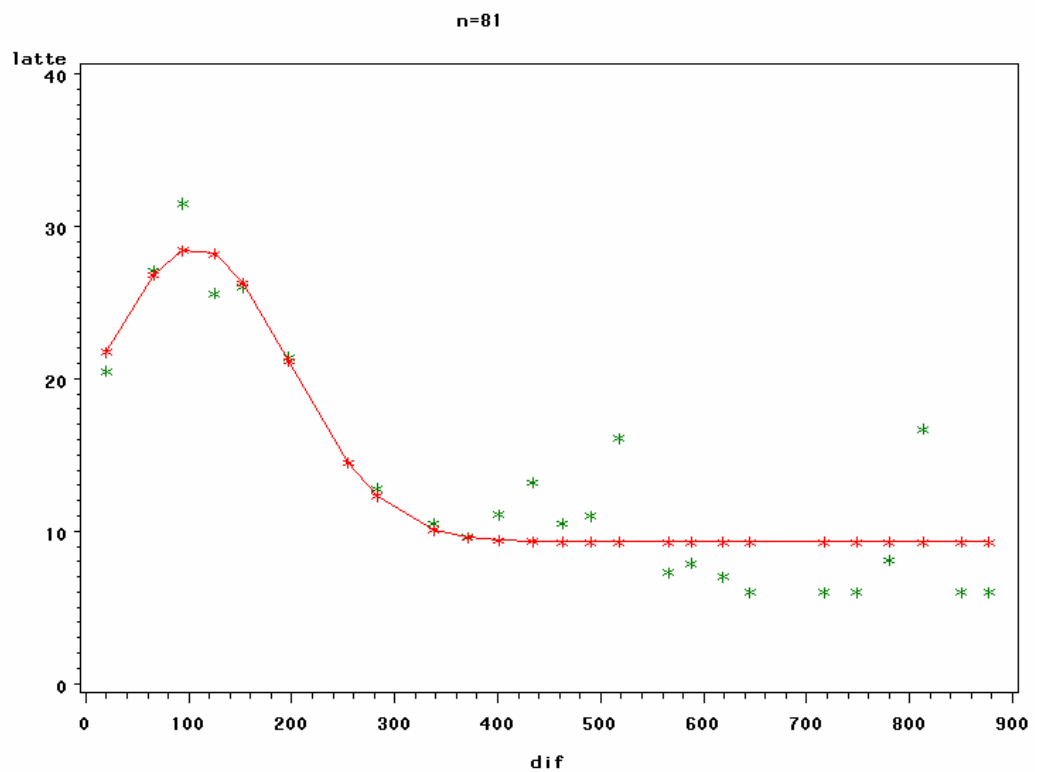*Indirizzo Scienze e Tecnologie Zootecniche*

- 73 -
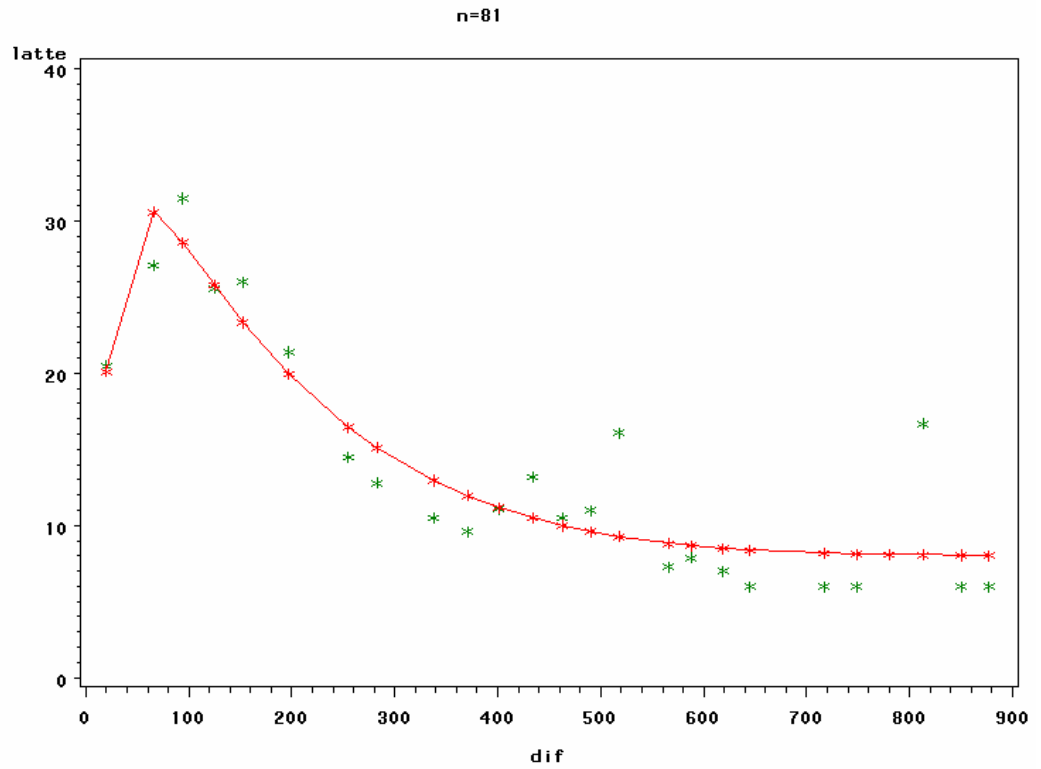
Figure 13. *example of lactation curves with decreasing phases tending to a low asymptotic level.*

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 74 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche
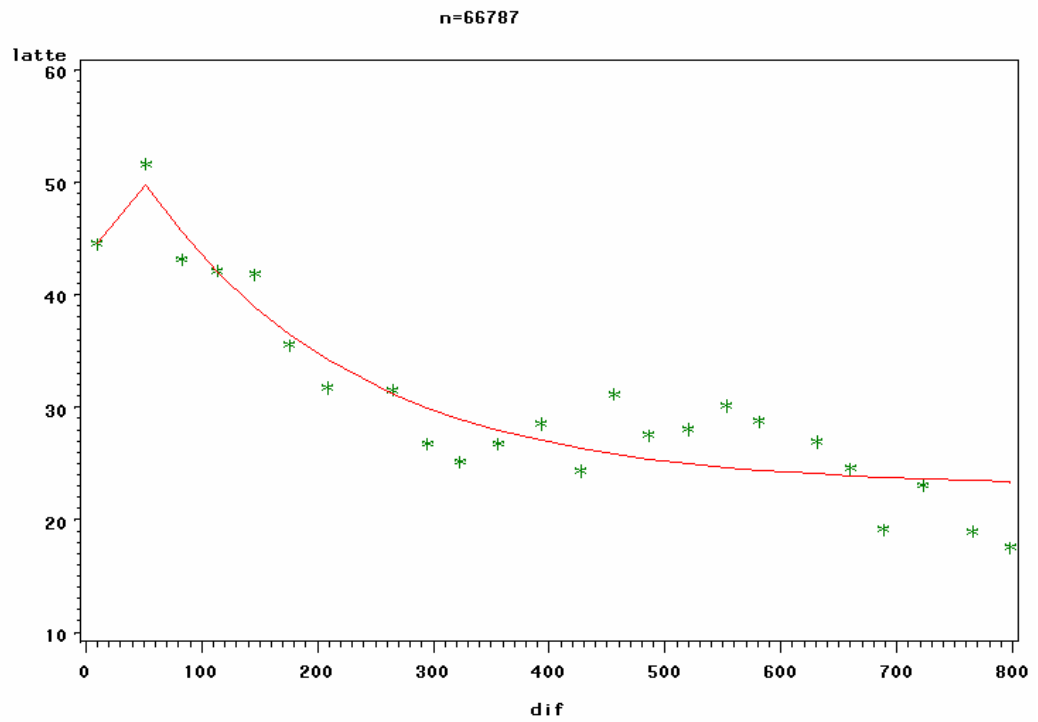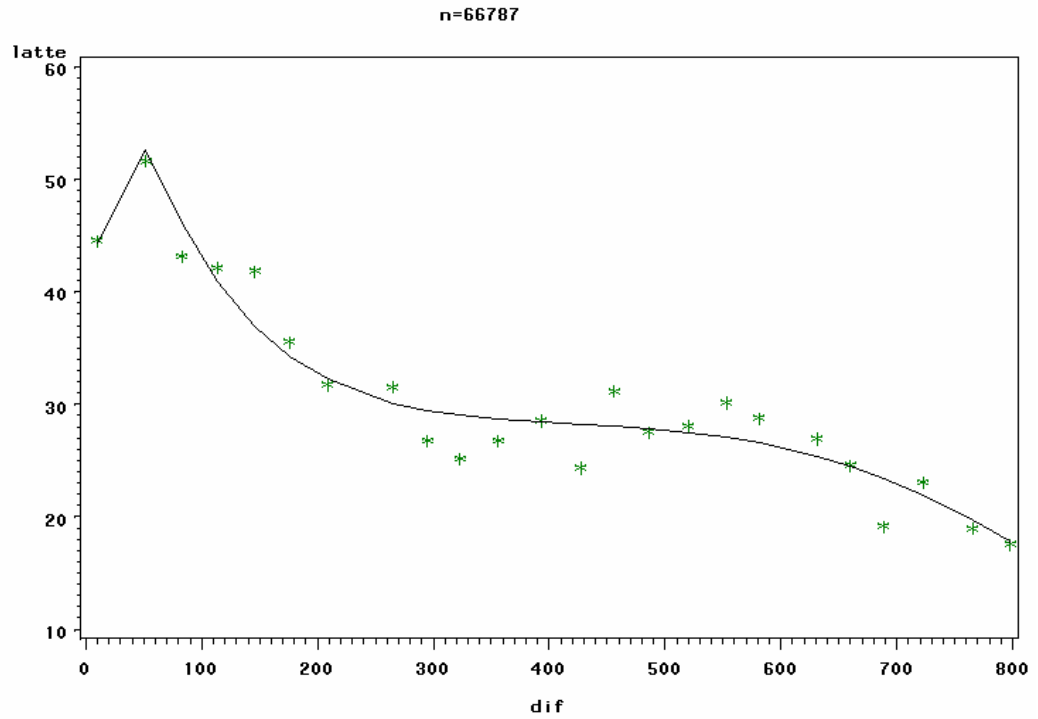
Figure 14. _example of lactation curves with decreasing phases tending to a high asymptotic level._

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 75 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

Finally, considering that a test day milk yield of 15 kg/d that can be considered in Italy as a reasonable threshold of profitability for a dairy cows, table 9 shows the frequencies of individual lactations with Ftd (sum of coefficients a_0, a_1 and a_2 for AS model; b_0 for DF model) greater or smaller of such value.

Table 12. frequency of Ftd in 651-1000d class length for AS and DF.

Model	Ftd	Frequency	Percent
AS	<15 kg	567	71.23
	>15 kg	229	28.77
DJ	<15 kg	582	73.12
	>15 kg	214	26.88

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 76 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

CHAPTER III

LACTATION CURVES OF SARDA DAIRY GOATS

Introduction

Knowledge of the main characteristics of the lactation curves is of great help for farmers and technicians of the dairy goat industry for management and breeding decisions (Gipson and Grossman, 1989). Lactation curve models are largely used in highly selected goat breeds for predicting total milk yield by using few available tests in early lactation (Gipson and Grossmann, 1990) and are becoming of interest for genetic evaluations based on Test Day models (Andonov et al., 2007; Breda *et al.*, 2006; Schaeffer and Sullivan, 1994).

Some of the mathematical functions proposed to model the lactation curve of dairy cattle have been used to study goat lactation patterns. Although the lactation pattern in goats, as in other ruminant species, is similar to the one described for cattle, mathematical modelling of lactation curves in this species is characterised by some specific problems.

First of all, a limited average number of records per lactation is available: not more than 6 for an average lactation length of 221 days for Italian goat breeds in 2005 (Italian Association of Animal breeders, 2005). For this reason, most of models proposed to fit the lactation curve of goats are characterized by a small number of parameters, usually three or four (Gipson and Grossman, 1990; Macciotta et al., 2008). An exception can be found in genetic evaluation using test day models, where the five parameter Ali and Schaeffer function was used to fit average (Schaeffer and Sullivan, 1994) or individual curves (Breda *et al.*, 2006). More sophisticated and flexible

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 77 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

functions as, for example, the diphasic that has been specifically suggested for dairy goats (Gipson and Grossman, 1989), require a large number of records and therefore it is suitable mainly for average curves.

In the case of goats farmed in extensive or semi extensive systems a further issue is represented by the absence of records for the first 30-40 days of lactation being the milk of this period suckled by the lamb. Such a peculiarity, common also for dairy sheep (Barillet, 1997), usually results in an inaccurate modeling of this stage of the lactation pattern and may lead to unexpected results such as the estimation of curves without the lactation peak or a great variability in the time at which the lactation peak occurs (Macciotta et al., 2008).

A third issue that is of great importance in autochthonous breeds is represented by the large variability of test day records, due to both the strong incidence of environmental factors and to the heterogeneity of the genetic background.

On the other hand, the study of the lactation curve could be useful also for goats that, despite the low level of production, have a considerable economic relevance representing an important source of food for rural population (Boyazoglu, 2005).

An example is represented by the Sarda goat, an autochthonous breed of the Island of Sardegna (Italy) that represents about 20% of the Italian goat stock (200.000 heads) (Macciotta et al., 2005). Sarda goat is farmed for milk, mainly destined to cheese making, with an average production of about 220 l per lactation (AIA, 2008) and a composition of 5.4 % and 4.4% of fat and protein content, respectively. Moreover, meat production, represented by the suckling kid slaughtered at about 40 days of age, is a remarkable income for farmers.

The main feature of the Sarda goat is a great fitting to adverse environmental conditions, due to a strong resistance, great capability to utilise rough forages, good

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 78 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

longevity and fertility (Brandano, 1982). For these reasons, goat farming in Sardegna has been traditionally located in mountain areas where Mediterranean scrubs is the main feeding source and only extensive farming systems may be implemented to economically exploit the natural resources (Macciotta et al., 2002). However, some flocks exist also on hill and plain, where goats are usually the result of crosses with other Mediterranean breeds (as the Maltese) and management conditions are generally better. Thus Sarda goat farming is characterised by a great variability in feeding and management techniques and by a strong genetic heterogeneity (Usai et al., 2006) Actually, the Sarda goat can be divided into three sub-populations on the basis of the altitude (plain, hill and mountain) of flocks location (Brandano and Piras, 1978a; Macciotta et al., 2002) that corresponds to morphological (Brandano and Piras, 1978a; Branca and Casu, 1988; Macciotta et al., 2002), genetic (Sechi et al., 2005; Sechi et al., 2007) productive and reproductive diversity (Brandano and Piras, 1978b). This variability affects lactation curve shape with remarkable differences in the average curves of flocks located at different geographical altitude (Macciotta et al., 2005).

Main features of the lactation pattern and their relationships with differences in genetic background, farming system, and environmental conditions should be further investigated for the Sarda goat. The method of fitting to actual data with continuous functions of time y=f(t) is particularly suitable for this purpose, being able to reconstruct specific traits of the lactation pattern such as curvature in different stages, peak production and its occurrence, and lactation persistency. However, in Sarda goat the great heterogeneity of both farming conditions and genetic background may represent a source of variation that is difficult to remove from the regular and continuous component over time evolution of milk production. Thus, in this work, the functional approach is tested also with a smoothing procedure, using the locally

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 79 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

weighted Scatterplot Smoothing (LOWESS) method. The LOWESS method was used by Gipson and Grossman (1989) for smoothing average lactation curve of five gat breeds farmed in the United states.

Materials and methods

Data

Data were 8,870 test day records for milk yield belonging to 1,610 lactations of 1,369 Sarda dairy goats from 74 flocks. Yields were recorded in the period from 1982 to 2004 by the Italian Breeder Association according to the AT method, that consists of one daily milking record (alternately at the morning or evening milking) taken every four weeks. The total daily yield is then calculated by doubling the yield recorded each day. Edits were on the number of records per lactation (>4), days in milk at the first test (<30), lactation length (≤240 d), milk yield (between 0.40 and 3 kg/d). Edit on the days in milk at first test was performed in order to have data also in the first part of the curve for a reliable estimation of peak yield and occurrence. Data were classified according to the following factors: parity (from first to sixth), kidding season (autumn = November and December; winter = January and February), kidding type (one kid or two kids) and altitude of location of flocks (mountain: 500 mt above the sea level; hill: from 200 to 500 mt a.s.l.; plain: <200 mt a.s.l.).

Basic statistics (mean and standard deviations) for milk yield, day at first test and age at first kidding, according to parity, kidding type, kidding season and altitude of flocks are reported in table 1.

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 80 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

Table 1. *Raw statistics for milk yield (kg/d), day of the first test date (d) and age at kiddng (month) according to parity, type of kidding, kidding season and altitude of flocks.*

Factor	levels	n. of tests	Milk yield (kg/d) Mean	St.dev.	Days at first test Mean	St.dev.	Age at kidding Mean	St.dev.
Parity	1	1350	1.15	0.56	22	6	18	9
	2	2068	1.25	0.59	22	6	28	8
	3	1782	1.17	0.54	22	6	40	9
	4	1533	1.22	0.54	22	6	53	8
	5	1178	1.27	0.57	22	6	64	6
	6	959	1.18	0.52	21	7	76	9
Kidding type	One kid	5574	1.16	0.55	21	6	43	29
	Two kids	3296	1.28	0.55	22	6	55	24
Kidding season	Autumn	6711	1.19	0.54	22	6	51	23
	Winter	2159	1.26	0.59	21	6	35	21
Altitude	Plain	4256	1.26	0.63	23	5	45	23
	Hill	3991	1.18	0.47	21	6	51	24
	Mountain	623	0.98	0.39	23	7	43	22

The trend of milk yield across the levels of classification factors confirms what already observed in literature: production tends to increase with parity, till about the fifth; goats with two kids at parturition have an higher yield than goats with a single kid; spring kiddings are more productive than winter kiddings; finally average yield tends to decrease with the altitude of location of flocks. However, all average values are characterised by a high standard deviation (coefficient of variation about 0,5) thus confirming the extreme variability of milk production records for extensively farmed goats. Such a variability justifies the use of a smoothing procedure able to remove local random variation from the underlying curve (Gipson and Grossman, 1989).

Lactation curve models

The choice of models used in this work was conceived by taking into consideration both the relevant in literature and also the known drawbacks in goat lactation curve modelling. Thus the first two selected functions were among those that have been most frequently used to fit lactation curves of small ruminants.

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 81 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

The first is the incomplete gamma function (WD), proposed by Wood (1967), that is the most popular model used in describing lactation curves in different ruminant species and also the most commonly used to fit lactation patterns of goats (Macciotta et al., 2008):

$$Y_t = at^b e^{-ct}$$ [1]

The second (CB) is a bi-exponential modification of the Wood model, proposed by Cappio-Borlino et al. (1995) to solve specific problems that occur in estimating the first part of lactation when few data are available:

$$Y_t = at^{b\exp(ct)}$$ [2]

The other two are more general mathematical functions that have not been specifically conceived to fit lactation curves and that are characterised by high flexibility.

In particular, one is a third-order Legendre orthogonal polynomials (LEG), often used in random regression models to fit individual patterns lactation curves:

$$Y_t = \sum_{i=1}^{n} \alpha_i P_j$$

[3]

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 82 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

where α_i are regression coefficients and P_j is a function of time calculated using values published by Schaeffer (2004).

Finally, a regression spline in linear (LS), quadratic (QS) end cubic (CS) form, with one (LS1, LS2, QS1) or two (QS2, CS1, CS2) knots are used. The general formulation of a regression spline is the following:

$$Y_t = \sum_{i=0}^{n} \beta_{0i} \cdot t^{i-1} + \sum_{j=1}^{m} \beta_j \cdot (t - t_j)^n \qquad [4]$$

where n is the degree of the spline, m is the number of knots and t_j is the knot point. In all models Y_t represents test day milk yield (kg) recorded at time t (days) whereas a, b, c, α and β are parameters to be estimated.

Parameters of WD and CB functions can be interpreted in terms of lactation curve shape (Macciotta et al., 2005; Muir et al., 2004). In WD model, *a* is a scaling factor, representing the production at the moment of kidding; *b* is linked to the rising phase of curve (before lactation peak); *c* regulates the decline of milk production after the peak yield. In the CB function, *a* represents the value of the horizontal asymptote and therefore it can be considered as the milk yield in the period immediately before drying off, *b* is related to production decrease after the peak yield and *c* controls the rate of variation of milk yield in the first part of the curve (Cappio Borlino et al., 1995; Todaro et al., 2000). Moreover, from the combination of these parameters, important features of the lactation curve can be calculated: the time at peak production, the milk production at peak and the persistency. Models with highest number of parameters (Legendre and

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives"   - 83 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

splines) are characterised by greater flexibility, but is often difficult assign to the parameters a clear meaning in terms of shape of the lactation curve.

Following the suggestions of Gipson and Grossman (1989), data were also analyzed after a procedure of smoothing obtained from the LOWESS (Locally Weighted Scatterplot Smoothing) regression. This technique is a useful method proposed by Cleveland (1979) which has the advantage of not being sensitive to outliers (it is robust) and allows the user to easily adjust the degree of smoothing without the curve having an excessively wiggly shape. It fits a simple straight line (or lower order polynomial function) in successive regions of the data, then iteratively reforms the results to create a smooth, continuous curve. The result of a LOWESS regression is a line which best fits the data locally, but is not constrained to be of a particular mathematical form. The crucial point in LOWESS is in fixing the windows regions of data, expressed as percentage of data. In other words, if q is the number of adjacent points to be used in estimation procedure of a set of n data, each region has a fraction of points given by q/n=f with f called the smoothing parameter. As the smoothing parameter increases the fitted line will be smoother until f =1 that corresponds to a single line (is the standard linear regression). Consequently, the lowess fit depends strongly on the smoothing parameter used (Cohen, 1999). In this work the best smoothing parameter was calculated for each level of each factor by minimising the bias corrected Akaike information criteria (Hurvich et al., 1998) using the SAS macro SMOOTH-SELECT (Cohen, 1999).

A nonlinear regression technique, based on the Marquardt compromise, was used for fitting WD and CB models, and also for Spline functions by introducing knot position as additional parameters to be estimated in the function. A linear least squares regression was used for estimating parameters of the LEG function. Each model was

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 84 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

fitted to both average lactation curves, calculated averaging for each day of lactation all test day recorded on the same date, and LOWESS-smoothed data (indicated as Av and Sm, respectively), for different parities, kidding season, kidding type and altitude of location of flocks.

Time of peak yield occurrence (Tm), peak yield (Ym), lactation persistency (S) and total milk yield (TMY$_{210}$) for a lactation length of 210 d (from 30 to 240 days in milking) were also calculated.

For WD model:

$$Tm = a(b/c)^b e^{-b}$$

$$Ym = b/c$$

$$S = - (b+1) \ln c$$

For CB model

$$S = 1/b^c$$

whereas Tm and Ym were predicted by model [3].

Total milk yield (TMY$_{210}$) was calculated for all models as:

$$TMY_{210} = \sum_{30}^{240} f(x)$$

Goodness of fit was assessed considering the adjusted coefficient of determination (R$^2_{adj}$), which adjust the R^2 for the number of parameters to be estimated and for the sample size. In this form, the coefficient of determination allows the comparison between the three-parameter models, Legendre polynomials and the spline functions. The Durbin-Watson statistic (DW) was also used to test for the presence of first order autocorrelation in the regression residuals. DW value ranges from 0 to 4: when the

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 85 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

residuals are randomly distributed the WD statistic is approximately 2.0, when residuals are positively or negatively autocorrelated, WD value is <1.5 or >2.5. (Macciotta et al., 2004). Moreover, the residual standard deviation (RSD) was also calculated.

RESULTS AND DISCUSSION

Model comparison

Table 2 shows the statistics of goodness of fit (R^2_{adj}, RSD and DW) for the nine models that were used to fit both Av and Sm milk production data. For each factor of variation (parity, kidding type, kidding season and altitude) the mean value, evaluated on all the levels of each factor, and the respective standard deviations were reported. As expected, values for the adjusted coefficient of determination for all models were higher in smoothed than in averaged raw data, with R^2_{adj} ranging from 0.97 to 0.74 in Sm and from 0.79 to 0.53 in Av, respectively. Moreover, the RSD for Sm data was around ten times lower than Av. On the contrary, the DW statistics showed values generally near to 2 for Av, indicating that residuals are randomly distributed, whereas in smoothed data, values of DW statistic were near to zero for all models, indicating high autocorrelation among residuals. A possible explanation for these results may be found in the fact that Sm values are the result of a previous regression (the LOWESS) and therefore a correlation among them exists. For example, figures 1 and 2 show the fitting of Wood model to the overall lactation curve, both for Av (figure 1) and Sm (figure 2) data. Residuals of Av tend to be more randomly distributed than those of Sm data.
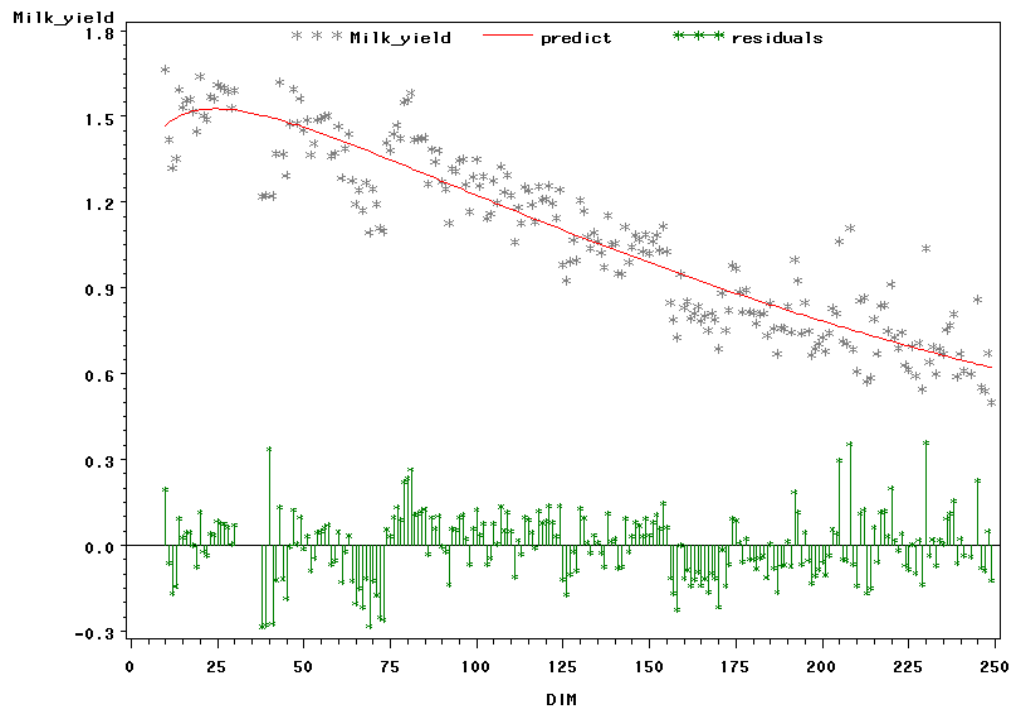
Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives"
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

- 86 -

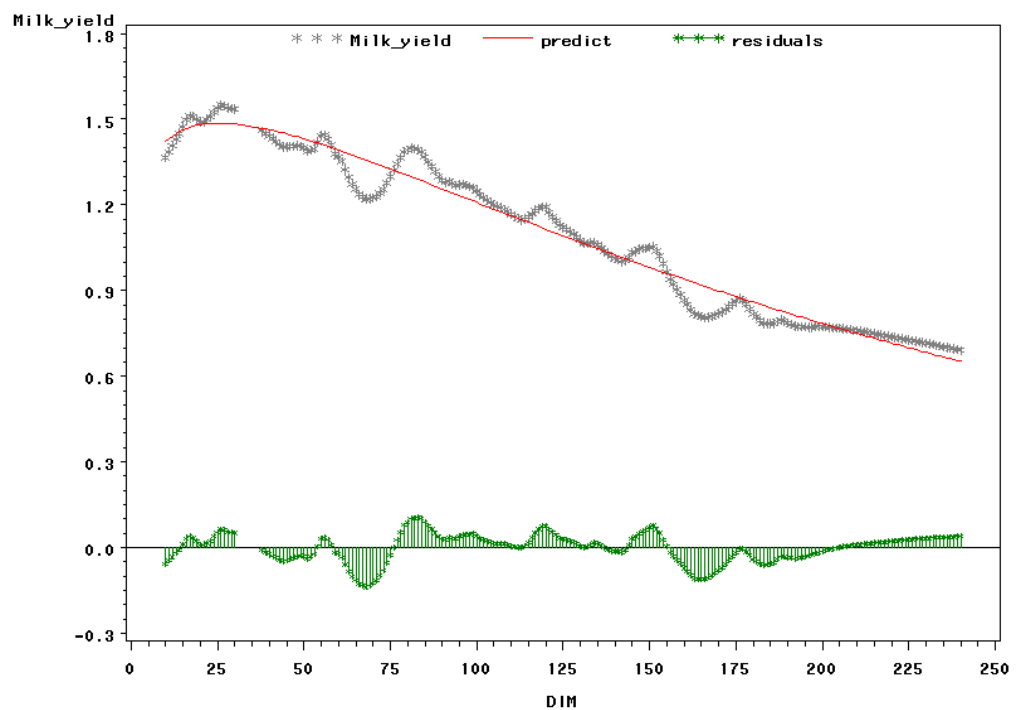***Figure 1**. Average data fitted by Wood's model*

***Figure 2**. Smoothed data fitted by Wood's model*

Table 2. *Mean and standard deviation (SD) for adjusted coefficient of determination (R^2_{adj}), residual standard deviation (RSd) and Durbin-Watson test (DW) according to parity, type of*

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 87 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

Data		Av								Sm							
		Parity		Kidding type		Kidding season		Altitude		Parity		Kidding type		Kidding season		Altitude	
Model		Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
WD	R^2_{adj}	0.59	0.11	0.78	0.04	0.69	0.16	0.55	0.30	0.95	0.03	0.96	0.02	0.90	0.08	0.78	0.25
	RSD	0.22	0.03	0.14	0.03	0.17	0.02	0.19	0.04	0.06	0.02	0.05	0.02	0.08	0.02	0.09	0.02
	DW	1.80	0.25	1.54	0.03	1.38	0.22	1.47	0.28	0.08	0.06	0.07	0.05	0.06	0.04	0.10	0.01
CB	R^2_{adj}	0.57	0.09	0.76	0.05	0.67	0.15	0.53	0.31	0.93	0.04	0.94	0.02	0.87	0.08	0.74	0.26
	RSD	0.22	0.03	0.15	0.03	0.18	0.02	0.19	0.04	0.07	0.03	0.07	0.02	0.09	0.01	0.10	0.01
	DW	1.73	0.25	1.41	0.03	1.29	0.26	1.41	0.27	0.10	0.05	0.07	0.02	0.07	0.01	0.10	0.01
LEG	R^2_{adj}	0.60	0.09	0.79	0.04	0.70	0.18	0.57	0.29	0.96	0.03	0.97	0.01	0.91	0.09	0.80	0.22
	RSD	0.22	0.03	0.14	0.03	0.17	0.03	0.19	0.04	0.05	0.03	0.05	0.02	0.07	0.03	0.08	0.02
	DW	1.84	0.28	1.56	0.04	1.45	0.13	1.52	0.30	0.09	0.06	0.09	0.05	0.09	0.03	0.12	0.03
LS1	R^2_{adj}	0.59	0.10	0.77	0.05	0.69	0.16	0.55	0.30	0.95	0.03	0.96	0.02	0.90	0.08	0.77	0.25
	RSD	0.22	0.03	0.15	0.03	0.17	0.02	0.19	0.04	0.06	0.02	0.06	0.02	0.08	0.02	0.09	0.02
	DW	1.79	0.27	1.51	0.03	1.37	0.26	1.44	0.24	0.08	0.06	0.07	0.06	0.07	0.03	0.09	0.01
LS2	R^2_{adj}	0.61	0.09	0.78	0.04	0.70	0.17	0.56	0.31	0.96	0.03	0.97	0.02	0.91	0.08	0.81	0.20
	RSD	0.21	0.03	0.14	0.03	0.17	0.03	0.18	0.04	0.05	0.03	0.05	0.02	0.08	0.02	0.08	0.02
	DW	1.83	0.27	1.55	0.03	1.43	0.19	1.50	0.29	0.07	0.05	0.07	0.04	0.05	0.03	0.11	0.02
QS1	R^2_{adj}	0.56	0.13	0.78	0.04	0.62	0.25	0.56	0.29	0.96	0.03	0.96	0.02	0.90	0.07	0.80	0.23
	RSD	0.23	0.04	0.14	0.03	0.19	0.04	0.18	0.04	0.05	0.02	0.05	0.02	0.08	0.01	0.08	0.02
	DW	1.71	0.41	1.53	0.01	1.17	0.01	1.50	0.28	0.08	0.04	0.06	0.04	0.05	0.04	0.13	0.04
QS2	R^2_{adj}	0.59	0.10	0.77	0.03	0.52	0.14	0.49	0.37	0.94	0.05	0.96	0.02	0.90	0.07	0.79	0.22
	RSD	0.22	0.03	0.15	0.02	0.23	0.06	0.20	0.04	0.06	0.03	0.05	0.02	0.08	0.01	0.08	0.02
	DW	1.79	0.30	1.45	0.11	1.05	0.92	1.31	0.28	0.06	0.03	0.06	0.04	0.05	0.04	0.13	0.06
CS1	R^2_{adj}	0.61	0.09	0.79	0.04	0.70	0.18	0.57	0.29	0.97	0.03	0.97	0.01	0.92	0.08	0.81	0.21
	RSD	0.21	0.03	0.14	0.03	0.17	0.03	0.18	0.04	0.05	0.03	0.05	0.02	0.07	0.03	0.08	0.02
	DW	1.86	0.27	1.59	0.05	1.45	0.13	1.53	0.31	0.07	0.05	0.08	0.05	0.07	0.02	0.12	0.03
CS2	R^2_{adj}	0.61	0.09	0.79	0.03	0.71	0.19	0.57	0.29	0.97	0.03	0.97	0.01	0.91	0.10	0.81	0.22
	RSD	0.21	0.03	0.14	0.02	0.17	0.03	0.18	0.04	0.04	0.02	0.04	0.01	0.07	0.03	0.08	0.02
	DW	1.86	0.27	1.63	0.11	1.49	0.07	1.54	0.30	0.09	0.05	0.09	0.05	0.10	0.02	0.13	0.02

In general, the different models used to fit the averaged or smoothed data, gave similar results in term of fitting performances. Among the different classification factors, goodness of fit was greater in kidding type and kidding season than parity and altitude of flocks. Moreover the high RSD for the altitude of location of flocks points out that one or some levels of this factor have a poor fit. This results can be explained with the limited availability of records of mountain goats (table 1). The same patterns was found for Av and Sm data.

Convergence problems occurred when the SPL models were fitted using a non linear regression. Actually spline functions had many convergence problems in both Av and Sm data. The curve fitting procedure failed to converge in most cases (44 times

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 88 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

out of 78), sometimes the parameter estimated were unrealistic or unreliable, with more problems for quadratic and cubic functions in the fit with two knots. Similar results were reported by Macciotta et al., (2008) who used the non linear regression to fit linear, quadratic and cubic splines for average curves of dairy cattle. They reported problems of convergence related to the increased number of knots from one to three.

The main technical features of lactation curves, for each factor of classification, are reported in tables 3 and 4. The estimated time at which the lactation peak occurs is about 4 weeks for CB and WD, in agreement with previous reports for autochthonous goats (Akpa et al., 2001; Ruvuna et al., 1995). The exception is represented by Tm for the goats farmed in mountain flocks (40 dim). LEG polynomials are able to predict the increasing phase at peak yield in four groups only (first and second parity, goats with two kids and goats kidding in spring). For the remaining cases the model has produced monotonically decreasing curves that lack of a peak. Thus Tm is equal or next to the first test day, and Ym is equal to yield at first test day. Later peak occurrence has been estimated for first and second parity goats, conforming previous reports for goats (Gipson and Grossman, 1990; Macciotta et al., 2008). This trend is evident also for the spline functions (table 4) although some of them gave a prediction of time at peak of 10 dim.

Both the production at peak and the total yield for 210 d show an expected behaviour across the different levels of the factors of variation considered. They tend to increase with parity till the fifth lactation. Goats with twins have higher yields than single kiddings. Lactation starting in spring have higher peak and total yield than those starting in winter. Finally the yield tends to decrease passing from plain to hill and mountain.

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 89 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

Table 3. *Time to the peak (Tm), production to the peak (Ym) and cumulative production until 240 day (TMY$_{210}$) according to parity, type of kidding, kidding season and altitude of location of flocks, for the parametric models, fitted with average (Av) and smoothed (Sm) data.*

Model	Factor	Level	Tm Av	Tm Sm	Ym Av	Ym Sm	TMY$_{210}$ Av	TMY$_{210}$ Sm
WD	Parity	1	27.6	26.3	1.33	1.36	172.19	174.62
		2	29.7	29.4	1.54	1.54	220.47	221.07
		3	25.5	25.3	1.43	1.44	216.96	218.46
		4	23.2	27.0	1.54	1.54	227.02	226.56
		5	25.9	31.6	1.56	1.56	225.53	226.80
		6	20.9	19.2	1.62	1.59	214.39	214.49
	Type of kidding	1	21.3	23.7	1.46	1.44	221.48	220.72
		2	29.5	28.1	1.55	1.58	236.24	240.16
	Kidding season	1	19.7	21.7	1.44	1.41	218.91	218.62
		2	32.1	32.7	1.55	1.55	216.61	219.39
	Altitude	1	20.1	23.4	1.64	1.62	228.35	229.45
		2	22.3	23.6	1.42	1.43	225.71	227.45
		3	42.9	39.4	1.08	1.09	138.71	139.85
CB	Parity	1	30	30	1.37	1.40	172.75	175.34
		2	39	30	1.58	1.60	221.68	222.26
		3	38	30	1.46	1.48	218.07	219.57
		4	30	30	1.56	1.56	228.32	227.83
		5	30	30	1.60	1.60	226.61	227.76
		6	30	29	1.66	1.61	215.95	215.76
	Type of kidding	1	29	30	1.49	1.48	222.60	221.83
		2	38	30	1.59	1.63	237.54	241.43
	Kidding season	1	30	28	1.47	1.44	219.65	219.38
		2	38	29	1.60	1.59	218.11	220.78
	Altitude	1	30	30	1.69	1.66	229.92	230.96
		2	30	30	1.44	1.48	226.76	228.48
		3	45	30	1.09	1.11	138.99	140.12
LEG	Parity	1	39	29	1.32	1.35	171.93	173.71
		2	30	30	1.51	1.51	219.42	219.98
		3	10	10	1.42	1.44	215.62	217.14
		4	10	10	1.52	1.52	225.81	224.96
		5	10	21	1.55	1.53	224.19	225.18
		6	13	10	1.60	1.60	214.49	214.51
	Type of kidding	1	10	12	1.46	1.43	220.46	219.58
		2	30	24	1.52	1.55	235.07	238.83
	Kidding season	1	10	10	1.49	1.46	218.46	218.21
		2	38	38	1.51	1.51	215.54	218.04
	Altitude	1	11	13	1.63	1.59	227.62	228.37
		2	10	10	1.43	1.43	224.52	226.12
		3	10	10	1.06	1.09	138.29	139.48

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 90 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

Table 4. *Time to the peak (Tm), production to the peak (Ym) and cumulative production until 240 day (TMY₂₁₀) according to parity, type of kidding, kidding season and altitude of location of flocks, for the splines models with one knot, fitted with average (Av) and smoothed (Sm) data.*

Model	Factor	Level	Tm Av	Tm Sm	Ym Av	Ym Sm	TMY_{210} Av	TMY_{210} Sm
LS1	Parity	1	20	28	1.38	1.39	172.68	174.99
		2	25	24	1.59	1.60	220.51	221.37
		3	25	25	1.47	1.47	216.73	218.32
		4	10	10	1.57	1.54	226.44	226.02
		5	10	29	1.57	1.62	225.00	226.91
		6	10	10	2.34	1.64	213.32	214.14
	Type of kidding	1	25	23	1.47	1.47	221.71	220.88
		2	10	26	1.64	1.62	234.90	240.09
	Kidding season	1	28	26	1.45	1.44	219.19	218.84
		2	10	10	1.53	1.52	215.96	218.75
	Altitude	1	16	15	1.69	1.67	228.05	229.28
		2	26	25	1.44	1.45	225.40	227.27
		3	28	26	1.13	1.13	138.51	139.78
QS1	Parity	1	30	26	1.45	1.34	173.09	174.67
		2	27	26	1.62	1.62	220.75	221.35
		3	16	23	1.48	1.46	216.72	218.30
		4	10	10	1.58	1.65	202.96	225.77
		5	18	24	1.60	1.62	225.30	226.86
		6	10	10	1.71	1.67	214.37	213.92
	Type of kidding	1	29	27	1.48	1.48	221.69	220.85
		2	17	26	1.61	1.62	235.82	240.10
	Kidding season	1	18	16	1.47	1.46	239.49	218.69
		2	29	27	1.59	1.60	216.18	219.07
	Altitude	1	27	10	1.64	1.61	228.56	229.34
		2	10	24	1.44	1.44	225.60	227.39
		3	50	43	1.06	1.06	138.62	139.84
CS1	Parity	1	27	30	1.36	1.38	173.04	174.98
		2	26	23	1.53	1.54	220.79	221.38
		3	19	18	1.44	1.44	216.89	218.31
		4	10	10	1.64	1.52	226.53	226.22
		5	20	23	1.56	1.58	225.44	226.85
		6	41	10	1.50	1.59	213.80	214.51
	Type of kidding	1	24	22	1.46	1.44	221.65	220.85
		2	24	21	1.53	1.57	236.25	240.17
	Kidding season	1	10	28	1.49	1.47	218.46	218.88
		2	38	30	1.51	1.51	216.52	219.21
	Altitude	1	16	19	1.63	1.60	228.52	229.57
		2	10	10	1.43	1.43	225.55	227.25
		3	20	22	1.08	1.10	138.47	139.75

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" – 91 –
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

One of the main problems in using regression splines is the optimisation of the number and position of knots. They should be placed in the points of curvature and, some authors, suggest that should be placed in the region of maximum density of data (Meyer, 2005). Actually there is not an assessed criteria and some studies that used spline function to fit lactation curves in dairy cattle fixed a priori the number and the position of knots (Druet et al., 2003; Silvestre et al., 2005). The non-linear procedure presented here attempts to optimise the position of knots treating them as parameters to be estimated (Fadel, 2004). Table 5 reports estimates of knot positions, according to parity, type of kidding, kidding season and altitude of location of flocks, for average (Av) and smoothed (Sm) data. The values are often out of the range of biological significance (i.e. negative values of the time or values that exceed the lactation length). However, it can be noticed that when the estimated values are of a reasonable magnitude, the first knot is positioned between 15 and 46 dim. Such a position corresponds, approximately, to the time of the peak yield. The location of the second knot is much more uncertain.

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives"
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

- 92 -

Table 5. *Estimated position of the knots, for the splines models, according to parity, type of kidding, kidding season and altitude of location of flocks, fitted with average (Av) and smoothed (Sm) data.*

			Model								
			LSPL			QSPL			CSPL		
			one	two		one	two		one	Two	
Data	Factor	Level	x1	x1	x2	x1	x1	x2	x1	x1	X2
Av	Parity	1	20.0	20.9	189.6	36.7	-3.8	36.7	28.0	34.2	23143.2
		2	25.0	25.0	234.4	30.6	30.6	30.6	23.4	-144.9	-45.4
		3	25.0	16.4	274.0	16.6	17.9	45.8	22.3	27.6	78.9
		4	56.0	101.8	228.5	11.7	21.8	22.9	46.8	25.6	124.2
		5	46.0	15.6	239.2	19.3	17.1	17.5	23.6	-5.3	114.8
		6	11.0	11.0	239.2	147.2	-0.3	18.9	34.5	28.6	1542.0
	Type of kidding	1	24.7	25.0	226.0	39.2	24.7	26.1	35.0	19.3	40.6
		2	-39.2	15.9	207.0	16.9	37.7	36.8	21.0	25.6	78.3
	Kidding season	1	28.0	14.0	217.1	18.3	64.0	62.5	-22.6	7.6	307.6
		2	72.2	26.0	222.0	35.3	13.3	27.6	10.6	42.9	60.6
	Altitude	1	16.0	20.4	220.0	52.4	52.0	51.6	20.5	17.2	98.6
		2	26.0	26.0	240.5	61.0	63.9	63.9	10.6	44.2	83.7
		3	28.0	19.0	218.6	15.9	64.9	65.3	23.0	23.4	256.8
Sm	Parity	1	27.5	33.3	169.1	108.0	47.7	47.7	42.6	8.0	3871.6
		2	22.4	21.0	191.6	29.2	27.7	27.8	24.0	43.1	78.1
		3	24.7	25.8	196.8	28.9	23.3	24.6	21.5	-7.1	98.2
		4	47.8	58.3	212.4	14.4	22.5	23.7	10.5	20.2	126.3
		5	25.1	16.7	248.5	25.0	26.5	28.6	26.8	38.7	100.4
		6	-2400.6	-311.4	191.0	2513.0	6.4	6.4	-20.2	18.4	91.4
	Type of kidding	1	22.5	24.7	187.0	31.8	25.2	26.1	24.9	323.8	116.0
		2	25.6	20.6	201.6	30.3	30.0	30.1	22.6	43.1	83.4
	Kidding season	1	25.7	14.5	241.2	16.2	13.6	15.2	45.7	10.6	3257.9
		2	66.0	25.7	196.2	31.2	23.2	24.3	20.2	34.5	59.3
	Altitude	1	15.0	16.3	184.0	140.7	103.6	104.0	21.1	26.2	81.8
		2	26.0	26.0	234.0	30.7	19.9	21.6	12.9	67.2	82.2
		3	26.0	18.7	168.7	18.1	15.2	16.0	27.0	30.7	916.0

Figures from 3 to 7 report lactation curves estimated with different models for the three levels of location of flocks. Only WD, CB and LS are able to clearly reconstruct the phase of increase and the peak yield in the first part of the lactation for all level. LEG, QS and CS produce some anomalous shape in many cases.
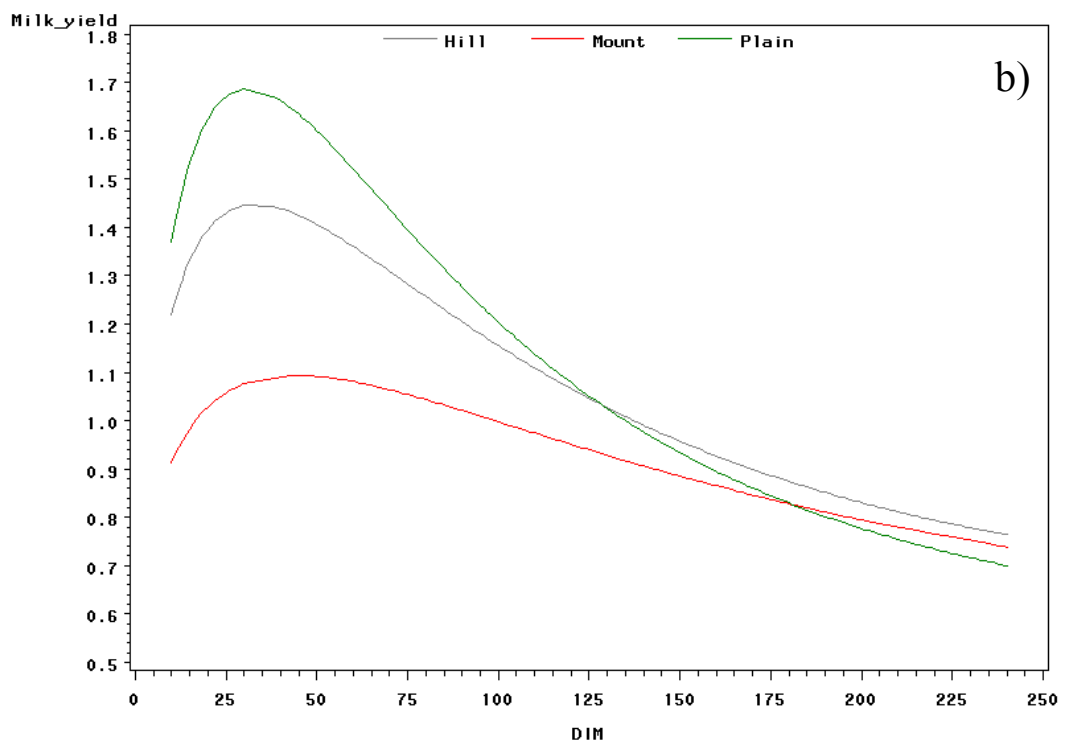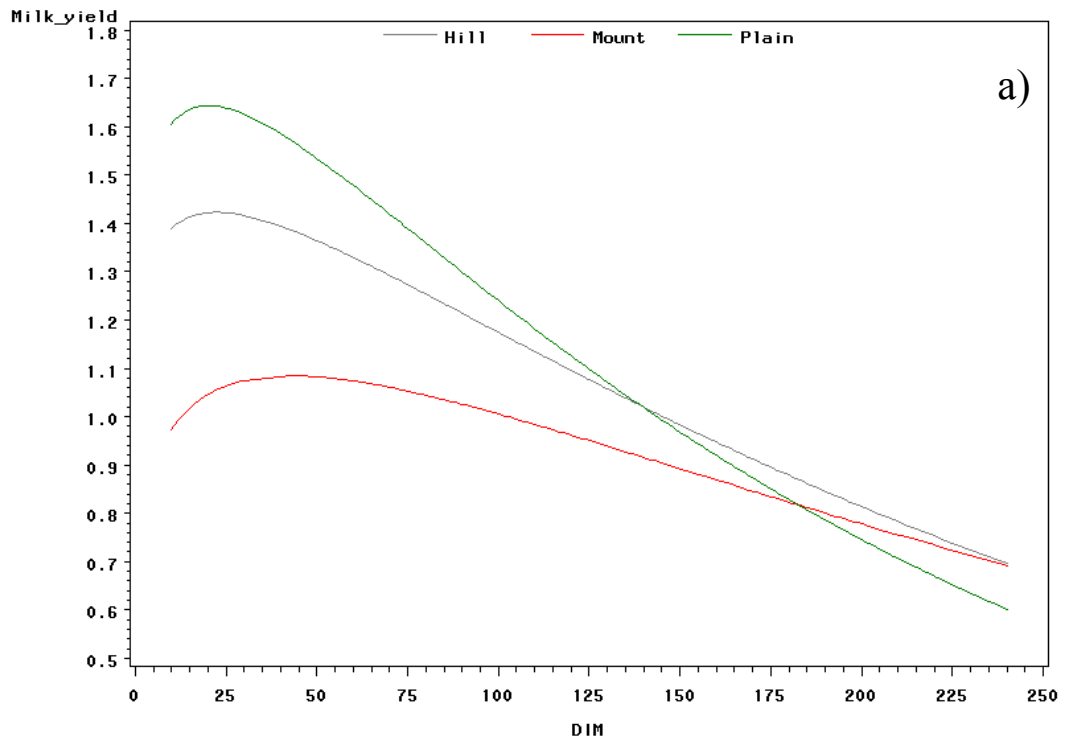
Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 93 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

Figure 3. *Average lactation curves for goats of flocks located at different levels of altitude estimated by different functions: Wood a), and Cappio-Borlino b) models.*
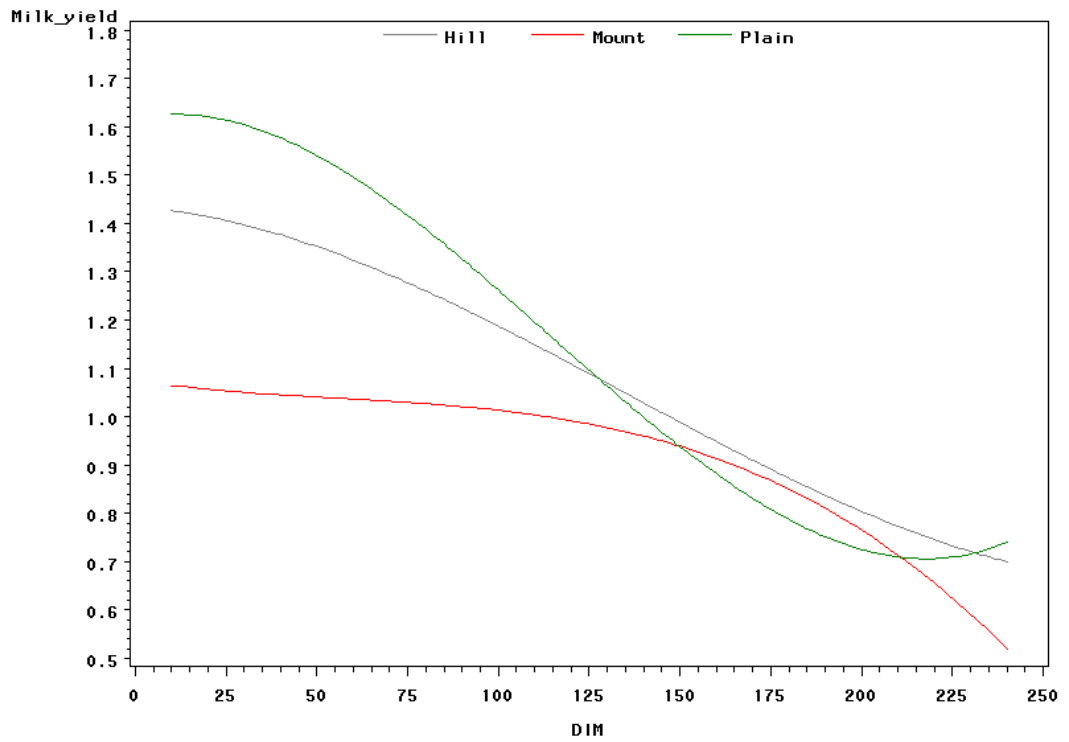
Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 94 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

Figure 4. *Average lactation curves for goats of flocks located at different levels of altitude estimated by Legendre polynomials.*
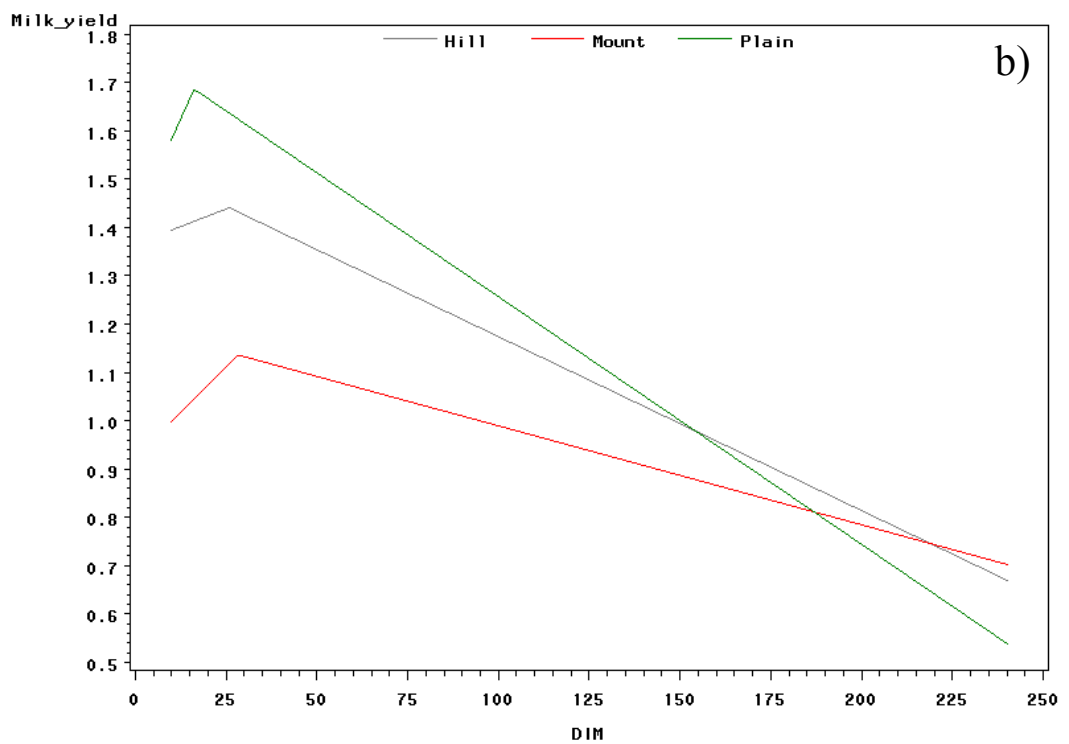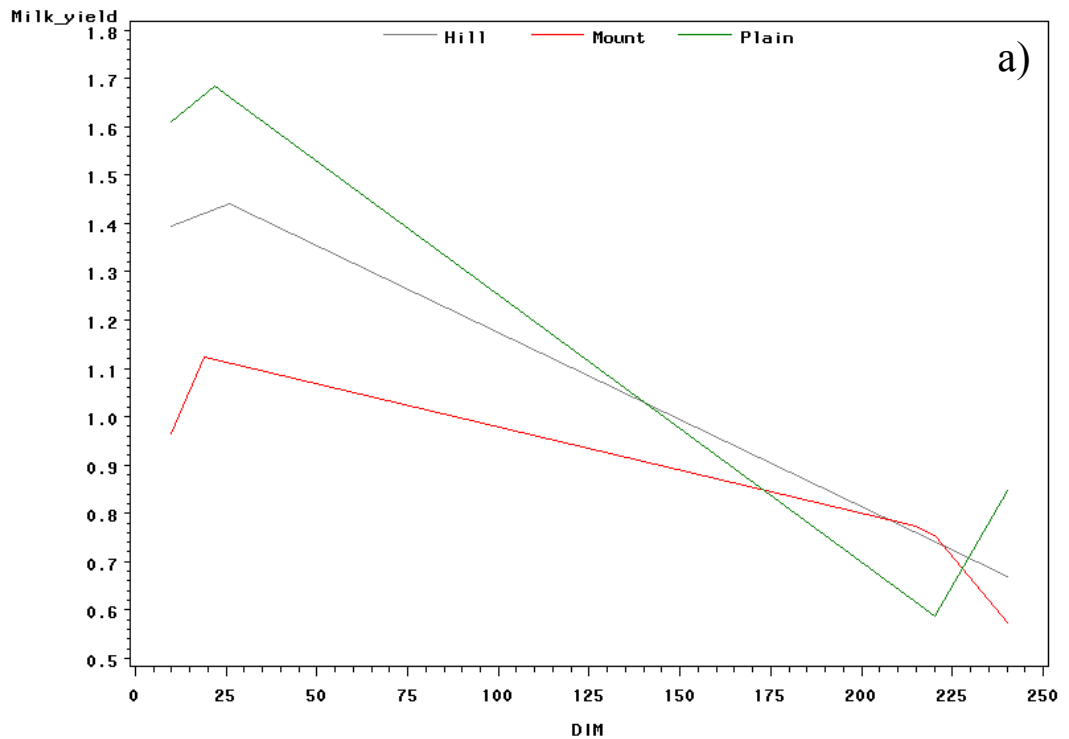
Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 95 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

Figure 5. *Average lactation curves for goats of flocks located at different levels of altitude estimated by linear splines one a) and two b) knots.*

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 96 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche
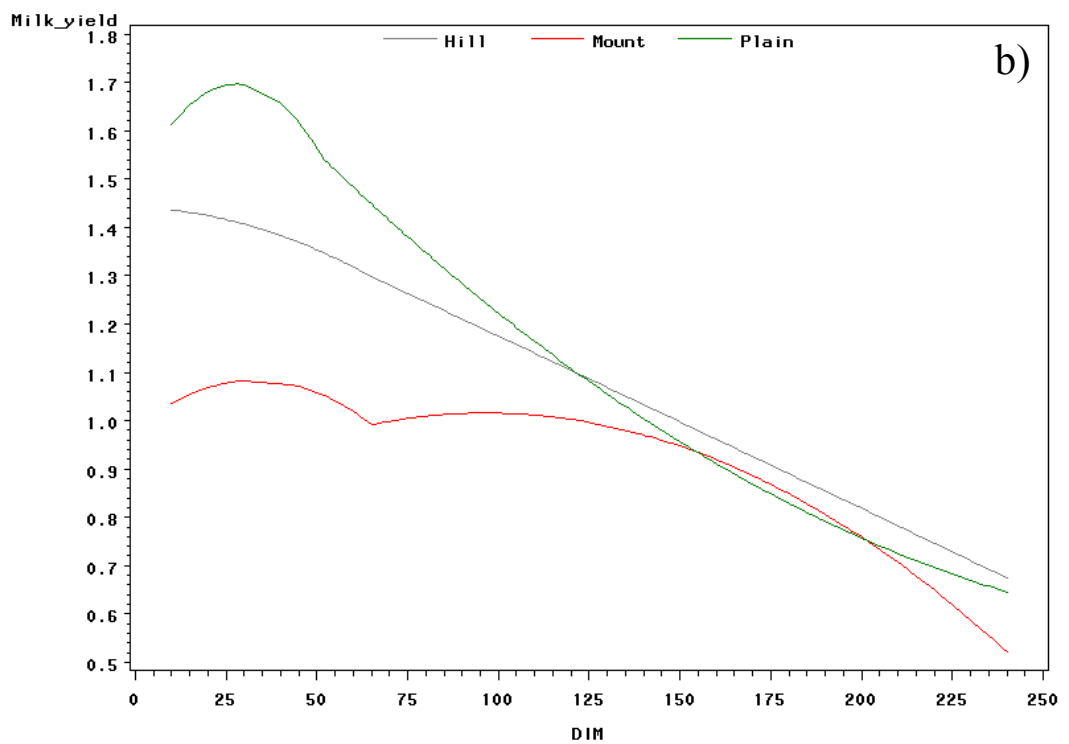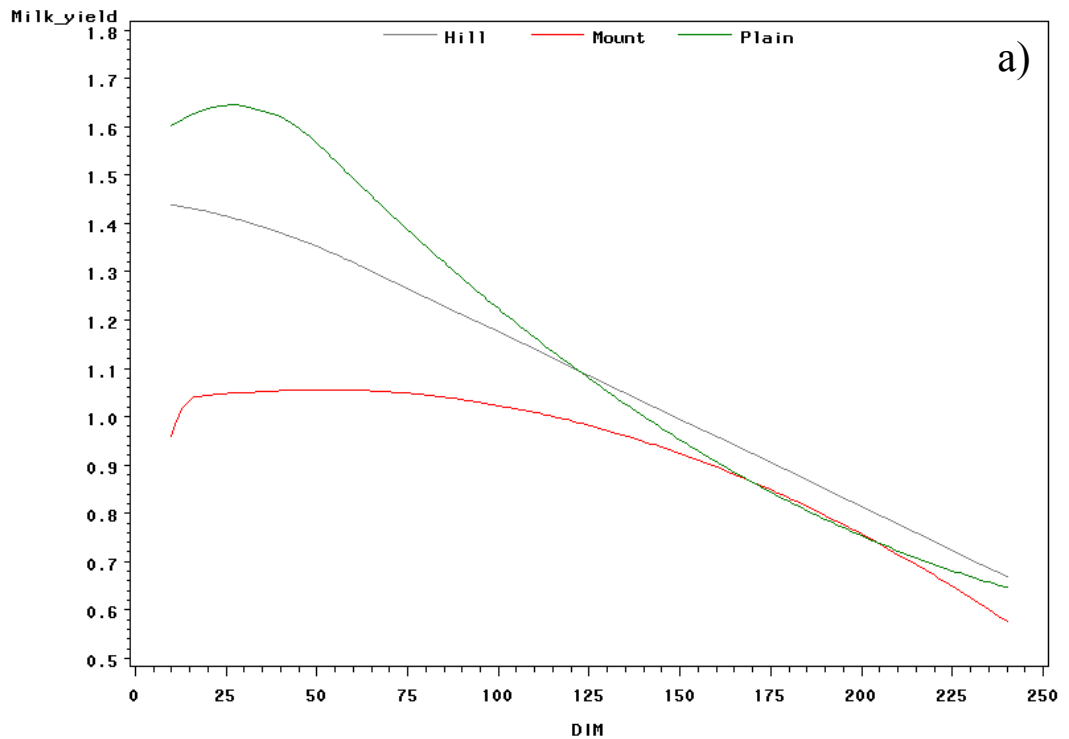
Figure 6. *Average lactation curves for goats of flocks located at different levels of altitude estimated by quadratic splines with one a) and two b) knots.*

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 97 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche
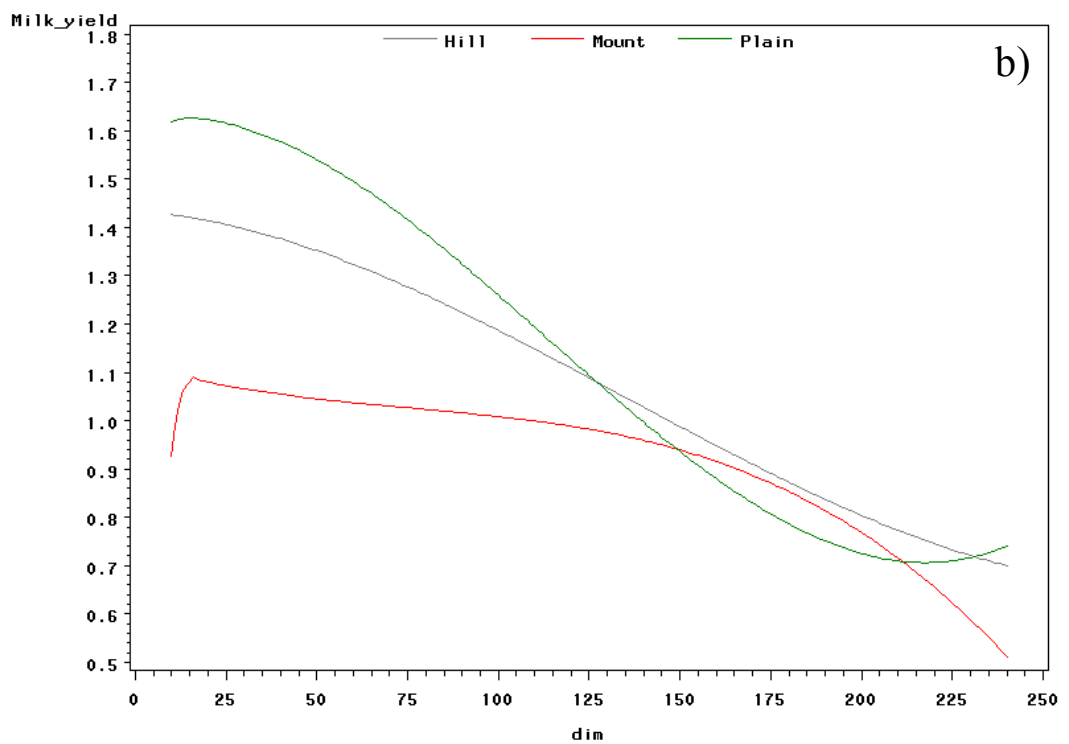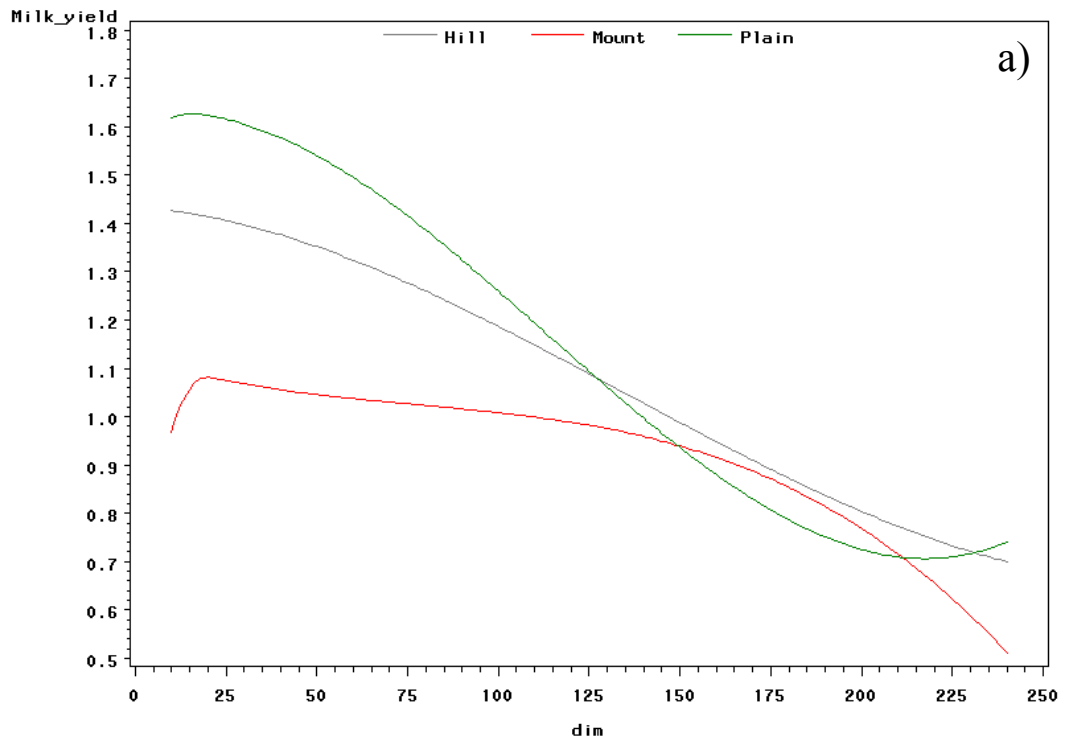
Figure 7. *Average lactation curves for goats of flocks located at different levels of altitude estimated by cubic splines with one a) and two b) knots.*

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 98 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

From the above reported results, it can be concluded that WD and CB functions, although having lower fitting performances than the other two general functions, were able to reconstruct the lactation curve shape of Sarda dairy goat.

Lactation curves of goats of different parities estimated with the WD and CB functions are reported in figures 8a and b, respectively.
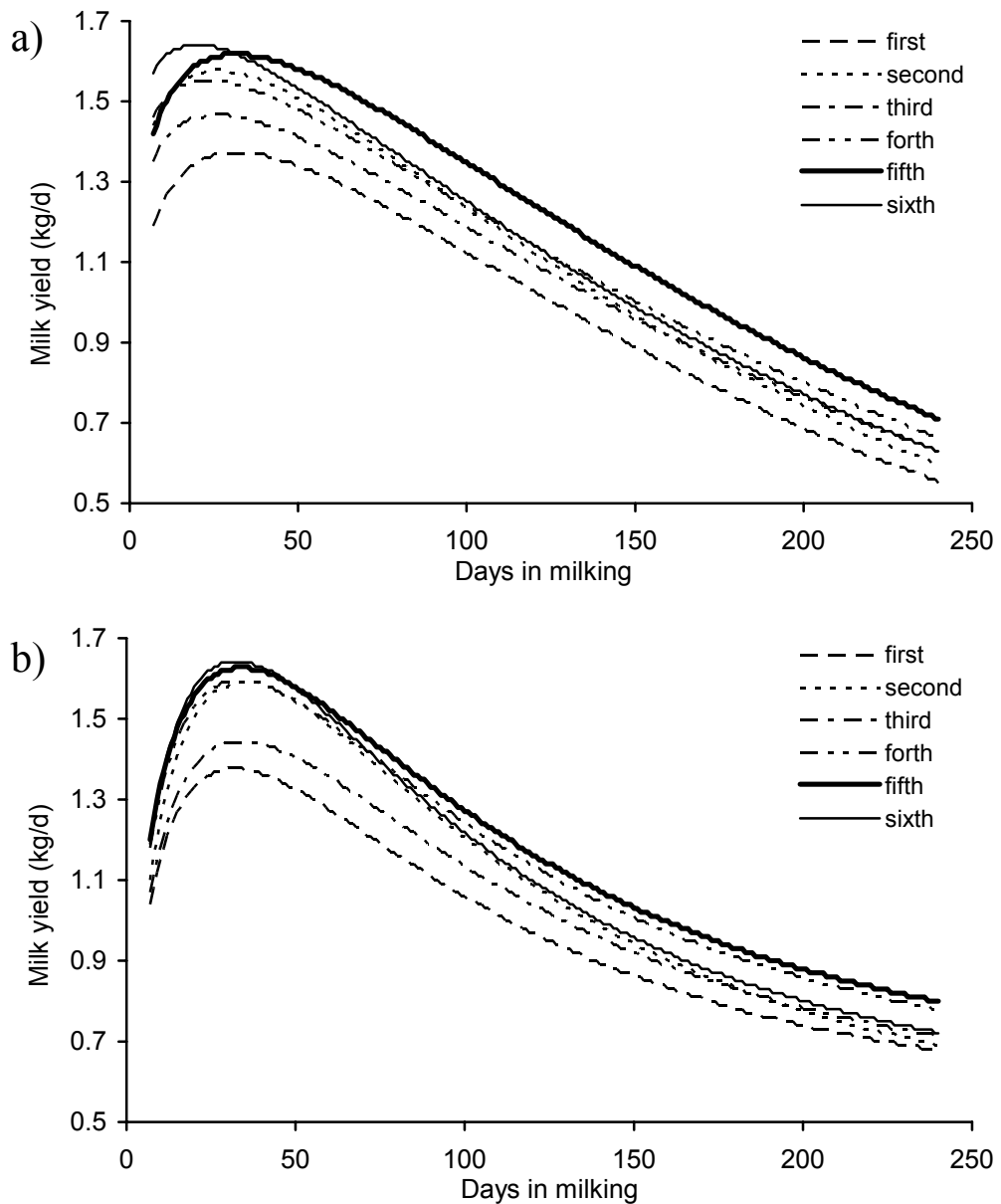
Figure 8. *Average lactation curves for goats of different parties estimated by the Wood a) and Cappio-Borlino b) function.*

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 99 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

The scaling effect of parity can be observed for both models. This behaviour can be observed also in the values of the *a* parameter estimated in the average curves (table 6). Furthermore, four parity goats show have the highest total lactation yield whereas six parity goats the highest peak production (table 3).

As far as lactation persistency is concerned, the S measure does not show the expected decreasing trend from first to older parities, observed in previous researches (Gipson and Grossman, 1989; Pena Blanco et al., 1999). This results is also confirmed by the pattern of lactation curves, substantially similar in different parities. Actually, a partial explanation can be found in the distribution of kiddings (Figure 9): first kiddings are manly concentrated in January and February and therefore the second part of these lactations occurs mainly during late spring-early summer, when in Sardegna there is a sudden decline of pastures that represent the main feeding source for goats. Such an unexpected result has been observed also for the lactation persistency of Sarda dairy sheep, where first lambing ewes that have lambings concentrated in early spring, do not show a higher persistency of lactation compared to older ewes (Macciotta et al., 2003).

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 100 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

Table 6. *Values of the parameters a, b, c and persistency (S) of average and smoothed lactation curves for different parities, type of kidding, kidding season and altitude of location of flocks, estimated with the Wood (WD) and Cappio-Borlino (CB) models with average (Av) and smoothed (Sm) data.*

Model	Factor	Level	a Av	a Sm	b Av	b Sm	c Av	c Sm	S[1] Av	S[1] Sm
WD	Parity	1	0.94	0.99	0.15	0.14	0.0053	0.0054	6.00	5.96
		2	0.98	0.99	0.19	0.18	0.0064	0.0063	6.01	6.00
		3	1.07	1.08	0.13	0.13	0.0051	0.0051	5.97	5.96
		4	1.21	1.10	0.11	0.15	0.0049	0.0054	5.92	5.98
		5	1.16	1.01	0.13	0.18	0.0051	0.0057	5.98	6.10
		6	1.27	1.31	0.12	0.10	0.0057	0.0052	5.79	5.79
	Type of kidding	1	1.18	1.11	0.10	0.12	0.0049	0.0050	5.87	5.92
		2	1.03	1.09	0.17	0.16	0.0058	0.0056	6.03	6.00
	Kidding season	1	1.23	1.18	0.08	0.09	0.0040	0.0040	5.95	6.00
		2	0.86	0.85	0.24	0.24	0.0075	0.0073	6.07	6.10
	Altitude	1	1.30	1.19	0.12	0.14	0.0059	0.0060	5.74	5.83
		2	1.16	1.14	0.10	0.10	0.0043	0.0044	5.97	5.99
		3	0.70	0.78	0.16	0.13	0.0037	0.0032	6.49	6.47
CB	Parity	1	0.54	0.54	0.36	0.37	0.0090	0.0090	311	303
		2	0.49	0.50	0.44	0.44	0.0081	0.0081	280	282
		3	0.54	0.55	0.37	0.37	0.0083	0.0083	323	322
		4	0.60	0.55	0.37	0.39	0.0085	0.0080	322	321
		5	0.61	0.55	0.37	0.40	0.0084	0.0077	325	325
		6	0.55	0.59	0.42	0.39	0.0089	0.0094	263	271
	Type of kidding	1	0.57	0.55	0.37	0.38	0.0090	0.0087	298	308
		2	0.52	0.55	0.41	0.40	0.0078	0.0080	312	308
	Kidding season	1	0.65	0.65	0.32	0.31	0.0093	0.0090	340	360
		2	0.41	0.42	0.50	0.49	0.0076	0.0076	260	268
	Altitude	1	0.54	0.53	0.44	0.44	0.0094	0.0088	242	257
		2	0.61	0.60	0.33	0.33	0.0086	0.0085	353	356
		3	0.54	0.59	0.24	0.21	0.0060	0.0064	684	728

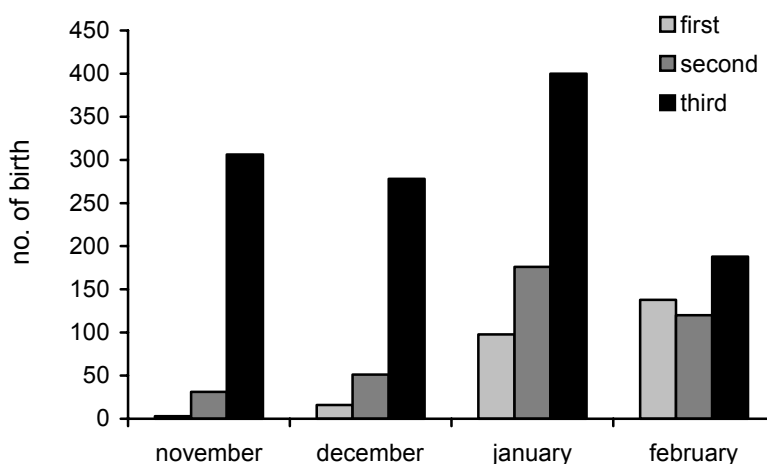[1] $S = -(b+1)\ln c$ for WD (Wood, 1967) and $S = 1/b^c$ for CB (Cappio-Borlino et al., 1995)

Figure 9. *Distribution of kiddings according to parity and month.*

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 101 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

The number of kids at parturition markedly affects lactation curve (figures 10a and b), especially in the first 100 dim. Goats with two kids have higher total and peak production and a more marked rising phase (tables 3 and 6). Some authors found that the effect of litter size on milk production for sheep and goat is mainly evident in the first part of the curve (Cappio-Borlino et al., 1995; Todaro et al., 2000).
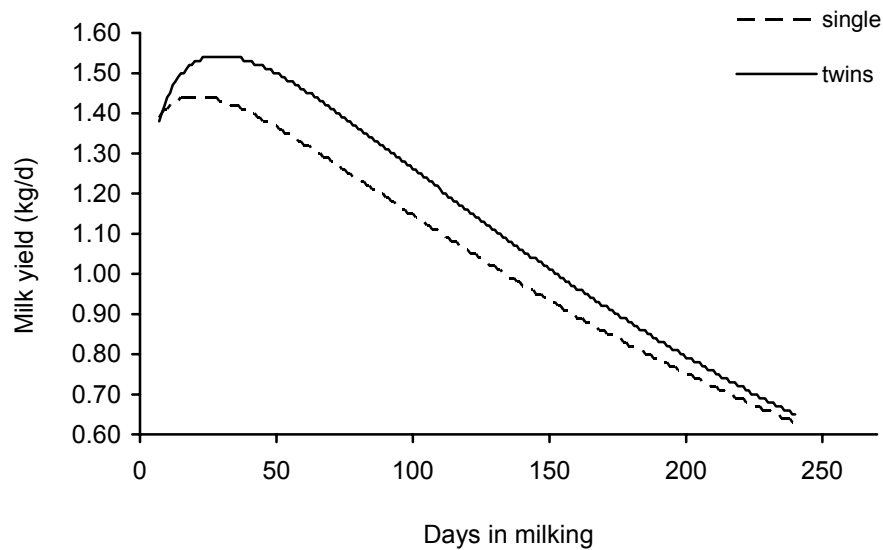

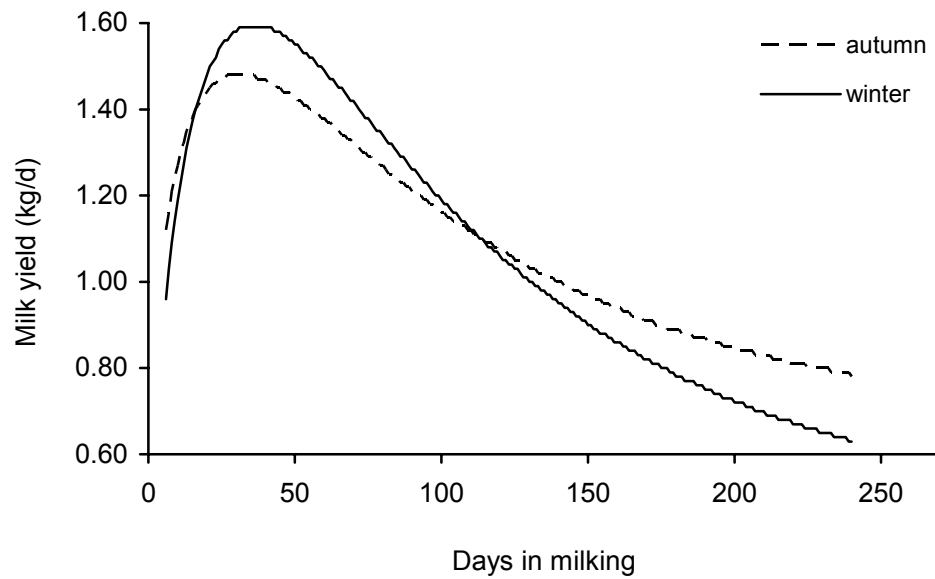**Figure 10a**. *Average lactation curves for goats of different type of kidding estimated by the Wood function*
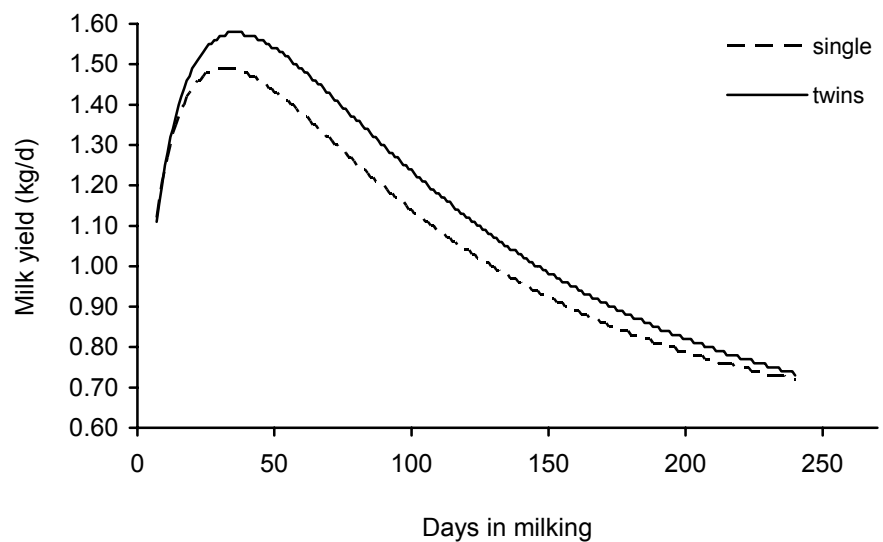
Figure 10b. *Average lactation curves for goats of different type of kidding estimated by the Cappio-Borlino function.*

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 102 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

The season effect (figures 11a and b) showed a remarkable difference between goat kidding in winter, with a pronounced rising phase and high level of production in the early lactation, in comparison to goat kidding in autumn, that show a lower initial yield but higher persistency after the peak. These patterns are related to the effects of climate and environmental conditions that for autumn kiddings are less favourable around the lactation peak (that occurs in winter) but that improve in late lactation, resulting in a higher persistency. On the contrary, late-winter kiddings benefit from the effect of spring on pasture availability (higher peaks) but are developed in the hot season in the second part of lactation. This behaviour is evident also in the value of parameters b and c related to slope of the curve before and after the peak yield (table 6). Also values of persistency (S) are different, with greater values for goats kidding in autumn (figure 11a and 11b; table 6), confirming previous results reported for dairy goat (Giaccone et al., 1995; Todaro et al., 2000).
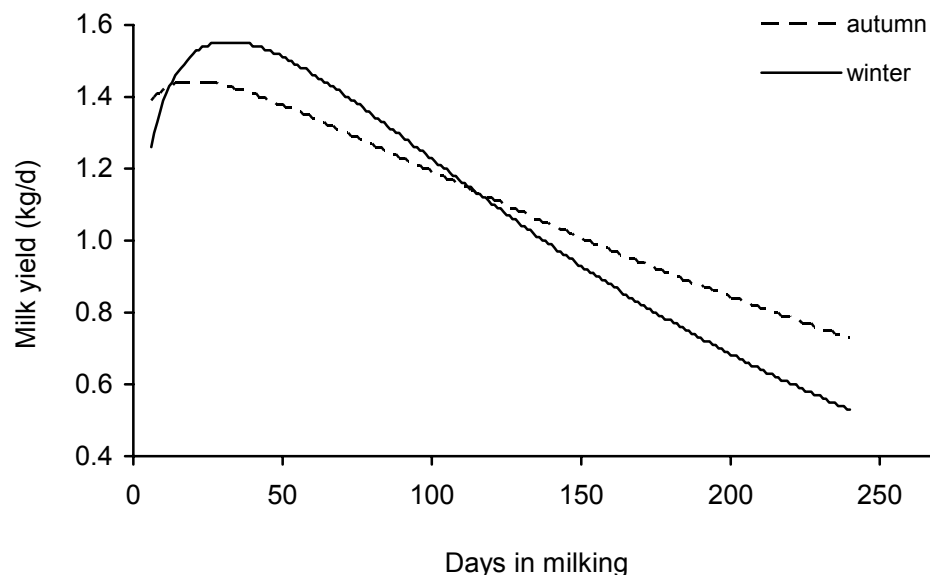
Figure 11a*. Average lactation curves for goats of different season of kidding estimated by the Wood function*

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 103 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

Figure 11b. *Average lactation curves for goats of different season of kidding estimated by the Cappio-Borlino function*

Interesting is the difference highlighted by both models between the curves of the three altitudes of flock location (figures 12a and b). This result confirms what already observed in lactation patterns estimated with mixed linear models in the Sarda goat (Macciotta et al., 2005). There is a marked decrease of peak yield, total lactation yield and an increase of lactation persistency (tables 3 and 6) passing from plain to hill and mountain. Moreover, of interest is also the trend of a delay of the lactation peak across different levels of altitude. All these differences can be ascribed to the different environmental conditions. In early lactation, occurring in December – January, environmental conditions are particularly adverse on mountain flocks, mainly due to low temperatures and scarce availability of pastures. Moreover, the later peak occurrence in these goats could be interpreted in terms of an effect of the improvement of conditions of production as lactation proceeds rather than the physiological raise to

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 104 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

the peak yield. Finally, the effect of the different genetic background of goats farmed in the different levels of altitude should not be neglected.
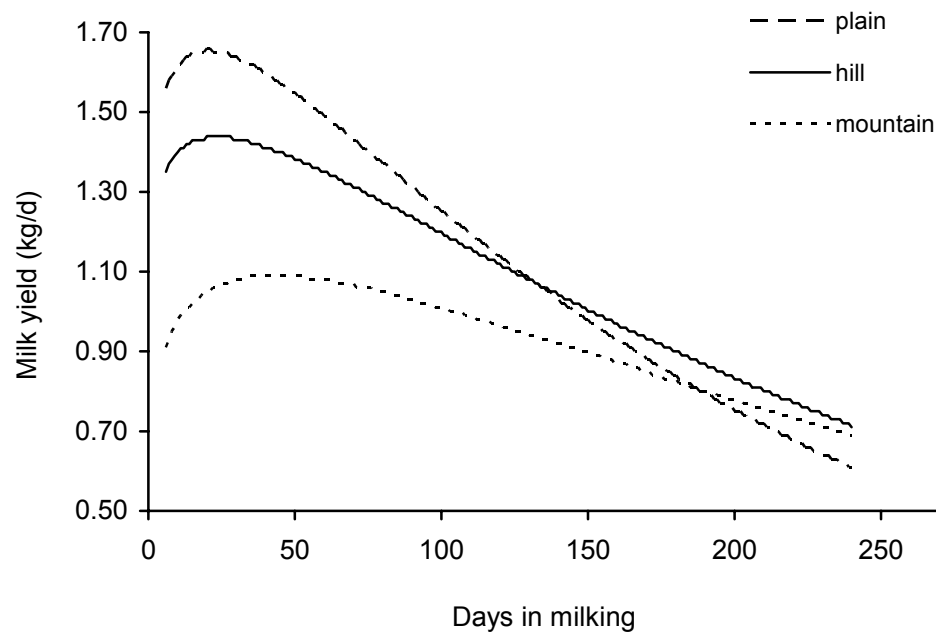
Figure 12a. *Average lactation curves for goats of different altitude estimated by the Wood function.*
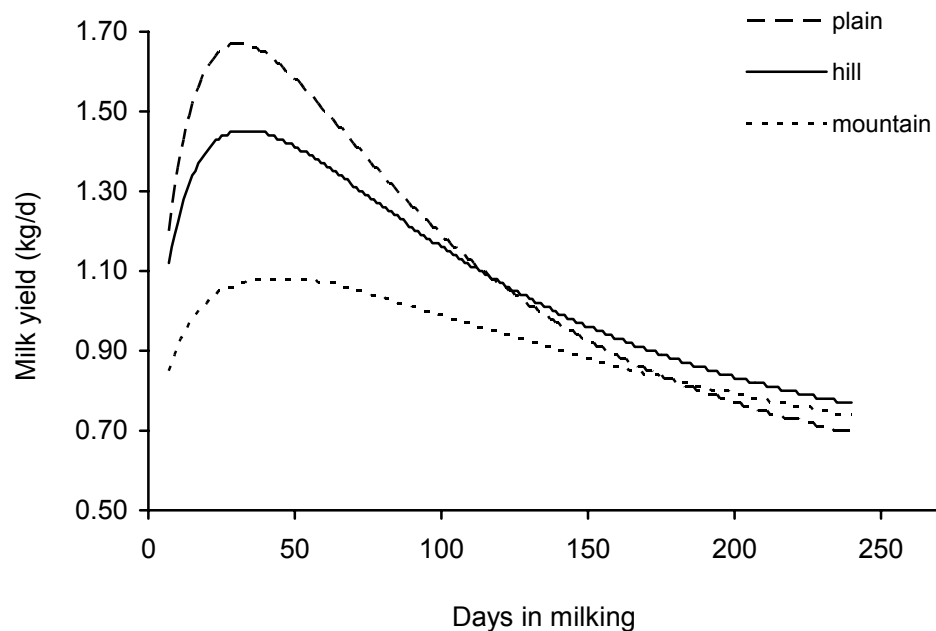
Figure 12b. *Average lactation curves for goats of different altitude estimated by the Cappio-Borlino function.*

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 105 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

CHAPTER IV

LACTATION CURVES OF MASSESE EWES

Introduction

Lactation is a physiological process characterised by the synthesis, secretion, ejection and removal of milk. The mathematical modelling of the temporal evolution of the milk is a fundamental step for a better understanding of the physiological mechanisms that underlie the milk production. Mathematical models of lactation curves are essentially aimed at disentangling the regular and deterministic component of lactation from the stochastic one that is peculiar of each animal and, therefore, unpredictable. The study of the shape of the first component and of the individual deviations from the continuous pattern gives useful information on physiology of milk synthesis and on the genetic and environmental factors that affect milk production. Such information is fundamental in the programs of genetic improvement, flock management, feeding and health monitoring and in the construction and validation of bio-economic models (Freeze and Richards, 1992; Pulina et al., 1995; Boe et al., 2005). Moreover, the mathematical analysis of the function that represents the lactation curve gives important technical indications for management choices in the specialized farming system: time at peak, peak production, persistence, total milk production.

Most of mathematical functions used for modelling lactation curves have originally been proposed for the dairy cattle and applied, with few modifications, in dairy sheep. Although the general pattern of the evolution of milk production over time is basically the same in the two species, the lactation curve of sheep shows some peculiarities due to biological and, mainly, management aspects.

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 106 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

A first specific feature is represented by the strict seasonality of reproductive and productive cycles that are synchronised with availability of natural pastures, the most common feeding source in Mediterranean countries where the largest concentrations of dairy sheep farms exists. As a consequence, milk yield and composition are strongly affected by environmental factors. A typical example is represented by double-peaked curves. The lactation peak in sheep is expected at 4-5 weeks from parturition, i.e. in winter for mature ewes, but it is often smoothed by a depressive effect of low temperatures and feed shortage availability. However, as lactation proceeds, environmental conditions improve and, due to the large availability of pastures in spring, a "false" peak in the second half of lactation occurs (see Figure 5 in the general introduction).

A further peculiarity is represented by the number and distribution of test day records throughout the lactation. As happens for dairy goats farmed extensively, also in sheep there is a limited availability of data at the beginning of lactation because milk of the first month is suckled by the lamb. Thus, in the typical Mediterranean farming system data recording start from about 30-40 day in milk and ends at the dry-off, with an average lactation length of approximately 210 days. The scarce availability of data in the first part of lactation can result in a scarce accuracy in modelling, and in several situation the lactation curves are estimated without peak yield (Macciotta et al., 2008). However, problems in modelling the first phase of lactation curves may occur also when milk yield dramatically falls immediately after the peak of lactation due to inadequate nutrition or environmental conditions (Cappio-Borlino et al., 1995). The existence of lactation curves without peak yield, named atypical, has been reported for cattle (Congleton and Everett, 1980; Shanks 1981; Macciotta et al., 2005; Olori et al., 1999; Rekik and Ben Gara, 2004), goat (Macciotta et al., 2004), sheep (Cappio-Borlino

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 107 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

et al., 1995; Portolano et al., 1997) and buffaloes (Dimauro et al., 2007). In cattle, the occurrence of atypical shapes has to be ascribed not only to biological variation between animals but also to the interaction between mathematical properties of the model used and the combination of values and distribution of test day records along the lactation (Macciotta et al., 2005).

A relevant occurrence of atypical shapes has been found in Massese breed sheep. Franci et al., (1999) reported about 50% of lactation estimated with Wood model without peak yield. The authors explained these results with a scarce suitability i of the model to fit lactations characterized by rapid increase in milk yield post partum. The Massese sheep is an autochthonous breed of north-west of Tuscany, farmed in flocks of medium or small dimension, with an extensive system based essentially on pasture as main feeding source. A peculiarity of this sheep is represented by the productive and reproductive cycles. Unlike most part of dairy sheep breeds farmed in Italy, which have lambings in autumn and late winter with a lactation length of about 180-210 days, the Massese sheep is characterized by a partial aseasonality of oestrus and births can occur at any time during the year (Acciaioli et al., 1999). Usually lactations start in late summer or autumn and last until early summer. However, they are frequently interrupted after a few months by another pregnancy, being ewes continuously exposed to mating. Thus a new shorter lactation starts in the spring. As a consequence, Massese ewes have normally three lambings every two year, alternating two short lactations and one long lactation a year (Pugliese et al., 2000). Franci et al. (1999) analysing the lactation curves of Massese sheep found a higher total production, greater persistency of lactation and lower peak yield level in sheep with long lactation compared to ewes with short lactation.

In the present study, the characteristics of lactation curves of Massese sheep with

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 108 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

different length are studied. Moreover, the ability of different mathematical models to fit the individual lactation curves is tested.

Materials and methods

Data

Data used in this work were recorded by the Italian Breeder Association and consisted of 9,374 test day records belonging to 2,066 lactations of Massese dairy sheep farmed in 7 flocks. In the data editing phase, lactations with a number of tests lower than 4 and with the first test after 50 days in milk were discarded. Data were then classified according to the length of lactation (short ≤ 160 days, long > 160 days), season of lambing (autumn = from August to December; winter-spring = from January to May) and the combination season-length of lactation (C1 = short lactation and autumn season, C2 = short lactation and winter-spring season, C3 = long lactation and autumn season, C4 = long lactation and winter-spring season). Average (calculated averaging for each day all records taken on the same date) and individual lactation curves were fitted.

Mathematical models

Three different mathematical functions chosen among the most frequently used for dairy sheep were fitted to the data (Cappio-Borlino et al., 2002).

The three models are:

I) The incomplete gamma function (WD) (Wood, 1967)

$$Y_t = a * t^b * e^{-ct} \tag{1}$$

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 109 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

fitted in the log linear form

$$\log Y = \log a + b \log t - ct$$

II) The combined exponential and linear model (WIL) (Wilmink, 1987)

$$Y_t = a + b_*e^{kt} + ct \qquad [2]$$

III) The bi-exponential function (CB) (Cappio-Borlino et al., 1995)

$$Y_t = at^{b\exp(ct)} \qquad [3]$$

Model [2] was fitted in the linear form by setting the parameter k to the fixed value of 0.40, obtained by fitting the WIL function to the whole data using a non linear regression procedure.

In all models, Y_t represents milk yield (kg) recorded at time t (days) and *a, b, c,* and *k* are parameters to be estimated. They can be easily interpreted in terms of lactation curve shape. In model [1] *a* represents the estimated milk production at lambing and, therefore, it is a scaling factor, *b* is linked the rising phase and *c* regulates the decline of milk production after the peak yield; In model [2] *a* is a scaling factor associated with level of production, *b* controls the rate of variation of milk yield in the first part of the curve, *c* is related to production decrease after the peak yield (persistency) (Macciotta et al., 2005a; Muir et al., 2004), whereas the *k* exponent is associated with the moment of peak yield (Wilmink, 1987). In model [3] *a* represents the horizontal asymptote to

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 110 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

which the milk production tends when t tends to infinite (for this reason the value of *a* can be considered as the milk yield immediately before the dry off), *b* controls the rate of variation of milk yield in the first part of the curve, and *c* is a regression coefficient related to production decrease after the peak yield (Cappio Borlino et al., 1995; Todaro et al., 2000). Moreover, the combination of the estimated parameters allows to calculate important features of the lactation curve, as maximum production (Ym), day of maximum production (Tm) and persistency (S). In particular:

I) WD model

$$Tm = a(b/c)^b e^{-b}$$

$$Ym = b/c$$

$$S = (b+1) \ln c$$

II) WIL model

$$Tm = -\frac{1}{k}\log\left(\frac{c}{kb}\right)$$

whereas peak production was predicted by model [2] at t=tm and S was assumed equal to parameter c.

III) CB model

$$S = 1/b^c$$

whereas Tm and Ym were predicted by model [3].

Total milk yield (TMY) was calculated for all models in the two classes of lactation length (160 d and 210 d).

Goodness of fit of average curves was assessed by examining:

a) the multiple coefficient of determination:

$$R^2 = 1\text{-RSS/TSS}$$

where

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 111 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

RSS = residual sum of squares

TSS = total sum of squares

b) the root mean square error

$$RMSE = \sqrt{RSS/(n-p)}$$

where:

n = number of observations

p = number of parameters in the model.

Serial correlations among residuals were evaluated with the Durbin Watson statistics (DW):

$$DW = \frac{\sum_{t=1}^{n}(e_t - e_{t-1})^2}{\sum_{t=1}^{n}e^2_t}$$

where: e_t e_{t-1} are the residual at time t and at time t-1, respectively. When there is no serial correlation among residuals the expected value of the DW coefficient is approximately 2.0. Values of DW<1.5 indicate a positive correlation, whereas values of DW>2.5 show existence of a negative autocorrelation (Macciotta et al., 2005a).

Individual curves were ranked according to five levels of R^2 (1<0.20, 2 = 0.20 to 0.40, 3 = 0.40 to 0.60, 4 = 0.60 to 0.80 end 5>0.80). Moreover, curves obtained with WD and WIL models were classified as standard or atypical according to the sign of parameter b (Macciotta et al. 2005b): standard = b>0 and atypical = b<0 for the Wood function; standard b<0 and atypical b>0 for the WIL model.

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives"   - 112 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

Results and discussion

Individual curves

Table 1 shows the percentage of individual lactation curves within each class of R^2. Goodness of fit shows a wide range of variation, although about 70% (WD), 59% (CB) and 78% (WIL) of curves have a $R^2 > 0.6$. For CB model, the class with $R^2 < 0.2$ has a number of lactation greater then WD and WIL because convergence problems occurred in several cases. Finally the value of DW statistics is always close to 2, indicating absence of correlations among residuals for all models.

Table 1. *Distribution of estimated individual curves across different classes of R^2*

R^2 class	Model					
	WD		WIL		CB	
	n.	%	n.	%	n.	%
<0.20	328	15.9	130	6.3	717	34.7
0.20-0.40	128	6.2	119	5.8	70	3.4
0.40-0.60	156	7.5	186	9.0	95	4.6
0.60-0.80	285	13.8	327	15.8	191	9.2
>0.80	1169	56.6	1304	63.1	993	48.1

A remarkable number of atypical curves was found (table 2) higher than the value reported by Franci et al. (1999) for Massese ewes. Results of the present work are in agreement with previous reports for dairy sheep (Cappio-Borlino et al., 1995; Portolano et al., 1996;).

Table 2. *Relative frequencies of standard and atypical shapes.*

Class[1]	Frequency (%)	
	WD	WIL
Atypical	57.84	63.94
Standard	42.16	36.06

[1]Atypical = b<0 in the Wood's model and b>0 in the Wilmink's model, Standard = b>0 in the Wood's model and b<0 in the Wilmink's model.

A higher occurrence of atypical curves was highlighted by the WIL model than WD model (63.94 vs. 57.84). This result, already observed in fitting individual curves of dairy cattle (Macciotta et al., 2005) can be explained with the mathematical structure of the different models. Being additive, the WIL function allows for a substantial independence between the first and the second part of the curve, thus it is more flexible in following particular patters. On the other hand, the WD model is multiplicative and, therefore, more rigid.

Average curves

At first, the three selected model were fitted to the overall average data. Figure1 shows actual data and estimated values for WD, WIL and CB models. Only the CB function is able to reconstruct the ascending phase to the peak yield whereas WD and WIL model yielded the pattern of an atypical curve. This is an expected result because the CB model is characterised by a great ability to describe immediate pre and post peak curvatures and to detect the position of the lactation peak (Cappio-Borlino et al., 1995).
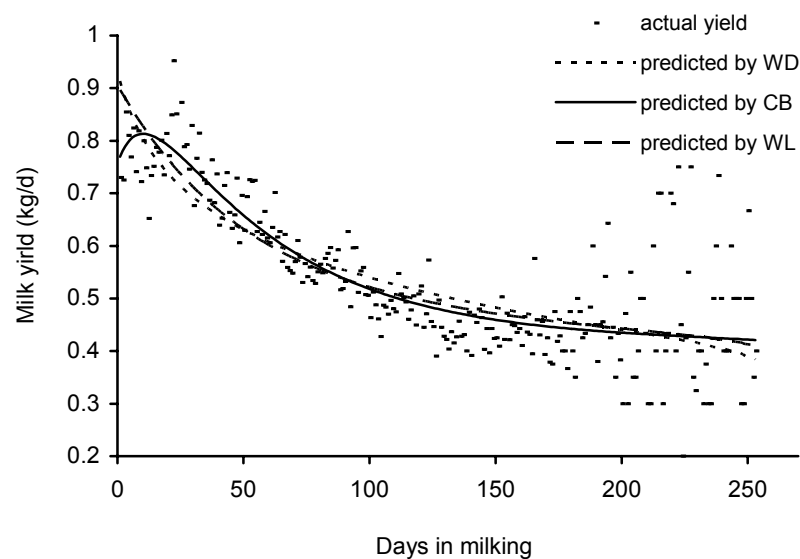
Figure 1. *Actual and predicted milk yield by Wood, Cappio-Borlino and Wilmink models for overall average lactation curves.*

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 114 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

It can be also observed a substantial underestimation of the peak yield for of all models and the great dispersion of data at the end of lactation. Parameters of the estimated curves are reported in table 3.

Table 3. Estimated parameters for overall average curve fitted by Wood, Cappio-Borlino and Wilmink models.

Model	a	b	c
WD	1.41	-0.19	0.0008
CB	0.42	0.32	0.0177
WIL	0.50	0.49	-0.0003

In order to remove possible biases in the fitting of average curves for different season and length classes, only patterns with the standard shape were considered. In figure 2, actual data and estimated values for WD, WIL and CB models for standard curves are reported. As expected all the three models are able to reconstruct correctly the first phase of lactation.
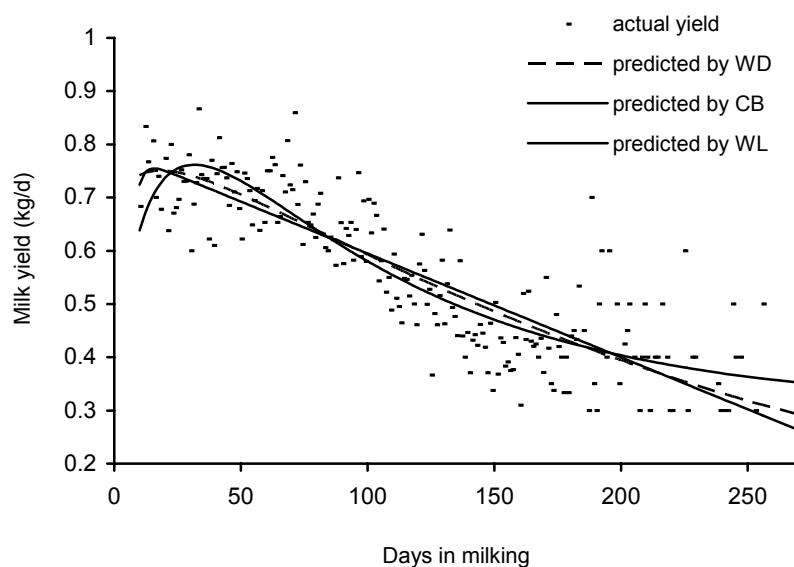
Figure 2. Actual and predicted milk yield by Wood, Cappio-Borlino and Wilmink models for overall average curve with only standard curves.

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 115 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

Estimated parameters for the curves depicted in figure 2 are reported on table 4

Table 4. Estimated parameters for overall average curve with only standard curves, fitted by Wood, Cappio-Borlino and Wilmink models.

Model	a	b	c
WD	0.64	0.08	0.0046
CB	0.30	0.36	0.0091
WIL	0.79	-2.53	-0.0019

The three models gave similar fitting performances when describing the average lactation curves for the four combination of lactation length and season of lambing. Short lactations (C1 and C2) have a higher value of R^2 and a lower RMSE than long lactations (C3 and C4).

Table 5. *Goodness of fit for Wood, Cappio-Borlino and Wilmink models (1 = short lactation and autumn season, 2 = short lactation and winter-spring season, 3 = long lactation and autumn season, 4 = long lactation and winter-spring season).*

Model	lactations type	R^2	RMSE	DW
WD	1	0.68	0.09	1.08
	2	0.66	0.11	1.96
	3	0.48	0.13	1.93
	4	0.55	0.15	2.07
CB	1	0.66	0.09	1.95
	2	0.64	0.11	1.85
	3	0.47	0.13	1.75
	4	0.51	0.14	1.93
WIL	1	0.65	0.09	1.92
	2	0.66	0.11	1.94
	3	0.46	0.13	1.76
	4	0.56	0.15	2.11

All three models were able to represent with good degree of accuracy the average lactation curves for the four combination of lactation length and season of lambing, and to underline significant differences between them, as reported by figures

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 116 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

3, 4, 5 and in table 6. In general, the average overall productive level is higher for lactations that start in spring, as evidenced by the high level of the curve (figures 2, 3, 4), the larger values of the scale parameter a and of the peak yield (table 6).
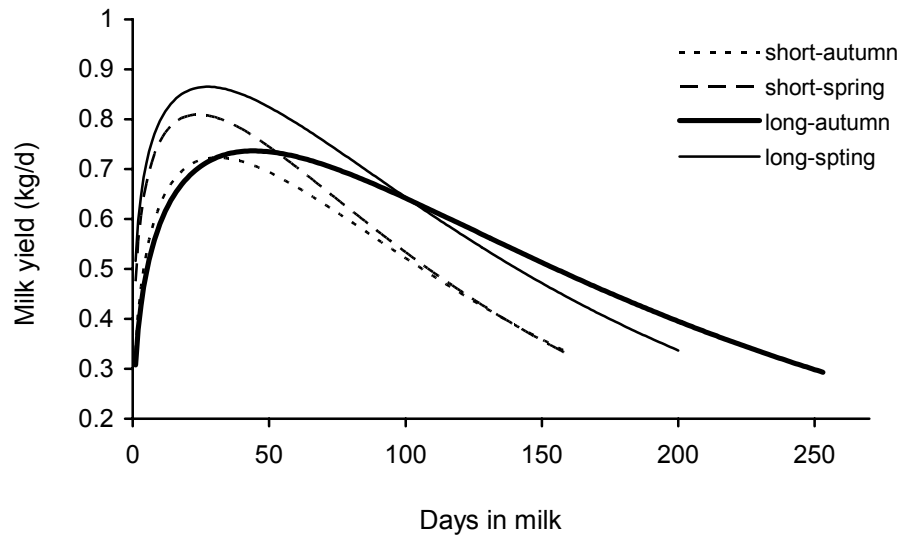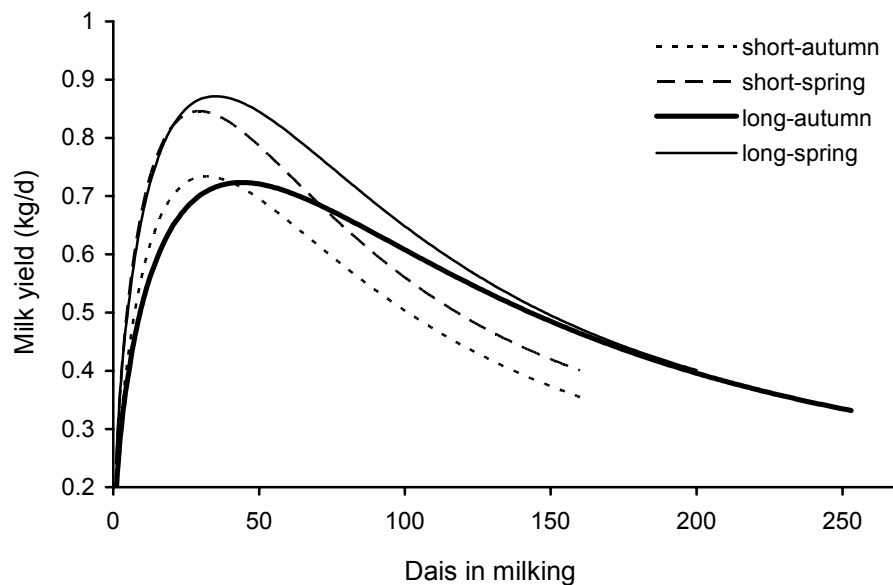

Figure 3. *Average lactation curves for different combination of lambing season - lactation length classes estimated with the Wood function.*

Moreover, long lactations are more productive than short lactations not only, as obvious expected, in terms of total milk yield (about 110 kg vs. 80 kg, respectively) but also in the peak yield (about 0.84 kg/d and 0,72 kg/d for the spring and autumn lambings, respectively).

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 117 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

Figure 4. *Average lactation curves for different combination of lambing season - lactation length classes estimated with the Cappio-Borlino function.*
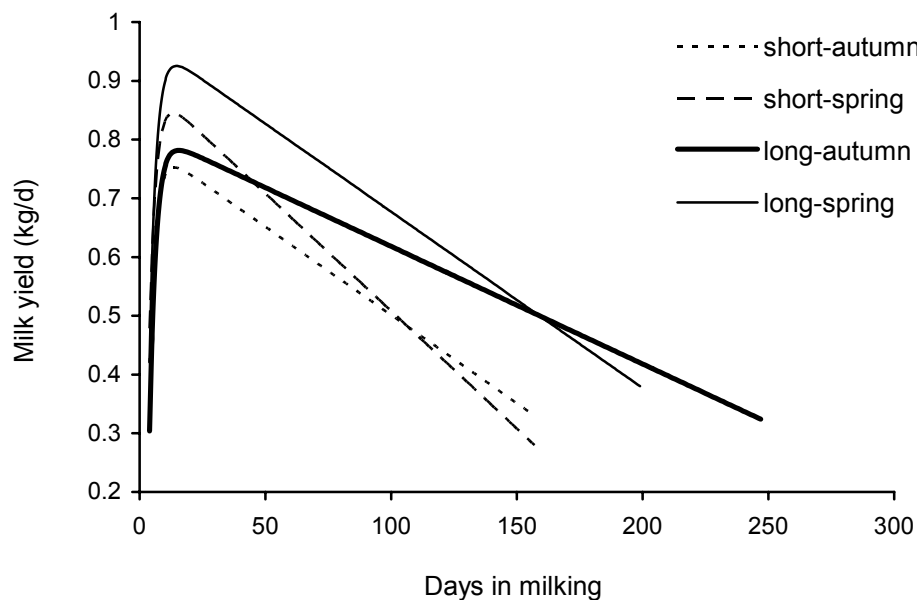
Figure 5. *Average lactation curves for different combination of lambing season - lactation length classes estimated with the Wilmink function.*

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 118 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

Table 6. *Values of the parameters a, b and c, the time to the peak yield (Tm), production to the peak yield (Ym), persistency (S) and total milk yield (TMY) of average lactation curves for different seasonal lambing-lactation length classes estimated with the Wood, Cappio-Borlino and Wilmink models.*

Model	lactations type[1]	a	b	c	k	Tm	Ym	S	TMY
WD	1	0.34	0.31	-0.010		31.1	0.72	6.04	77.7
	2	0.48	0.24	-0.010		25.5	0.82	5.78	85.6
	3	0.31	0.31	-0.007		43.7	0.73	6.48	107.4
	4	0.52	0.22	-0.008		27.9	0.87	5.91	110.9
CB	1	0.19	0.52	0.009		33.0	0.66	220	77.7
	2	0.24	0.50	0.010		29.0	0.77	198	86.2
	3	0.19	0.46	0.006		44.0	0.69	364	102.8
	4	0.24	0.48	0.008		27.0	0.81	249	107.9
WIL	1	0.81	-6.08	-0.003	-0.4	7.8	0.74	-0.003	76.7
	2	0.92	-6.79	-0.004	-0.4	7.0	0.83	-0.004	85.2
	3	0.83	-27.63	-0.002	-0.4	4.8	0.78	-0.002	107.2
	4	0.98	-4.01	-0.003	-0.4	8.5	0.92	-0.003	110.3

[1]1=short lactation and autumn season, 2=short lactation and winter-spring season, 3=long lactation and autumn season, 4=long lactation and winter-spring season

The time at peak occurrence is about 4-6 weeks from the lambing, as reported by several authors for dairy sheep (Macciotta et al., 2005; Cappio-Borlino et al., 2004), delayed in sheep with long lactation. The persistency is greater for the long lactation and, within these, for the sheep lambing in autumn (figure 2, 3 and 4). A greater persistency of lactation in ewes lambing in winter was reported also by Portolano et al. (1996).

As far as differences among the three models are concerned, it can be observed that WIL predict the time of peak yield around 8 day, whereas WD and CB between 27 and 44 day from the lambing. Moreover CB tend to underestimate the peak yield in comparison to the other models.

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 119 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

CHAPTER V

GENERAL CONCLUSIONS

Mathematical modelling of complex biological systems has always to handle several theoretical and practical issues. The basic need is to translate in mathematical terms an observed outcome in order to reproduce as closer as possible its general pattern. Beside this problem of generalization, models have also to cope with specific sources of perturbation affecting the phenomenon under study that, depending of the aim of the research, have to be removed or investigated. The mathematical description of milk production in ruminants has to address two main issues. One is represented by the requirement of reconstructing the regular and continuous pattern of evolution of milk yield along the lactation. A second issue is the need to account for deviations from the regular pattern due to environmental perturbations. The theoretical development of mathematical modelling applied to the study of lactation curve in ruminants during the last forty years has tried to give an answer to these problems using different approaches.

Mechanistic modelling should be preferred when the main task is to tests scientific hypothesis on regulatory mechanisms involved in the determinism of milk production. The core of a mechanistic model should be able to mimic the standard shape of the lactation curve. Several papers have assessed that the number and the activity of mammary secretory cells and their rates of differentiation and apoptosis represent the key state variables for building the main part of the machinery. Further developments are aimed at specifically studying some particular aspects of the phenomenon: examples are submodels of mammary gland alveoli, hormone actions, cellular apoptosis, energy supply. Such a deep theoretical understanding is however reached at the expense of a progressively larger number of parameters to be estimated with a subsequent increase of

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 120 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

the mathematical complexity. Actually, this can be considered the main reason of the limited practical use of mechanistic modelling in animal science. Furthermore, the inputs required (rates of cell proliferation and apoptosis, hormone concentrations etc.) are always nnt available. In some cases, as the modification of the Dijkstra function proposed by VanRaden et al. (2006) and used in the present thesis for modelling extended lactations, mechanistic models can be modified in order made then more "easy to use". The simplification obviously leads to a reduced explanatory power of the model but it can still be able to supply outcomes of technical interest. Modern software technologies as computer aided design may also be of help in making easier the use of mechanistic functions. The use of analog simulators allows the development of complex models based on non-linear differential equations also by non pure mathematicians scientists.

Fitting empirical functions able to describe a first ascending phase till a maximum followed by a declining pattern, regardless any link with the underlying physiological mechanism, has undoubtedly been the most frequent approach used in animal science. Starting from the pioneer work of Brody (1925), several continuous function of time have been proposed, differing in the type of regression (linear or non linear), number of parameters and their degree of relationship with main traits of lactation curve shape. Whereas the early goal was to reconstruct the general shape essentially for management purposes, in recent years the need for modelling individual deviations both for animal monitoring and for genetic evaluation has become relevant. As a consequence, for empirical modelling there has been a progressive tendency to move from functions specifically conceived to model the standard shape of the lactation curve, as the milestone paper of Wood (1967), to more general functions as Legendre polynomials. These latter functions, due to their great flexibility, are more suitable to fit

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 121 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

individual deviations. However, their ability to reconstruct the standard pattern is more or less comparable with the one of simpler models. Multiphasic functions can be regarded as a sort of good "hybrid" between empirical and mechanistic models, being based on the partition of lactation pattern in an increasing curve followed by one or more decreasing curves. They have been successfully used for fitting curve of cattle and goats but a widespread use is strongly constrained by the huge number of parameters to be estimated.

Thus the choice of a model should be based on several elements. First of all the specific scenario of production. Fitting production records of dairy cows highly selected, managed intensively is very different from fitting curves of sheep or goats farmed in marginal areas. Second, the mathematical properties of the model should fit the peculiarities of the lactation pattern considered. For example, Cappio-Borlino et al. (1995) started from the relevant occurrence of atypical shapes in sheep and suggested a modification of the Wood function able to detect the peak also when it is very close to parturition. Third, computational complexities should be taken into account. Non linear equations often gave problems of lack of convergence and may be sensitive to prior values. Splines seem to be more attractive for their ability to detect also slight inflections of the curve but they usually fail to converge with a number of knots greater than two. Thus different models have different advantages and drawbacks. This is probably one of the main reasons for the still large use of the Wood function: besides its well known limitations, it is characterised by a great capacity to reconstruct the standard shape of the lactation curve, has a limited number of parameters that have a clear relationship with curve shape and it can be easy linearised.

All the above mentioned considerations lead to the more general conclusion that does not exist a perfect model and for each specific problem a selection of model should

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 122 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

be made. Experimental contributions of this thesis deal with various scenarios of temporal evolution of milk yield in the main livestock species reared for milk production. The man aim of the researches has been to identify suitable functions to fit different types of lactation curve shape.

The first case that has been considered is the modelling of extended lactations in dairy cows. a frequent situation for highly producing dairy cows. This should be one of the most likely challenge for the dairy cattle industry in the very near future. The comparison of several empirical mathematical models currently used to fit lactations with a function developed specifically for long patterns and the study of main traits of extended patterns has yielded some useful indication. As far as model comparison is concerned, the Ali and Schaeffer polynomial regression gave similar performances of the modified Dijkstra functions both for average and individual curves, suggesting that models used for describing lactations of standard length can be used also for extended ones. Moreover, it has been confirmed the difficulty for non linear models to converge when they are used to describe individual patterns. The two functions used were able to calculate two traits, the inflection point and the level of production at the end of lactation, that may have some relevance for management and genetic purposes. In particular, the yield at the end of lactation is a basic tool for deciding whether a cow at this stage is profitable or not. Considering a daily yield production of about 15 kg as cut off value, about 25% of cows considered in the study had higher yields in late lactation. The study of genetic basis of these traits may be of great interest for a possible consideration as selection goals. Extended lactations have also been found to have higher 305d yields compared to standard yields. These results, confirming previous reports on dairy cattle obtained in other countries, seem to indicate the extension of lactation length as a valid management strategy. However, it must be remembered that

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 123 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

this research, as most of studies in literature, has been carried out on an archive where extended lactations were in the majority of cases the result of reproductive failure and not the consequence of management choices. Thus conclusion on the efficiency of extending lactations should be tested on planned experimental groups.

The second experimental contribution has approached a common problem when small ruminant lactation curves are modelled: the great intrinsic variability of data. Reasons are well known: the farming system, the recording system (many animals are still hand milked), the great genetic variability. In the specific case of the Sarda goat, the partial overlapping of altitude of location of flock with the partition into three different genetic subpopulation represents a further peculiarity. In spite of all of these limitations, the functional approach has been able to catch some of the main features of average curves of different classification factors such as party, number of kids at parturition, season of kidding. Polinomials or splines did not results in better fittng performances compared to the Wood or the Wilmink functions. The results confirm that, also in a situation of great heterogeneity of data structure, if the main aim is to reconstruct the regular component of milk production pattern, model specifically conceived to reconstruct the standard lactation curve shape are more suitable. The extra flexibility supplied by non parametric regressions do not represent in advantage in this case. On the contrary, they often were not able to detect the increasing first phase of the curve, as happened for Legendre orthogonal polynomials. Finally a previous data smoothing by using the LOWESS regression resulted in a relevant improvement of goodness of fit. The use of this technique may be of interest for traits characterised by huge variability as, for example, somatic cell counts.

The third study was a investigation on the peculiar situation of the Massese breed ewes, where the intensification of reproductive cycle results in an alternate

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 124 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

sequence of long and short lactations for each ewe. A frequent issue in modelling lactation curves is represented by relevant occurrence of atypical shapes, i.e. those that lacks of the peak yield and consist of a monotonically decreasing pattern. Such a situation is particularly relevant in small ruminants. It can be remembered that in the first part of the curve the ewe is nursing the progeny and for this reason data are not available Such a behaviour is particularly evident in the Massese. The research has highlighted the ability of the Cappio-Borlino function, specifically concei.ved to fit the first part of the curve, to describe both the short and the long lactations of the Massese

Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 125 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

CHAPTER VI

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Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 126 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

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Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 127 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

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Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 128 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

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Roberto Steri "The mathematical description of the lactation curve of Ruminants: issues and perspectives" - 130 -
Tesi di Dottorato in Scienze dei Sistemi Agrari e Forestali e delle Produzioni Alimentari
Indirizzo Scienze e Tecnologie Zootecniche

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Indirizzo Scienze e Tecnologie Zootecniche