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RABBIT MILK: A REVIEW OF QUANTITY, QUALITY AND NON-DIETARY AFFECTING FACTORS.

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Abstract: This literature review focuses on the milk yield and milk composition of rabbits and the non-nutritional factors affecting both quantity and quality. Actual highly efficient hybrid does have an average daily milk yield of 250 g or 60 g/kg of live weight during the 4-weeks lactation period. However, compared with cow and sow milk, rabbit's milk is much more concentrated in fat (12.9 g/100 g), protein (12.3 g/100 g) and energy (8.4 MJ/kg) which explains the extremely rapid growth of the young (weight × 6 after 3 weeks). Characteristic of rabbit milk is also the nearly absence of lactose (<2 g/100 g). At peak lactation, protein output per kg metabolic weight (13.4 g/day/kg$^{0.75}$) exceeds even those of Holstein milk cows. The non-nutritional factors having the largest impact on the milk yield are the number of suckling kits, the parity order (primiparous *vs.* multiparous) and the gestation overlapping degree (rapid decline after 17-20 days of gestation). However, also through the reduction of feed intake, heat stress has a detrimental impact especially when the night temperature remains above 25°C. Rabbit milk lipids are highly saturated (70.4% SFA) due to the high content of $C_{8:0}$ – $C_{12:0}$ (50% of total FA) and further characterised by nearly equal quantities of oleic and linoleic acid and an ω-6/ω-3 ratio around 4. Finally some data about the amino acid, milk proteins including the immmunoglobulins, mineral and vitamin composition are presented.

Key words: rabbit, milk, quantity, quality, affecting factors, review.

INTRODUCTION

Rabbit does are in general allowed to nurse their kits till weaning age (4-5 weeks of age). Kits are until 18-19 days of age exclusively depending from the milk of their mother (Maertens and De Groote, 1990; Fortun-Lamothe and Gidenne, 2000). Newborn rabbits have high energy requirements and a low thermal isolation. Therefore early liveability and growth performances are closely related to the quantity and quality of the milk ingested (Lebas, 1969 and 1976; McNitt and Moody, 1988; Fraga *et al.*, 1989; Szendrö and Maertens, 2001). Recently, this relationship has been stressed by Szendrö *et al.* (2002) using 2 nursing does per litter.

The lactation requires a great energy effort of the doe and is closely related to some variables as corporal condition, fecundity and foetal growth (Fortun-Lamothe and Bolet, 1995; Pascual *et al.*, 2003; Xiccato *et al.*, 2004). Moreover, genetic selection in maternal lines has focussed mainly on prolificacy resulting in parental lines with a litter size of over 10 kits (Tudela *et al.*, 2003). Consequently, demands and requirements of does for milk yield have increased greatly. However, strains were primarily successfully selected for increased litter size but weaning weight of kits dropped (Rochambeau, 1998). This indicates that the relative increase of milk yield was smaller than that of litter size, leading to smaller amounts of milk available per kit (Szendrö and Maertens, 2001).

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Rabbit milk is collected for the production of recombinant proteins in transgenic animals (Castro *et al.*, 1999; Bõsze and Houdebine, 2006). The high protein content of rabbit milk together with the high yield/kg live weight and the rapid reproduction rhythm are attractive characteristics to use rabbits for this purpose. Nevertheless, milking of rabbit does remain an exceptional goal. Consequently, information relating with milk yield and composition remains relatively scarce although interesting work was already executed, mainly in France, already 35 years ago (Lebas, 1968, 1969, 1971 and 1976; Lebas *et al.*, 1971). The present review intends to update this information and to discuss the main factors influencing milk yield and milk composition of does used for meat production. Dietary effects on milk yield and composition were recently reviewed by Pascual *et al.* (2003) and thus they should be only marginally mentioned in this review.

METHODOLOGY USED TO MEASURE THE MILK YIELD OR TO COLLECT SAMPLES

Direct method

In larger animal species (e.g. cows, sheep), mechanical or manual milking is used as direct method to measure milk production. Also for rabbits milking machines were developed and described (Lebas, 1970; Schley, 1975; Marcus *et al.*, 1990). Milking or sampling is always done after a 24-hour separation of mother and kits avoiding the free suckling of kits. Females have to be treated with oxytocine in order to stimulate the milk ejection. When the females are fixed in a comfortable position with suitable milking equipment, equivalent or higher amounts than that ingested by the kits at one suckling can be collected (Lebas, 1970). This methodology is generally used for the collection of milk from transgenic rabbits (BioProtein Technologies, 2006). However, in animal research studies, this methodology is not used to determine the milk yield capacities during the whole lactation period.

Indirect measurement

The nursing behaviour of the rabbit is characterised by a daily short event of only 3-4 minutes (Cross, 1952; Hudson *et al.*, 2000). Although most does show a strong circadian basis with one nursing event every 24 hours, a limited number of females nurse their kits more than once a day (Zarrow *et al.*, 1965; Hoy and Selzer, 2002; Matics *et al.*, 2004). However, it has not been demonstrated that more milk is produced or that kits grow faster when the doe performs (or is allowed or not) more than one nursing a day (Hudson *et al.*, 2000). For example Zarrow *et al.* (1965) have observed exactly the same daily gain, day after day, from 2 to 30 days after kindling for kits able to suckle their mother freely, only once or twice a day. An explanation could be found in the observations of Calvert and Knight (1982) that milk secretion is performed at a constant speed during the 24 hours following a nursing and thereafter dropped dramatically. Nevertheless with the double suckling method, Gachev (1971b) observed a slight reduction of milk production during the last 6 hours fraction of the 24 hours period (19.4% of the total yield vs 24.8% to 28.0% for the 3 others 6 hours periods).

As a consequence of the nursing behaviour, daily milk yield can easily and accurately measured by determining the weight difference of the doe before and after nursing (Lebas, 1968). This weight-suckle-weight method is widespread used for research purposes and has an advantage over weighing of the kits. Kit weighing is more difficult because they are nervous and the accuracy is lower because kits show some urine losses even during the suckling event (Lebas, 1971).

During the first stage of the lactation period, the next box can be closed and daily opened to nurse the kits and to determine the milk yield. However, once the kits starts to consume solid feed, from day 18 onwards (Fortun-Lamothe and Gidenne, 2000), housing of the kits has to be in a separated cage or in an adapted cage to allow both the milk yield determination as the normal development of the kits (Fortun-Lamothe *et al.*, 2000).

The indirect measurement of the milk yield is a time and labour consuming method. However, when only 3 measures per week are executed, total yield can be calculated with a high accuracy (R^2=0.982; RSE=5.2) (Fernández-Carmona *et al.*, 2004). Using a quadratic regression model obtained from 3 measurements per week (9 in total), Fortun-Lamothe and Sabater (2003) estimated daily and total milk yield of each doe in the 0-21 days lactation period.

Estimation based on the growth of the suckling kits
There exist a high correlation between the milk production and the growth of the kits because rabbit kits do not show significant feed intake before the age of 18-19 days (Maertens and De Groote 1990; Fortun-Lamothe and Gidenne, 2000). The highest correlations reported are for the period between birth and 21 days of age and amount to 0.90 (Lebas, 1969), 0.91 (Fortun-Lamothe and Sabater, 2003) or even 0.99 (Lukefahr *et al.*, 1983). Weight gain of the litter at a later stage is much less correlated with the milk yield in the corresponding period (Lebas, 1969). Although litter weight at 21 days is highly correlated with the milk yield (R^2=0.917; RSE=11.5) (Fernández-Carmona *et al.*, 2004), litter weight gain at 21 days is a better predictor of the doe milk yield than litter weight at 21 days (Fortun-Lamothe and Sabater, 2003).

For actual high productive hybrid does the following equation was drawn (Fortun-Lamothe and Sabater, 2003):

Milk yield 0-21 d (g) = 1.69 × weight gain of the litter 0-21 d (g) + 362   (r=0.91)

Collection of samples
There are different methods to collect milk samples. Apart from a milking machine, samples can be collected by manual milking by gently pushing on the mammary gland. An experienced person can collect during 1-2 minutes easily 20 ml even without injection of oxytocin (authors' personal observations). Although Lebas (1971) did not find significant differences in the composition of 4 consecutive samples of 45-70 g, he recommends for analysis a sample quantity of at least a quarter of the total amount present. However, it was never proved that the composition of the first 20 g by e.g. hand milking is not representative for the total quantity.

Another milk collection method is to take, immediately after the nursing, a sample out of the kit's stomach by means of an orally introduced stomach tube (Fraga *et al.*, 1989; De Blas *et al.*, 1995). This method is easy but some contamination may occur with gastric secretions and with the residual milk still contained in the stomach even after a 24 hours period (authors' personal observations).

MILK YIELD

The usual lactation period of does is between 4 and 5 weeks depending on the reproduction rhythm and management system. However, mainly for experimental purposes, early weaning is sometimes executed and a shorter lactation period is considered (Xiccato *et al.*, 2004). In absence of a new pregnancy, milk production can continue up to 6 weeks or even a longer period (Cowie, 1968; Lebas, 1969).

Papers dealing with milk yield of does are quite limited and most of them are linked with nutrition experiments. In Table 1 only papers that have measured the milk yield and when does were fed *ad libitum* are considered. Milk yield is often expressed in different ways: i) as the total quantity produced in a certain period ii) as an average production during a period or iii) as the sum of a limited number of determinations. Therefore, it is not easy to compare the data in the different papers including milk yield data. Moreover, many of the results published are strongly influenced by diet or does genotype but also by reproduction rhythm, environmental temperature, parity, and so on. A detailed discussion about their impact on milk yield is presented below.

Based on the data of Table 1, actual strains used for commercial meat production have a 28-days milk yield in their first lactation of about 5.5 kg (Xiccato *et al.*, 1995; Pascual *et al.*, 2002b, Maertens *et al.*, 2006). Multiparous hybrid does, nursing 9-10 kits, have a yield that exceed 7.0 kg during a 28-days lactation period or 250 g/d or around 60 g/d when expressed per kg of live weight (LW) (Fortun-Lamothe and Sabater, 2003; Xiccato *et al.*, 2005; Maertens *et al.*, 2006).

Table 1: Description of the papers dealing with milk yield.

						Milk yield				
Reference	Diet	Breed/ Strain/Line	Parity	Litter size	No. of lactations	Period (d)	Total (g)	Top (g/d)	Average (g/d)	g/kg LW[2]
Lebas, 1968	Reproduction diet	Fauve de Bourgogne	Different	8-9	143	0-42	7090	242	169	42.3
Partridge and Allen, 1982	a) Low protein diet	New Zealand x Californian	2+	8	6	0-28	3890		139	34.8
	b) Medium protein diet				6	0-28	4820		172	43.0
	c) High protein diet				6	0-28	5270		188	47.0
Lukefahr *et al.*, 1983	Reproduction diets	NZW	Different	NSLS[1]	In total: 225	0-21	3970		189	47.2(3)
		Californian				0-21	3060		146	38.4(3)
		Cal x NZW				0-21	4030		192	49.2(3)
		NZW x Cal				0-21	3650		174	44.6(3)
Maertens and De Groote, 1988	Low energy diet	Hybrid (Elco)	2-5	8	15	0-28	6140		219	51.2
	Medium energy diet				16	0-28	6330		226	53.4
	High energy diet				15	0-28	6810		243	57.3
Fraga *et al.*, 1989	Different reproduction diets	Californian x New Zealand		NSLS	22	0-28	5680		203	50.7
					17	0-28	4700		168	42.0
					17	0-28	5020		179	44.8
					17	0-28	4600		164	41.0
McNitt and Lukefahr, 1990	Reproduction diet	Californian	Different	NSLS	19	0-29	4582		158	40.0
		New Zealand			23	0-29	3973		137	31.9
		Palomino			22	0-29	3480		120	29.0
		White Satin			21	0-29	3683		127	29.9
Mohamed and Szendrö, 1992	Reproduction diet	Californian (3.8 kg)	?	6	4	0-21	3567		170	44.7(3)
				8	8	0-21	3686		176	46.3(3)
				10	8	0-21	3776		180	47.4(3)
Khalil, 1994	Commercial diet	Giza White (3.2 kg)	Different		222	0-35	3493		100	31.3
Taboada *et al.*, 1994	L-lysine level:									
	a) 0.64%	New Zealand x Californian	2+	NSLS	14	0-30	5820	299	194	50.0
	b) 0.68%				14	0-30	6280	313	209	53.3
	c) 0.71%				14	0-30	6440	330	215	55.4
	d) 0.76%				14	0-30	6850	351	228	59.0
	e) 0.82%				14	0-30	6550	337	218	56.1
De Blas *et al.*, 1995	Lactation diets with different starch and fat content	New Zealand x Californian	2+	NSLS	16	0-30	5830	297	194	47.8
					16	0-30	5820	296	194	49.2
					16	0-30	6060	307	202	51.3
					16	0-30	5940	292	198	49.4
					16	0-30	5730	297	191	48.8
Xiccato *et al.*, 1995	Medium energy level	Hybrid (Provisal)	1	8	16	0-30	5130		171	42.3
	High energy level				17	0-30	5400		180	44.3
	High fat level				15	0-30	5730		191	47.3
De Blas *et al.*, 1998	Threonine level:									
	a) 0.54%	Hybrids (Hyplus)	2+	NSLS	16	0-30	5400	277	180	43.2
	b) 0.58%				16	0-30	5650	290	188	45.4
	c) 0.63%				16	0-30	5680	287	189	45.5
	d) 0.68%				16	0-30	5830	300	194	46.3
	e) 0.72%				16	0-30	5780	300	193	46.6

Continuation Table 1.

Pascual *et al.*, 1998	a) Starch rich lactation diet	Crossbreed (V x A rabbit does)	2	8	20	0-28	5348		191 236	50.7
	b) Soy oil rich lactation diet		2		18	0-28	6608			61.8
Pascual *et al.*, 1999a	a) Control reproduction diet	Crossbreed (V x A rabbit does)	2+	8 or 11	40	0-35	5540		158	40.2
	b) With added vegetable fat				40	0-35	6263		179	47.3
	c) With added animal fat				40	0-35	6365		182	46.0
Pascual *et al.*, 1999b	a) Low energy diet	Crossbreed (V x A rabbit does)	1-2+	± 8	21-46	0-35	5740-6090		164-174	44.5(3)
	b) Medium energy diet		1-2+		20-38	0-35	5430-5425		155-155	40.8(3)
	c) High energy diet		1-2+		18-49	0-35	5240-5495		150-157	40.3(3)
Xiccato *et al.*, 1999	Lactation diet	Hybrid (Provisal)	1	8	23	0-30	6150		205	52.6
Fraga *et al.*, 1989	Different reproduction diets	Californian x New Zealand		NSLS	22	0-28	5680		203	50.7
					17	0-28	4700		168	42.0
					17	0-28	5020		179	44.8
					17	0-28	4600		164	41.0
Pascual *et al.*, 2000b	a) Reproduction diet	Crossbreed (V x A rabbit does)	1+2	8	51	0-28	5376		192	50.5(3)
	b) Alfalfa based diet				52	0-28	4480		160	42.1(3)
	c) Alfalfa based + animal fat				49	0-28	4788		171	45.0(3)
Pascual *et al.*, 2002a	a) Animal fat enriched diet	Crossbreed (V x A rabbit does)	1	10	20	0-28	5087		182	49.7
	b) Vegetable oil enriched diet				21	0-28	5055		181	46.2
	c) Starch rich diet				23	0-28	4550		163	42.2
Pascual *et al.*, 2002b	a) Control reproduction diet	Crossbreed (V x A rabbit does)	1	8	22	0-28	4844		173	43.0
	b) High fibre followed by control diet				24	0-28	5404		193	48.8
Fortun-Lamothe and Sabater, 2003	Standard reproduction diet	Hybrid (INRA)	2+	10	50	0-21	5300	315	252	62.2
Khalil *et al.*, 2004	not defined	Gabali x Spanisch V line crosses (3.5 kg)	1-2+	NSLS	2141	0-28	4331		155	44.3(3)
Xiccato *et al.*, 2004	Lactation diet	Hybrid (Hyplus)	1; 2; 3	9	22	0-21	4242		202	53.6
					23	0-26	4964		191	52.3
					24	0-32	5774		180	49.8
Xiccato *et al.*, 2005	Lactation diet	Hybrid (Hyplus)	2+	10	31 23	0-21	5417		258	64.0
						0-25	6296		252	61.5
Zerrouki *et al.*, 2005	Reproduction diet	Kabylian (2.8 kg)	1-4+	2-8	299	0-21	2180	147	104	37.2(3)
Maertens *et al.*, 2005	a) Lactation diet	Hybrids (4.2 kg)	1-6	8-9	179	d3,5,9,			244	58.1(3)
	b) ω-3 lactation diet				205	12,16,19			236	56.2(3)
Maertens et al., 2006	Lactation diet	Hybrids	1 2	7.4	45	0-29	5900	256	203	50.2
				8.8	35	0-29	7600	317	262	61.8

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[1] NSLS: not standardised litter size; [2] Recalculated using the given average doe live weight (LW); [3] Recalculated using average strain LW if data were lacking

Table 2: Comparison of daily milk yield, fat and protein output at lactation peak between multiparous high productive rabbit does, cows and sows.

	Hybrid rabbit does[1]	Holstein cows[2]	Hybrid sows[3]
Live weight (kg)	4.2	650	230
Peak milk yield (kg)	0.320	47.5	8.9
Milk fat (g/100 g)	12.9	3.7	6.5
Milk protein (g/100 g)	12.3	2.84	5.1
Output/kg live weight (LW)			
Milk (g/d)	76	73	39
Fat (g/d)	9.8	2.7	2.5
Protein (g/d)	9.4	2.1	2.0
Output/kg metabolic weight ($LW^{0.75}$)			
Milk (g/d)	109	369	151
Fat (g/d)	14.1	13.7	9.8
Protein (g/d)	13.4	10.5	7.7

[1]Based on data of Table 1 and Table 5; [2]Kay *et al.* (2005); [3]Lauridsen and Danielsen (2004)

Average peak lactation of multiparous commercial hybrids is around 320 g/d (Fortun-Lamothe and Sabater, 2003; Xiccato *et al.*, 2005; Maertens *et al.*, 2006). Expressed per kg LW, peak yield is around 75 g/d and exceeds those of milk cows (Kay *et al.*, 2005) or sows (Lauridsen and Danielsen, 2004) (Table 2). When expressed per kg of metabolic weight, which is preferred by some scientists because of its physiological basis (but not really accurate because it is a production of a milk mass by a body mass), milk production of rabbit is still lower than that of productive Holstein cows or hybrid sows.(Table 2).

FACTORS INFLUENCING MILK YIELD

Lactation stage

Average lactation curves of multiparous hybrid does at different physiological status are presented in Figure 1 (adapted from Lebas, 1968; Szendrö *et al.*, 1985; Xiccato *et al.*, 1995; Maertens *et al.*, 2006).

The top lactation is situated on day 18-19 after kindling (Lebas, 1968; Maertens and De Groote, 1991; Fortun-Lamothe and Sabater, 2003; Casado *et al.*, 2006). However, in case of deficiencies in amino-acid supply (De Blas *et al.*, 1995; Taboada *et al.*, 1994) or when primiparous does are submitted to the intensive reproduction rhythm, the lactation peak is reached 2-3 days earlier (Maertens and De Groote, 1991; Xiccato *et al.*, 1995; Pascual *et al*, 1999b). Moreover, Lebas (1968) observed a breed difference; Fauve de Bourgogne does reached top lactation 3-4 days (day 21) later than Californian does.

The lactation curve of rabbits is asymmetric with a convex ascending and a concave descending period (Lebas, 1968). The principle component analysis executed by the same author (Lebas, 1976) using 975 lactation curves, revealed that 74.3% of the variability between lactation curves could be explained by 3 main factors. The most important was the total daily amount, followed by a factor expressing the asymmetry of the curve and finally a factor determining the amplitude of the curve, explaining respectively 58.3, 10.1 and 5.8% of the variability.

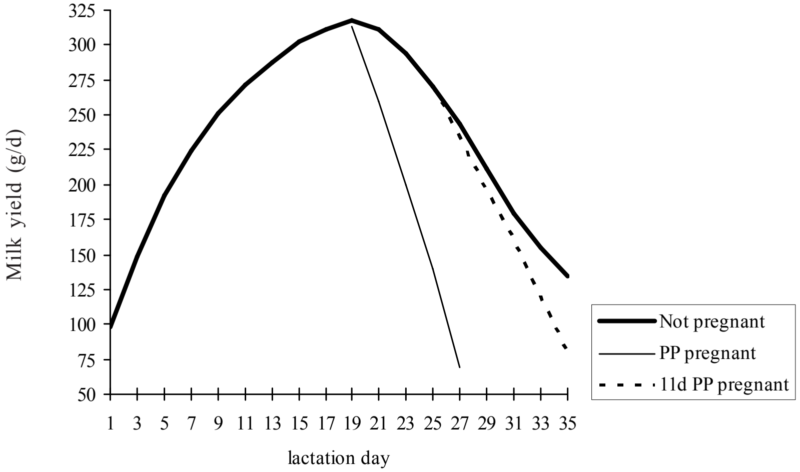

Figure 1. Lactation curve of multiparous does according to their physiological status.

Recently Casado *et al.* (2006) proposed different empirical models for the 28-day lactation curve, based on 550 lactation records. The beta-modified equation had a better fit suitability than the quadratic model and the advantage of a greater biological interpretation of its parameters. The following prediction model is proposed (Casado *et al.*, 2006):

Milk yield (g/day) = $k \times (\text{day}/30)^{a} \times (1- (\text{day}/30))^{b}$

where k regulates the height of the curve and a and b regulate the milk yield of the ascending and descending period, respectively. In the equation given by these authors, values for the parameters k, a and b are respectively 470.156; 0.489 and 0.371 (R^2=0.986, RSD=5.648).

There are only few data available concerning the weekly yields of does. When we recalculate the data of Lebas (1968) based on 143 lactations, on a 4 weeks lactation basis, 15.9, 24.4, 32.0 and 27.3% were produced in weeks 1 till 4, respectively. The analysis of Fernández-Carmona *et al.* (2004), based on 943 records obtained in their experimental farm, revealed a similar weekly partition of 18, 27, 30 and 25%, respectively for weeks 1-4. However, the partition between lactation weeks is strongly dependent if the doe is concurrent pregnant or not (Lebas, 1972; Xiccato *et al.*, 1995). According to Lebas (1968), if the litter weaning is delayed to 35 or 42 days post parturition, and if the doe is not pregnant, the milk production during the 5th or the 6th week represents 19.5% or 12.9% respectively of the 0-28 days milk production.

Gestation overlapping degree

The negative impact of the gestation overlapping on milk yield was already clearly demonstrated by Lebas (1972) and confirmed in several other studies. In practise only 3 reproductive rhythms are frequently used: intensive with complete overlapping, semi-intensive with overlapping from 11 days after parturition and a rhythm without significant overlapping. Does submitted at the intensive reproduction rhythm (mating or artificial insemination (AI), within 48 h after kindling) begin showing decreased milk production after 17 days (Maertens and De Groote, 1991; Fraga *et al.*, 1989; Xiccato *et al.*, 1995 and 2005; Pascual *et al.* 2002a) to 19 days (Lebas, 1972; Partridge *et al.*, 1986a; Szendrö *et al.*, 1985; Kustos *et al.*, 1996; Xiccato *et al.*, 1995) of lactation with a sharp and quite linear decrease during the last 10 days of pregnancy (Figure 1). However, in primiparous does that are concurrently pregnant shortly after parturition, this decline starts already at day 16-17 of the lactation (Maertens and De Groote, 1991; Xiccato *et al.*, 1995; Pascual *et al.*, 2002a). Moreover in some experiments peak yield was lower in does pregnant immediately after parturition compared to does not pregnant before day 11 post parturition (Szendrö *et al.*, 1985; Xiccato *et al.*, 1995).

The decrease in milk yield due to the gestation overlapping during the entire 28-day lactation period was between 19-22% according to the diet (Maertens and De Groote, 1988) and in line with the 20% decrease determined by Xiccato *et al.* (1995). Although the milk yield decrease between 21 and 28 days was 38% in the experiment of Pascual *et al.* (2002a), for the whole lactation period only a 9% lower yield was determined in post-partum pregnant females compared to does without gestation overlapping. When compared to females pregnant from day 9 post parturition off, total milk yield was 9% lower in females with complete gestation overlapping (Fraga *et al.*, 1989).

When females are submitted to the usual semi-intensive reproductive system with AI 11 days postpartum, the milk yield is only slightly decreased from day 25 off compared to females inseminated after weaning (Szendrö *et al.*, 1985; Casado *et al.*, 2006). The decrease is limited to around 25 g during the last days of a 28-day lactation period. If weaning is performed later, a sharp decline of the milk yield is observed with virtual dried up does after 35 days of lactation (Figure 1). However, when no concurrent gestation occurs, still a significant (70 g) yield was measured at day 38 (Szendrö *et al.*, 1985).

The decline in milk yield due to the gestation overlapping is a result of the pregnancy requirements that consistently increase with the exponential foetal development (Parigi-Bini and Xiccato, 1998), the increasing volume of the uterus reducing the voluntary feed intake and due to hormonal changes caused by the imminent kindling contrasting with those for lactation.

Number of suckling kits

In various studies it has been demonstrated that the number of suckling kits is the main factor affecting milk yield of does and by consequence the intake of the suckling kits (Lebas, 1969; Torres *et al.*, 1979; Partridge and Allen, 1982; McNitt and Lukefahr, 1990; Pascual *et al.*, 1996 and 1999a). In Figure 2, the relationship between the number of suckling kits and the milk yield is presented (Lebas, 1987). Based on these data, the following quadratic model was fitted between milk yield and number of suckling kits:

Milk yield (g/day) $=37.47x - 1.56N^2$ ($R^2=0.999$, RSD=3.77)

where N is the number of kits (range=5-11).

In the experiments of Partridge and Allen (1982), does allowed to nurse 8 kits had a 24.1% higher yield compared to does with only 4 kits. Mohamed and Szendrö (1992) found an increase with 3.3% and 5.4% of the milk yield with increasing litter sizes from 6 to 8 and 10 kits, respectively. Pascual *et al.*

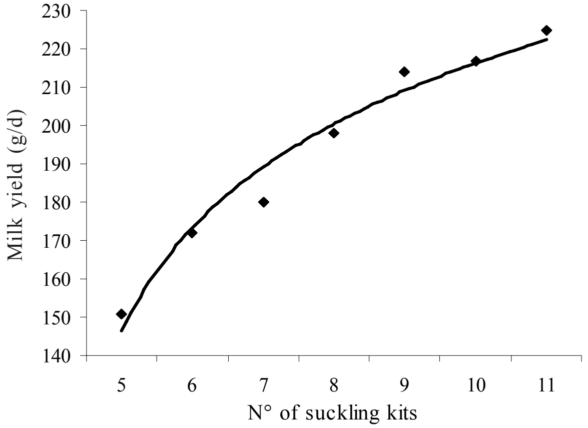

Figure 2. Relationship between the number of suckling kits and milk yield (Lebas, 1987).

(1996) determined even a difference of 32% in milk yield in favour of litters of more than 10 kits compared to litter sizes of 7-8 kits.

The effect of the number of suckling kits on milk yield was even clear if litter size was reduced from 10 to 4 kits at day 16 of the lactation (Fortun-Lamothe and Gidenne, 2000). Milk yield between 16 and 32 days of lactation dropped by 45% in does nursing only 4 kits. This indicates that the intake capacity of the kits, suckling only once a day, is limited because in the experiments of Szendrö *et al.* (2002) kits that nursed in morning and evening by 2 different does had a 89% higher intake compared to single nursed kits.

However, not only an increasing number of suckling kits favours milk yield but also an increasing litter weight at birth increases milk production as consequence of the uterine induction. Vásquez Martínez *et al.* (1999) studied the interaction between both factors using a complete kit exchange at birth and standardized litter sizes of 7, 8 or 9 suckling kits (Figure 3). Does with low litter weight (<450 g) showed no increase in milk yield with increasing number of suckling kits. On the contrary, does with medium and high litter weight at birth (>450 g) had a significant higher yield by assigning additional kits. Due to the limited number of kits born or suckling kits in some non selected lines or populations, maximum milk production can therefore not be reached as demonstrated by Bolet *et al.* (1996). However, Zerroucki *et al.* (2005) demonstrate in a local population that maximum does milk production capacity can be reached for a number of kits lower than the maximum litter size naturally observed in this population: in theses author's observations milk production increases regularly with the suckling kits number until a maximum (7 in the present case) above which a plateau production is observed whatever the kits number (7, 8 or 9).

Both for experimental purposes as under commercial field conditions, due to the common practise of cross fostering between does littering on the same day, the effect of litter size on milk yield is minimised. Nevertheless when comparing does milk production published in the literature, attention must be paid to the number of kits to which the litter size was adjusted in each case.

Parity order

The milk yield of does has a curvilinear relationship with parity (Khalil, 1994) and increases until the third lactation and stabilizes thereafter (Casado *et al.*, 2006). McNitt and Lukefahr (1990) reported even an increase till the 7th litter; however because less productive females were progressively culled out, their selection policy has favoured the milk yield with increasing parity order.

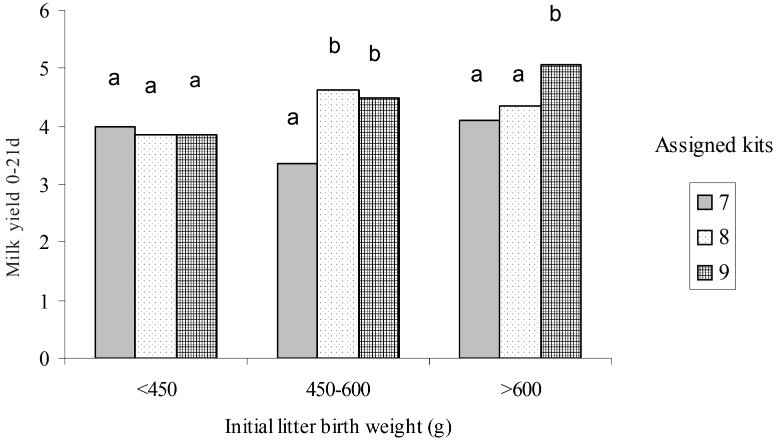

Figure 3. Effect of number of assigned kits on the milk yield of does dependent of the initial litter weight at birth (Vásquez Martínez *et al.*, 1999).

The highest difference is found between the 1st and 2nd lactation. Even at standardised litter size, Xiccato *et al.* (2004) reported an increase of 10% and 8% of the milk yield during lactation 2 and 3, respectively. Pascual *et al.* (1999b) found a much more modest increase between primiparous and multiparous does, on average only 3.6%. This difference was more pronounced (6.3%) when using a low energy diet. Based on the litter weight at 3 weeks, Vicente and Garcia-Ximénez (1992) report a difference of 14% in favour of multiparous does. Maertens *et al.* (2006) determined a 19.9% higher yield in lactation 2 compared to lactation 1 even after a correction for the difference in litter size. Part of this great difference could be explained by the early first insemination (15-16 weeks) compared to the aforementioned studies.

The milk production increase is a response to the higher live weight and feed intake capacity of multiparous does (Pascual *et al.*, 1999b; Xiccato *et al.*, 2004). Parigi-Bini and Xiccato (1998) mentioned an increase of the voluntary feed intake of 10-20% from the first to the 2nd lactation and 7-15% from the 2nd to the 3rd lactation. Moreover, primarily primiparous does have to share the energy between the demands for milk (and eventually concurrent pregnancy) with those for body accretion because they have not yet reached their adult weight (Parigi-Bini and Xiccato, 1998).

Number of nipples

A majority of does has 8 to 10 productive teats with independent mammary gland, although there is a variation between 6 and 12 (Szendrö and Holdas, 1984; Fleischhauer *et al.*, 1985). Nevertheless in lines selected for litter size, teats number was increased as a passive answer to selection, and females with 10 nipples may become the most numerous: 37% to 51% in 2 selected lines *vs* 27% in the control line (Rochambeau *et al*, 1988). Females with less than 8 teats have a significant lower milk yield than those with 8 or more teats (Fleischhauer *et al.*, 1985). However, in this study, females with 6 teats were obtained after surgically removing of 2 mammary glands. In the same study, females having more than 8 teats showed a slightly higher milk yield (+2.2%). Szendrö and Holdas (1984) as did not found significant differences in weight gain of kits till 21days of age between does having 8, 9 or 10 productive teats, although the highest value was obtained for does with 10. However Rochambeau *et al.* (1988) considering only litters with more than 10 kits born alive, *i.e.* with kits number exceeding that of nipples, observed higher litter weaning weights (28 days) for does having 10 nipples compared to 8 (+13.2%), which implies a higher milk production.

Later on, limited attention has been putted on this factor. Only Mohamed and Szendrö (1992) compared females with 8 and 10 nipples and determined a 4.8% higher milk yield in does having 10 nipples.

According to the observations of Petersen *et al.* (1989), milk secretion is higher in the middle pairs of teats than in pairs 1 and 4.

Genotype

In the intensive rabbit meat production, pure breeds are still seldom used and replaced by specialised strains or lines selected for a higher litter size and therefore indirectly for a higher milk yield (Garreau *et al.*, 2004). The populations originating these actual selected strains or lines belonged near exclusively to breeds of medium size, as mainly the New Zealand White or/and Californian. Usually, the females on commercial rabbit farms are obtained by crossbreeding of these strains or lines to gain the heterosis effect. These females are named crossbreds or “commercial hybrids”.

Literature data comparing milk yield of different breeds are scarce. Lukefahr *et al.* (1983) demonstrated that New Zealand White does are superior (+ 30%) to Californian does and that crossbred rabbits of both breeds are superior than the pure breeds. However, in another study, the same team determined a comparable milk production for the 4 breeds tested (Calfornian, New Zealand White, Palomino and

White Satin) (McNitt and Lukefahr, 1990), which indicate that the genetic background of the particular populations is perhaps more important than the breed itself.

Vicente and Garcia-Ximénez (1992) found significant higher litter weights after the 2nd and 3rd lactation week in 2 synthetic lines compared with purebred New Zealand White and Californian. Native breeds as Giza White (Khalil, 1994) or Kabylian rabbit population (Zerrouki *et al.*, 2005) have a modest yield (average over the whole lactation period of 100 and 104 g/d, respectively) compared to the actual production level of over 200 g/d for commercial parental does (Fortun-Lamothe and Sabater, 2003; Xiccato *et al.*, 2005; Casado *et al.*, 2006). However, these native breeds have a low adult weight. When their milk yield is expressed per kg LW, the difference with medium-size breeds or hybrids is less pronounced (Table 1). Moreover, comparing milk yield between different experiments (and strains) remains difficult because especially for these native breeds temperature conditions were not favourable. Under favourable housing conditions, recent reported data of multiparous females of hybrid dam lines demonstrate an average daily yield of 250-260 g during the 4-weeks lactation period (Xiccato *et al.*, 2005; Maertens *et al.*, 2006).

Even in the same population a large individual variability has been observed. Fernández-Carmona *et al.* (2004) used the records of 943 lactations of crossbreds from 2 lines selected for litter size (V x A) and milk yield ranged between 46 and 306 g/d during the 28 days lactation period. Also Khalil *et al.* (2004) obtained, using a large data set, a variation coefficient of 38% for milk yield (0-21 d). Moreover, heritability of milk production is low and amounts only 0.14 (Lukefahr *et al.*, 1996) or 0.18 (Khalil *et al.*, 2004) for the cumulative 1 to 21 days of lactation. However, under current field conditions, litters are equalised at parturition and by consequence milk yield is much more homogeneous with the exclusion of the initial litter size effect (Casado *et al.*, 2006).

Finally, in a study using transgenic does (for obtaining the presence of human clotting factor VIII, hFVIII in their milk) milk yield was not significantly different from non-transgenic does descending from the same founder females (Rafay *et al.*, 2004). However, as the authors pointed out, it is necessary to verify these preliminary results on a larger set of animals before to generalize this observation for all transgenic does.

Temperature

High environmental temperatures have a detrimental effect on milk yield of does. Several studies have clearly demonstrated that the effect of high temperature can be explained by the drop in feed intake which is in the same range as the drop in milk yield (Rafai and Papp, 1984; Maertens and De Groote, 1990; Pascual *et al.*, 1996; Szendrö *et al.*, 1999a).

Under constant ambient temperatures, Rafai and Papp (1984) found a decrease of 7.7 g/d with each centigrade of temperature rise above 20°C. Moreover, the relative decrease is depending from the lactation stage, being largest in the week with the highest yield (3rd week) (Rafai and Papp, 1984; Pascual *et al.*, 1996; Szendrö *et al.*, 1999a). The detrimental effect of high temperature on milk yield was also clearly observed by Fernández-Carmona *et al.* (2000). When housed in a climatic chamber at 30°C, milk yield dropped with 30-40% according to diet compared with housing under conventional circumstances (Pascual *et al.*, 2000b).

In the study of Szendrö *et al.* (1999a) the heat stress was not yet pronounced on milk yield when housed at 23°C (Figure 4). However, at 30°C, average daily milk yield was reduced with 29% (114 g *vs.* 161 g/d).

Under natural housing conditions, with varying temperature between day and night, heat stress is less pronounced and seems to be linked with the minimal temperature during the active feeding

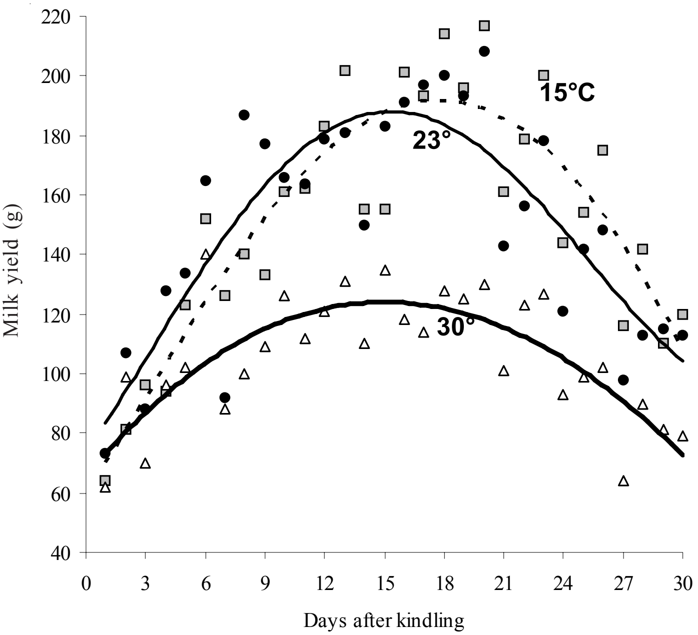

Figure 4. Effect of temperature (▫ 15°C ◆ 23°C △ 30°C) on milk yield of does (Szendrö *et al.*, 1999a).

period (Maertens & De Groote, 1990). However, when the minimum temperature was above 24°C total lactation yield was reduced with 17.3% compared to conditions below 24°C (Pascual *et al.*, 1996).

Rearing, feeding, body weight and body condition

The litter size in which does were raised in before weaning did not influence their later milk yield (Rommers *et al.*, 2001). However, it has been shown that the feeding regime during the rearing period has an influence on the subsequent litter weight (milk yield) of primiparous does and even in multiparous does. Primiparous does fed restrictively during rearing and *ad libitum* later had an increased litter weight at 16 days (Rommers *et al.*, 2004) or 21 days (Gyovai *et al.*, 2004) compared to always *ad libitum* fed young does. The significant increased feed intake during the subsequent lactation observed in previously restricted reared does seems responsible for this effect in primiparous does (Rommers *et al.*, 2004). However, in the 2 following lactations an effect on the feed intake was not more clear in this study indicating that some other factors could be involved, such as higher body weight and/or appropriate body condition. Gyovai *et al.* (2004) observed higher body weight (at 1st kindling and maintaining during the successive cycles) in does reared under feed restriction. In contrast, Rommers *et al.* (2004) reported higher body weight in *ad libitum* reared does but their lower milk yield fall essentially on the very heavy young does (>4,5 kg at first insemination at 17.5 weeks of age), perhaps excessively fatty (Rommers, 2004). In earlier experiments, Coudert and Lebas (1985) did not observe any significant effect of feed restriction during rearing on does LW measured 7 days after the kindling in the 3 first lactations. Thus some factors other than rearing conditions seem to be as well important for milk production or does body weight as the feed restriction itself.

Complementarily, in *ad libitum* reared does inseminated at early age (14.5 weeks), small young does (<3.5 kg, averaging 3.18 kg at insemination) had significant lower litter weight at 16 days (milk yield) than heavier, in their two first lactations (Rommers *et al.*, 2002).

Body weight of different dam lines did not have a significant effect on milk yield although their weight differed by 10% at their first parturition (Fortun-Lamothe and Bolet, 1998). However, Pascual *et al.* (2002a) observed that does presenting a better body condition at *partum* showed higher milk yield. Perirenal fat thickness at parturition used as indicator for body condition revealed to be positively correlated (r=+0.36) with the subsequent milk yield. However, the change of the body condition during the lactation is negatively correlated with milk yield (r=–0.24 and –0.61, Fortun-Lamothe and Lebas, 1996 and Pascual *et al.*, 2002a, respectively). This shows that does exhibiting higher body-fat losses during the lactation have also a higher milk yield. This relation could be reinforced or reduced according to diet's composition as demonstrated by Pascual *et al.* (2003) in their review.

MILK COMPOSITION

Major components

The average chemical composition of rabbit milk is presented in Table 3 and Figure 5. In total 20 original publications were found with determined data of the macro nutrient composition from does fed a standard diet. Data referring to experimental diets with high fat content were excluded from the dataset used for this review. Literature data are grouped per lactation week.

The lactose content of doe milk was determined only in few experiments because of the minor importance due the low content (<2 g/100 g) especially at a later stage of the lactation (Lebas, 1971). Moreover, in several experiments the content was calculated by difference with the other nutrients. As a result, the variation coefficient is high for lactose (Table 2).

There exists little information concerning the composition of the colostrum of does (Lebas, 1971; El-Sayiad *et al.*, 1994; Christ *et al.*, 1996). Based on these data the colostrum DM is higher than milk DM (33 *vs.* 30 g/100 g) due to a higher protein content and fat content. However, this composition has to be taken with caution because the samples were collected on the day after kindling. The real colostrum is already consumed by the kits during the initial suckling which takes place during the parturition (Hudson *et al.*, 2000).

Based on the overview of literature data (Figure 5), the composition of rabbit milk is quite stable during the 2nd and 3rd week of the lactation, except for the protein content which shows a decreasing trend (from 12.8 till 11.9 g/100 g) with increasing daily milk yield. This quite constant composition during the 3 first weeks of the lactation (with exception of the first days) is remarkable because milk yield increases in that period with a factor of 2 till 3.

Already in week 4, the DM content is on average 2.6 points (+ 8.7%) higher and the fat and protein content increase by 1.1 g/100 g (+ 8-9 %) compared to the average of the first 3 weeks (Table 3). In week 5, a strong concentration of the milk is observed which results in a DM, fat and energy content of 36.9 g/100 g, 18.7 g/100 g and 10.5 MJ/kg, respectively. Ash and protein increase more slowly in the final week of the lactation.

The changes in composition in the later stage of the lactation period are closely related with the decrease in milk yield (Lebas, 1971; Partridge at al., 1986a). The dramatic reduction of the lactose content is even higher than the corresponding drop in milk yield (Lebas, 1971). In does immediately pregnant after parturition, dry matter, protein and fat increases one week earlier than in does not concurrently pregnant (Kustos *et al.*, 1996). An interruption of the lactation by omission of one suckling leads to changes in milk composition similar to those observed with declining milk yield (Szendrö *et al.*, 1999b). However, some days later the composition returns to levels approaching the original values.

Table 3: Chemical composition of rabbit milk depending of the lactation stage

	Lactation week	Mean	Range	CV(%)	n[1]
Dry matter (g/100 g)	Colostrum	32.6	31.4-33.7	5	2
	1	29.8	25.6-31.4	9	5
	2	30.0	25.7-33.1	9	9
	3	29.5	25.8-33.2	7	19
	4	32.4	29.8-33.7	5	6
	5	37.7	34.2-42.1	7	6
Ash (g/100 g)	Colostrum	1.8	1.7-2.0	18	2
	1	1.9	1.8-2.0	6	3
	2	1.9	1.3-2.2	16	7
	3	2.2	1.5-2.6	13	13
	4	2.4	1.8-2.6	15	5
	5	2.4	2.0-2.8	12	5
Protein (g/100 g)	Colostrum	14.7	13.5-15.9	12	2
	1	12.8	11.2-14.8	11	6
	2	12.2	10.1-14.1	10	11
	3	11.9	9.9-14.3	10	20
	4	13.4	10.6-15.5	12	7
	5	14.1	12.4-16.9	11	6
Fat (g/100 g)	Colostrum	16.3	13.7-20.4	22	3
	1	12.7	9.1-16.1	20	5
	2	13.1	8.9-17.0	19	9
	3	12.9	10.0-16.6	16	19
	4	14.0	12.2-15.7	11	5
	5	18.9	16.9-21.4	9	6
Lactose (g/100 g)	Colostrum	1.9	1.6-2.1	18	2
	1	1.6	1.0-2.0	36	3
	2	1.4	1.0-1.9	33	3
	3	1.9	0.3-3.2	50	8
	4	1.8	0.8-2.6	51	3
	5	1.0	0.2-1.8	9	2
Energy (MJ/kg)	Colostrum	9.3	-	-	1
	1	8.4	8.4-8.4	0.1	3
	2	8.5	7.5-9.6	10	6
	3	8.3	7.1-9.2	7	9
	4	9.2	8.5-10.0	8	3
	5	10.5	9.8-11.6	9	3

[1] n= number of literature references used to calculate the values in table.

References: Castellini *et al.* (2004), Christ *et al.* (1996), Cole *et al.* (1983), El-Sayiad *et al.* (1994), Fraga *et al.* (1989), Kowalska and Bielanski (2004), Kustos *et al.* (1999), Lebas (1971), Lebas *et al.* (1996), Maertens *et al.* (1994, 2005 and 2006), Partridge and Allan (1982), Partridge *et al.* (1983, 1986a and 1986b), Pascual *et al.* (1996, 1999a and 2000a) and Xiccato *et al.* (1999)

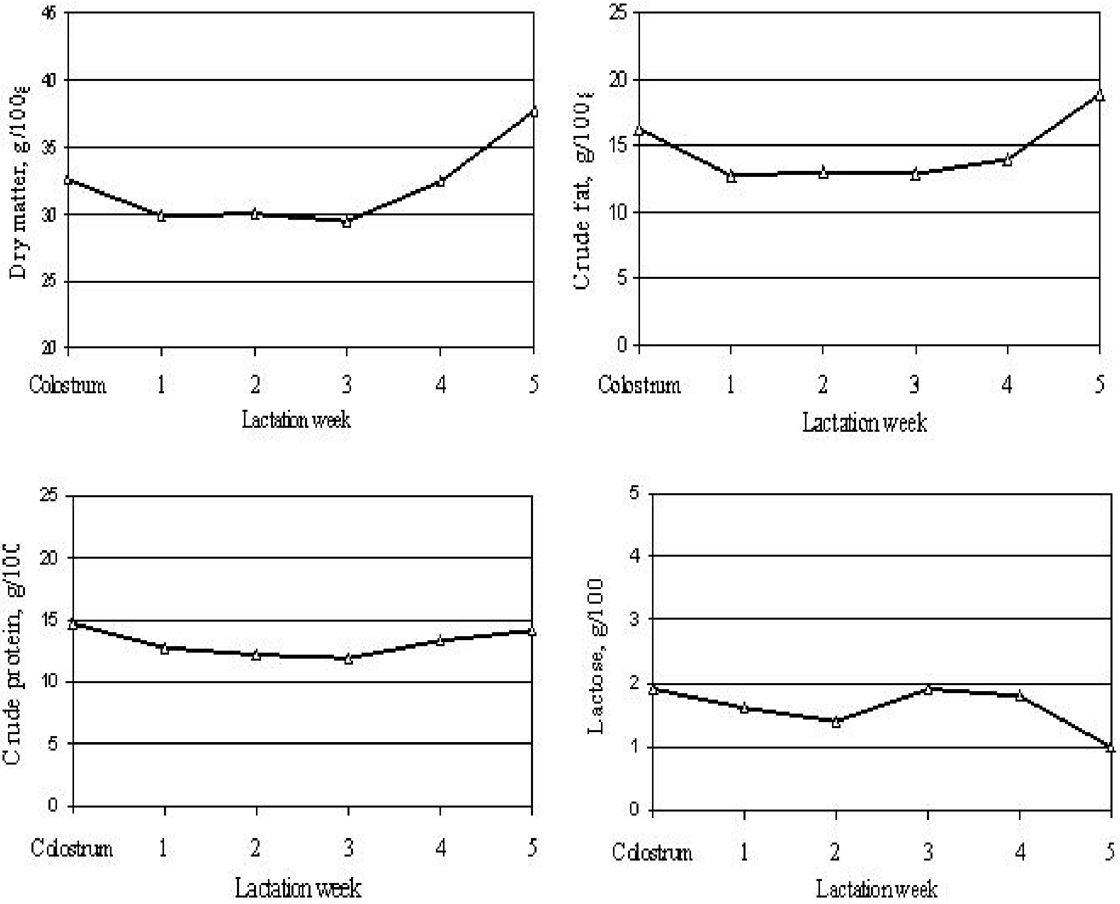

Figure 5. Milk composition changes during the lactation period (literature compilation, see Table 3).

Milk composition did not vary significantly between New Zealand White and Duch rabbits (Cowie, 1968) or between commercial hybrids (Maertens *et al.*, 2006). However, El Sayiad *et al*, (1994) found significant higher crude protein levels in Californian does (12.02 g/100 g) than in New Zealand females (11.02 g/100 g) The effect of temperature or the feeding level seems not very outspoken. Only at 30°C a trend to decreasing fat, protein and especially lactose content was observed (Kustos *et al.*, 1999).

In general, rabbit milk can be characterised as a very protein and fat rich milk (12.3 and 12.9 g/100 g, respectively) but with low lactose content (1.7 g/100 g). Compared to cow and sow milk, rabbit milk is respectively 2 and 3 times more concentrated in fat and protein (Table 5). The lactose content is only one third of the 2 other species. Remarkable is also the high energy content of rabbit milk (8.4 MJ/kg) which explains the rapid growth of the kits (LW x 6 after 3 weeks).

At peak lactation, fat and protein output per kg LW are 3 to 4 times higher in rabbits compared with cows and sows (Table 2). This explains why rabbits are searched as bioreactor for the production of recombinant proteins. The fat production per kg metabolic weight at peak lactation equals (14.1 g/kg$^{0.75}$) that of high productive Holstein cows and exceeds that of hybrid sows (Table 2). The protein production (13.4 g/kg$^{0.75}$) exceeds largely those of both cows and sows.

Milk lipids

With an average lipid content of 12.9 g/100 g (Table 5), it is clear that the greatest energy source quantitatively for the suckling kit is the fat component. The milk lipids are composed mainly of triglycerides with small proportions of di- and monoglycerides, phospholipids, cholesterol, fat-soluble vitamins and free fatty acids (Smith *et al.*, 1968; Perret *et al.*, 1977; Demarne *et al.*, 1978; Christie, 1985). Triglycerides of acyl carbon number less than 42 made up about 75% of the total glycerides in rabbit milk (Smith *et al.*, 1968).

The fatty acid (FA) profile of rabbit milk is characterized by a very high content of short-chain FA, mainly caprilic ($C_{8:0}$), capric acid ($C_{10:0}$) and, to a smaller extent, lauric acid ($C_{12:0}$), which represent 50% of the total FA (Table 4). Consequently, milk fat of rabbits differ very markedly from the carcass depot fats. On average 70% of the milk FA are saturated (SFA), 13% monounsaturated (MUFA) and 16% polyunsaturated FA (PUFA). Nevertheless it must be pointed out that in the suckling kit, the fate of the saturated FA is very different according to the carbon chain length: short chained FA (70.0% of saturated FA) are almost exclusively used as energy source (or basis for length elongation) and only the longer ones are transferred in the body fat (Ouhayoun *et al*, 1985).

The milk contains nearly equal proportions of oleic and linoleic acid, and some ù-3 linolenic acid. Concerning the longer ω-3 FA searched for their potential as beneficial for health, small amounts of $C_{20:5,\omega\text{-}3}$ (EPA: 0.04%) and $C_{22:6,\omega\text{-}3}$ (DHA: 0.06%) are mentioned by Castellini *et al.* (2004) and Kowalska and Bielanski (2004). Moreover, these last authors found also a small amount of conjugated linoleic acid (CLA) (0.08%). The proportions of these polyunsaturated FA are mainly dependent of the lactation diet.

Fatty acids in milk are derived from blood triglycerides and *de novo* synthesis in the mammary gland. Short-chain FA are synthesized within the mammary gland rather than by FA uptake from circulating blood or by oxidation of long-chain FA (Carey and Dils, 1972). Acetate is an important precursor of both $C_{8:0}$ and $C_{10:0}$ (Jones and Parker, 1978).

Diet has a very strong influence on the FA profile of rabbit milk especially on the medium and long-chain FA (see the review of Pascual *et al.*, 2003), but only little information exists concerning the non-nutritional factors affecting FA composition. Perret *et al.* (1977) determined an increase of short triglycerides (C<36) at the expense of long triglycerides (C>46) after the 10th day of lactation and the same effect but less pronounced for FA (Hall, 1971). Significant changes of the FA profile during the lactation stage were confirmed by Pascual *et al.* (1999a). Short-chain FA and by consequence SFA showed a significant increase at the 21st and 28th day. The trend for medium-chain FA was opposite, showing the highest proportions on day 7 of the lactation except for $C_{15:0}$ and $C_{17:0}$ that remained constant during lactation (Pascual *et al.*, 1999a; Christ *et al.*, 1996).

The FA profile of rabbit milk is strikingly different from cow and sow milk (Table 5). Data refer to a standard feeding of these species because especially fat-enriched diets manipulate to a large extend the FA profile (Pascual at al., 2003). The high concentration of short-chain FA ($C_{6:0}$ to $C_{12:0}$) results in a more saturated milk compared to especially sow milk. On the contrary, medium-chain FA ($C_{14:0}$ to $C_{17:1}$) are nearly three times as high in cow and sow milk. Due to the low content of $C_{18:1}$, rabbit milk has a rather low MUFA content MUFA (12.8%) compared to cows (30.1%) and sows (41.5%). The PUFA content is comparable with sows and much higher than in cow milk. The ratio ω-6/ω-3 FA (around 4) is intermediate between sows and cow milk.

The FA profile is also remarkable different from the hare or rodents fed the same diet. The concentration of short-chain FA are 2.1 times lower in hare milk compared to rabbit milk (Demarne *et al.*, 1978).

Table 4: Fatty acid composition of rabbit milk.

	Mean	CV(%)	n[1]
Fatty acids (% of total fatty acids)			
$C_{4:0}$; $C_{5:0}$; $C_{7:0}$	Traces	-	1
$C_{6:0}$	0.4	20	3
$C_{8:0}$	26.3	27	6
$C_{10:0}$	20.1	21	6
$C_{12:0}$	2.9	30	5
$C_{14:0}$	1.6	39	6
$C_{15:0}$	0.8	79	3
$C_{16:0}$	12.8	23	6
$C_{17:0}$	0.7	55	3
$C_{18:0}$	2.9	11	6
$C_{20:0}$; $C_{22:0}$	Traces	-	2
Total saturated fatty acids (%)	70.4	14	7
$C_{14:1}$;$C_{17:1}$; $C_{20:1}$	Traces	-	2
$C_{16:1}$	1.5	59	6
$C_{18:1}$	11.3	18	6
Total monounsaturated fatty acids (%)	12.8	17.6	7
$C_{18:2}$	12.8	37	7
$C_{18:3}$	2.5	36	7
CLA	0.08	-	1
$C_{20:4}$	0.5	49	2
EPA ($C_{20:5}$ ω-3)	0.04	47	2
DHA ($C_{22:6}$ ω-3)	0.06	64	2
Total polyunsaturated fatty acids (%)	15.6	35	7

[1] n= number of literature references used to calculate the values in table.

References: Castellini *et al.* (2004), Christ *et al.* (1996), Fraga *et al.* (1989), Kowalska and Bielanski (2004), Lebas *et al*. (1996), Maertens *et al.* (2005), Pascual *et al.* (1999a).

Short-chain FA are even absent in guinea pig milk, and to a much lesser extent are present in mouse (one third of rabbit) or rat milk (half of rabbit) (Smith *et al.*, 1968).

Rabbits are known for their sensitivity to dietary-induced hypercholesterolemia but their milk cholesterol levels can be normally maintained unless the maternal plasma cholesterol concentration is extremely elevated (Whatley *et al.*, 1981). Milk cholesterol concentration increases from 28.0 (day 5) till 89.7 mg/100 ml (day 35 of the lactation) in close correlation with the milk triglycerides and drying up of the females (Whatley *et al.*, 1981). In the mammary gland the cholesterol excretion in milk is regulated but without local synthesis: nearly all the milk cholesterol derived from the blood plasma cholesterol (Connor and Lin, 1967).

Milk protein composition

Rabbit milk proteins have been studied intensively in view of biomedical research for e.g. the production of recombinant proteins in the milk or serum. A recent successfully example is the human α-glucosidase produced in the milk of transgenic rabbits to treat the Pompe´s disease (Van den Hout *et al.*, 2001). However, in this review the information will be limited to the composition of the main constituents, referring for specific information to other reviews (Fan and Watanabe, 2003; Bõsze and Houdebine, 2006).

Table 5: Comparative composition of milk from rabbits, cows and sows.

		Rabbit does[1]	Cows[2]	Sows[3]
Dry matter (g/100 g)		29.8	12.5 - 13.5	17.9
Protein (g/100 g)		12.3	3.0 - 4.0	5.1
Fat (g/100 g)		12.9	3.5 - 5.0	6.5
Lactose (g/100 g)		1.7	4.5 - 5.0	5.7
Energy (MJ/kg)		8.4	2.7- 3.2	4.5
Fatty acids (% of total FA)	$C_{6:0}$	0.4	1.5	n.r.
	$C_{8:0}$	26.3	0.9	n.r.
	$C_{10:0}$	20.1	2.0	0.4
	$C_{12:0}$	2.9	2.4	0.5
	$C_{14:0}$	1.6	14.3	5.6
	$C_{16:0}$	12.8	24.4	29.4
	$C_{16:1}$	1.5	1.7	13.7
	$C_{18:0}$	2.9	11.9	6.3
	$C_{18:1}$	11.3	27.5	27.6
	$C_{18:2}$	12.8	1.6	13.3
	CLA	0.08	1.26	n.r.
	$C_{18:3}$	2.5	0.71	1.4
	$C_{20:1}$	n.r.[4]	n.r.	0.2
	$C_{20:4}$	0.5	0.04	0.09
	$C_{20:5}$ (EPA)	0.04	0.01	0.16
	$C_{22:6}$ (DHA)	0.06	0.04	0.20
	Other	4.2	6.3	1.2
	Total SFA	70.4	60.0	42.2
	Total MUFA	12.8	30.1	41.5
	Total PUFA	15.6	3.6	16.3
	Ratio ω-6/ω-3	4.1	2-3	7.2

[1]Average composition of lactation weeks 1-3 (Table 2). [2]FA adapted from Rego *et al.* 2005 (Control diet, pasture). [3]Lauridsen and Danielsen, 2004 (Control diet). [4]Not reported.

The protein-rich milk of rabbits provides primarily the amino acids essential for tissue growth and maintenance but also to continue a certain degree of immune protection through the presence of specific whey proteins. Information concerning the amino acids composition is given in Table 6. However, the data of rabbit milk have to be taken with caution because the total sum of amino acids expressed per 100 g amino acids is 118.6 g (recalculated data from Uribe *et al.*, 1980) or only 76.9 g (Kustos *et al.*, 1999).

Rabbit milk proteins as for other mammals, are grouped in two main types: caseins which precipitate in the isoelectric conditions (pH 4.6) and represent about 70% of the total milk proteins and whey proteins which do not precipitated in these conditions (Dayal *et al*, 1982). After numerous attempts to identify the various types of casein present in rabbit milk (Allais and Jollès, 1970; Majumder and Ganguli, 1970; Testud and Ribadeau-Dumas, 1973; Al Sarraj *et al.*, 1978; Dayal *et al.*, 1982; Baranyi *et al.*, 1995; Grabowski *et al*, 1991, Virag *et al.*, 1996), 4 types can be clearly distinguished now: α_{S1}-casein, α_{S2}-casein, α-casein and κ-casein. Total of caseins represent about 90 g/l with a specific contribution for example of 45 g/l of β-casein and 16 g/l of α_{S1}-casein (Grabowski *et al*, 1991). Virag *et* *al.* (1996) mentioned a micelles size of skimmed rabbit milk varying from 210 to 230 μm in relation with the 8 patterns of α_{S2}-caseins observed in the milk of New Zealand White does. One of the functions of the κ-casein is the formation, stabilisation and aggregation of the micelles (Gerencsér *et al*, 2002). In addition some hydrolysed fractions of α_{S1} and β-casein have a clear antibacterial activity which most probably participate in the protection of digestive tract of suckling kits (Baranyi *et al.*, 2003).

The main types of whey proteins are α-lactalbumin, tranferrin, serum albumin, whey acidic protein (WAP) and immunoglobulins (Baranyi *et al*; 1995). Transferrin is present at 17 to 23 g/l (Jordan and Morgan, 1970) and is an iron binding protein identical to the serum transferrin (Baker *et al.*, 1968) which has no immunological reaction with the classical lactoferrin (Lyster, 1967). This specificity explains for example why Masson and Hermann (1971) failed to find lactoferrin in the rabbit milk in an extensive study of lactoferrin in different species conducted with an immuno-methodology. Despite its identity with serum transferrin, the milk transferrin is almost exclusively synthesised and secreted in the mammary gland (Jordan and Morgan, 1970). This protein has an *in vitro* antibacterial activity against *Escherichia coli*, but it is not clear if this function is still active *in vivo* in the kits digestive tract (Baker *et al.*, 1968).

As previously mentioned, other whey main proteins detected in rabbit milk are serum albumins (4-5 g/l), different lactalbumins, WAP (15 g/l) (Jordan and Morgan, 1970; Grabowski *et al*, 1991; Baranyi *et al.*, 1995) and different immunoglobulins but no protein resembling to the cow β-lactoglobulin (the main whey protein in cow milk) was detected (Lyster, 1967). Nevertheless this affirmation disagrees with the results of Stambolova and Gachev (1972) which have identified a rabbit whey protein with an electrophoretic pattern identical to that of the bovine β-lactoglobulin.

The γ-globulin concentration is around 10 g/l and increases in milk during lactation (Jordan and Morgan, 1970; Maertens *et al.*, 1994). According to Berthon and Salmon (1993), the specific immunoglobulins concentration decreases from colostrum to milk. They are represented mainly by the IgG form, which represents 95.2% of the total immunoglobulins of colostrum (30 g/l) and 98% of milk ones (5 g/l). The IgA represent a higher proportion in colostrum (4.7%) than in milk (2.0%). In addition the presence of few IgM can be noticed in colostrum (0.1% of the total) but only traces are present in milk. During γ-globulin secretion in the mammary gland, the initial serum IgA is modified and T-Chains are added (Asofsky and Small, 1967). The immunoglobulins present in the first suckled colostrum seem to be transferred to the kit serum (Goszinska *et al*, 1969). But later, absorption

Table 6: Amino acid composition of rabbit and sow milk.

	g/100 g amino acid			g/100 g amino acid	
Amino acid	Rabbit[1]	Sow[2]	Amino acid	Rabbit[1]	Sow[2]
Lysine	9.0-7.6	7.5	Valine	8.0-5.9	4.7
Methionine	3.0-1.6	1.7	Tryptophan	1.3 -3	1.4
Cysteine	-[3]	1.5	Arginine	6.4-4.8	5.2
Histidine	5.3-2.3	2.4	Proline	3.2 -3	11.3
Phenylalanine	4.9-3.3	3.9	Glycine	1.5-3.7	2.8
Tyrosine	6.2-2.6	4.2	Glutamic acid	25.0-12.7	21.6
Threonine	7.3-4.1	3.9	Aspartic acid	8.1-4.0	7.9
Isoleucine	4.2-3.6	3.8	Serine	5.6-6.1	5.2
Leucine	11.9-8.9	8.8	Alanine	7.7-5.7	3.2

[1] Left values from Uribe *et al.* (1980); right values from Kustos *et al.* (1999). [2] According to Darragh and Moughan (1998). [3] Traces for Uribe *et al.* (1980) and not determined by Kustos *et al.* (1999).

throught the intestinal epithelial cells of the kits in direction of blood is generally stopped inside the enterocytes (Krahenbuhl and Campiche, 1969).

The immunisation of does against specific agents such as *E. coli* or *Vibrio cholerae* induce the presence of specific IgA antibodies in the milk during the whole lactation (Yoshiyama and Brown, 1987; Milon and Camguilhem, 1989). These IgA can be immediately locally active in the kit digestive tract. But their short half-life (3 days) makes them ineffective after weaning (Milon and Camguilhem, 1989).

Also prolactin and growth hormone binding proteins have been identified in rabbit milk (Postel-Vinay *et al.*, 1991) as well as thyroid hormones (Slebodzinski and Gawecka, 1983). In addition a lot of active enzymes are detectable in rabbit milk (Hellung-Larsen, 1968).

Mineral content

The ash content of rabbit milk (Table 3) increases from about 1.8% during the first weeks of the lactation till 2.4% in the 4th and 5th week of the lactation. This increase can partly be ascribed to the drying up of the does and as consequence of the higher dry matter content with declining milk yield. Rabbit milk is rich in calcium although its concentration varies according to the source (Table 7). Also sodium and potassium concentration is high compared to sow milk (Darragh and Moughan, 1998). Since lactose and sodium are two of the main constituents concerned in maintaining the constancy of the osmotic properties of milk it is not surprising that the low level of lactose in rabbit milk is compensated by a sodium concentration higher than in cow milk (Coates *et al.*, 1964). The reduction of milk lactose concentration observed after the lactation peak is clearly associated with a decrease of sodium and a correlative increase of potassium content because of the osmolarity regulation (Gachev, 1971a)

As for the major components, mineral composition changes substantially after lactation peak especially when does are concurrently pregnant and a very rapid drying up of their milk yield occurs. Calcium concentration and to a lesser extend phosphorus increase with progressing lactation stage (Lebas *et al.*, 1971; Perret *et al.* 1977; Kustos *et al.*, 1996) while the effect for potassium and sodium is less clear. Potassium concentration drops dramatically with decreasing milk yield according to Kustos *et al.* (1996) but this was not very outspoken in earlier work of Lebas (1971), Gachev (1971a) and El-Sayid *et al.* (1994). El Sayid *et al.* (1994) reported a gradual increase of the sodium content

Table 7: Mineral composition (g/kg milk) of rabbit milk[1].

	Lebas *et al.* (1971)	Perret *et al.* (1977)	El-Sayid *et al.* (1994)	Kustos *et al.* (1996)	Kustos *et al.* (1999)
Sodium	1.03	0.82	1.16	0.84	
Potassium	1.98	1.77	1.68	2.01	
Calcium	5.36	3.64	4.82	2.76	2.71
Magnesium	0.35		0.36		0.45
Phosphorus	3.28		2.61	2.44	
Chlorine			0.66		
Zinc	0.02			0.021	0.034
Iron				0.003	0.003
Copper				0.002	0.002
Manganese				0.0001	0.0002

[1] Average value determined during lactation (colostrum excluded).

while Lebas *et al.* (1971) and Kustos *et al.* (1996) mention a tendency to a higher content at the beginning and near the end of the lactation period. Magnesium content increases with lactation stage (Lebas *et al.*, 1971; Kustos *et al.*, 1999) while the microelements (zinc, copper, iron and manganese) decrease gradually in concentration as lactation progressed (Kustos *et al.*, 1996 and 1999). For example, Tarvydas *et al.* (1968) observed a reduction of iron content from 3.9-4.6 mg/l 3-4 days after kindling down to 2.3 mg/l on day 17.

Phosphorus concentration decreases in pregnant does at the end of the lactation period probably due to more phosphorus being derived to foetal growth (El-Sayid *et al.*, 1994; Kustos *et al.*, 1996). However, the pregnancy effect was much less clear in the work of El-Sayid *et al.*, (1994), because females were not remated immediately after parturition. Calvert *et al.* (1985) observed a rise in milk sodium and chlorine concentration and a decline in potassium and lactose during the milk accumulation 24 h after the last nursing.

Vitamin content

Few data can be found about the vitamin content of rabbit milk. The research done by Coates *et al.* (1964) can therefore still be considered as basic information although only 1 or 2 samples per lactation day were analysed. Rabbit milk is richer than cow milk in all the water-soluble vitamins and vitamin A (Coates *et al.*, 1964). The high level of vitamin A in the colostrum (6-7 µg/ml) was confirmed by El-Sayiad *et al.* (1994) and also the gradually decreasing levels as the lactation proceeds. This fits with the function of retinol being important for the kit eye development. Basic level of vitamin D_3 is fairly low in milk (0.6 mg/l or 24 IU/l), but very sensitive to doe circulating vitamin D_3 level, since a single injection of a massive vitamin D_3 dose increases the milk vitamin D_3 for minimum 5 days (Hidiroglou and Williams , 1985)

The following levels for biotin (0.45 µg/ml), folic acid (0.30 µg/ml), niacin (4.9 µg/ml), pantothenic acid (14.5 µg/ml), riboflavin (4.6 µg/ml), thiamin (1.6 µg/ml), pyridoxine (B_6) (3.6 µg/ml) and B_{12} (0.07 µg/ml) were determined on the 18th day of the lactation (Coates *et al.*, 1964). However, some effects of stage of lactation were observed e.g. an increase for biotin between 1st and 40th day of lactation (multiplied by 2.7), and simultaneously a decrease of pyridoxine (divided by 6) (Gogeliya, 1970). More recently, Cole *et al.* (1983) determined comparable levels for folic acid and vitamin B_{12} as the aforementioned values.

Some other components

It has been shown that rabbit milk has antibacterial effects (Canas-Rodriguez and Smith, 1966; Marounek *et al.*, 2002). When rabbit milk is added in cultures of rabbit caecal contents, a significantly decreased production of microbial metabolites was determined, whereas no inhibitory effect of a corresponding mixture of cow milk fat, casein and lactose was observed (Marounek *et al.*, 1999).

The bactericidal effect is linked to the short-chain FA ($C_{8:0}$ and $C_{10:0}$) which make that suckling rabbits are unique amongst other species in the contents of the stomach and small intestine that are almost completely sterile. This is a natural protection against the risks of the very high milk intake in only one meal a day. In rabbit milk triglycerides, $C_{8:0}$ and $C_{10:0}$ are mainly in the external position on the glycerol molecule while $C_{16:0}$ is mainly in the central position (Demarne *et al.*, 1978; Christie, 1985). This explains the quickly hydrolysis in the stomach which enables their antibacterial role in this gut segment. In addition and as shown in the protein section, some proteic milk components have their own anti-bacterial activity such as α_{S1} and β-casein fractions or transferrin, in addition to the classical immunoglobulins activity. However, rabbit milk contains only few orotic acid (0.5 mg/l, compared to the 18 mg/l of cow milk; Gajos and Krêzlewicz, 1974), a residue of arginine catabolism sometimes used in human medicine in diarrhoea control.

Finally, rabbit milk can contain undesirable components transferred from contaminated diets or treatments. For example an effective transfer of ochratoxin A from plasma to milk has been demonstrated (Galtier *et al.*, 1977; Ferrufino-Guardia *et al.*, 2000). Also antibiotic residues are found in milk as has been demonstrated after a tilmicosin treatment of does (Saggiorato *et al.*, 2004).

CONCLUSIONS

Due to the time consuming determination of the milk yield and the divergent methodology used, published data concerning the production capacities of does are quite scarce and difficult to be compared. However, the production level of actual highly efficient hybrids used for commercial rabbit production can be situated around 250 g/d (or 60 g/d/kg LW). By consequence, during a 30 days lactation period, total milk yield exceeds 7 kg in multiparous does.

There are much more data available of the macro nutrient composition of rabbit milk. Both the macro composition as the fatty acid composition is widely different from cow or sow milk. Due to the high yield of does and their concentrated milk, at peak lactation protein output per kg LW and even per kg$^{0.75}$ exceeds those of Holstein cows.

Rabbit milk distinguishes from other milks by its extremely high content of short chain FA. Their antibacterial effects in the gut protect the kits against enteritis risks which are high due to the natural suckling behaviour (only one daily quantitatively rich meal).

The non-nutritional factors having the largest impact on the milk yield are the lactation stage, the number of suckling kits, the gestation overlapping degree (rapid decline after 17-20 days of gestation), the parity order and heat stress (through feed intake depression for the later factor). However, due to the common practise of equalizing the litter size at parturition, commercial strains are capable to express their maximal yield aptitude.

Milk production has had little attention in selection programs in spite of its large importance in kit survival and post-weaning growth.

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