Effects of Energy Intake on Performance, Mobilization and Retention of Body Tissue, and Metabolic Parameters in Dairy Cows with Special Regard to Effects of Pre-partum Nutrition on Lactation - A Review -

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ABSTRACT : The present review focuses on the effects of energy intake on performance, changes in body tissue during lactation, and metabolic parameters in dairy cows. Especially, pre-partum nutrition and its influence on lactation are emphasized. In recent decades the increase in genetic potential of dairy cows has increased milk yield. This fact sharpens the problem of a negative energy balance in early lactation because the amount of energy required for maintenance and milk production exceeds the amount of energy cows can consume. Around parturition, reduced feed intake reinforces the situation. Continuing negative energy balance causes decreasing milk yield, fertility problems, and incidence of metabolic diseases. Hence, the cow has to rely on body reserves that were stored in late lactation and the dry period. It is evident that the nutritional status pre-partum acts as the key factor for milk yield and fertility parameters in the following lactation. Cows overfed during the foregoing gestation and which have gained large quantities of body fat have lower dry matter intake along with the need to mobilize larger quantities of body reserves in lactation. The milk yield in the following lactation is lower than in cows fed according to their requirements. Cows restrictively fed in late gestation have a higher feed intake in lactation and a lower mobilization of body reserves. The effect of energy intake post-partum plays only a minor role for performance parameters in lactation. Lipid mobilized from body reserves makes a substantial contribution to the energetic cost of milk production in early lactation and adipose tissue undergoes specific metabolic alterations. Adipose tissue is degraded to free fatty acids, which are used in liver for energy purposes. High lipid mobilisation promotes the development of a fatty liver and therefore a reduced gluconeogenesis. (**Key Words :** Dry Matter Intake, Milk Production, Dry Period, Health, Mobilization, Metabolic Parameters)

INTRODUCTION

During early lactation, the energy requirements for maintenance and milk production exceed the amount of energy obtained from dietary sources. Thus, the high energy requirement at the onset of lactation results in a negative energy balance (NEB) that begins a few days pre-partum and usually reaches its maximum two weeks post-partum (Butler and Smith, 1989; Bell, 1995), which may adversely affect post-partum health and fertility (Butler and Smith, 1989; Reist et al., 2002). Not until two months or more

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post-partum, energy balance (EB) reaches a positive value (Knight, 2001). In the study of Beever et al. (1998) a positive EB was still not restored after 20 weeks, despite feeding the cows with a high-quality diet at an intake level of >28 kg dry matter (DM)/d and showing positive weight gain.

EB has been defined as the difference between energy intake of the animal and energy required for maintenance and pregnancy in the gestating cow, and that required for maintenance and milk production in the lactating cow (Butler and Smith, 1989; McNamara et al., 2003a). NEB becomes more intense and prolonged with increasing milk yield (Staufenbiel et al., 2003). The degree of NEB in early lactation and the recovery rate from NEB are critical for health status and productivity (Reist et al., 2002). Energy intake and supply change throughout lactation. In the period around parturition, both an oversupply and an undersupply could lead to detrimental consequences for the animal. The

incidence of metabolic diseases increase and performance declines (Gelfert et al., 2003). After parturition an inadequate energy supply may result in a higher risk of metabolic disorders (Fronk et al., 1980), in poor reproductive performance (Fronk et al., 1980; Butler et al., 1981; Butler and Smith, 1989; Staples et al., 1990), and in elevated occurrence of inflammatory disease (Markusfeld, 1985).

Energy requirements of lactating cows are met by a genetically determined combination of dietary intake and mobilization of body reserves (Farries, 1983a; Butler and Smith, 1989). High-yielding dairy cattle cannot meet energy requirements by intake during early lactation and have to mobilize body energy sources (Coppock et al., 1974; Nebel and McGilliard, 1993; Ferguson, 1996). Homeorhetic controls in early lactation assure that body tissue, primarily adipose stores, will be mobilized to support milk production despite insufficient nutrient intake (Baumann and Currie, 1980). Excessive body condition loss acts as an indicator for energy management (Ferguson, 1996). During early lactation, the maximum NEB occurs at peak yield of energy corrected milk, followed by a return towards zero. The magnitude and duration of NEB between individual animals could be quite different (Butler et al., 1981). The use of increasing concentrates in the ration reduces the time for animals to reach energy equilibrium but does not eliminate the problem (Coppock et al., 1974).

In the last decades, the increase of milk performance per cow and lactation was correlated with a reinforcement of NEB combined with a decline of reproductive parameters within the period of highest milk yield (Kanitz et al., 2003). Due to a priority of milk production in early lactation the high-yielding cow cannot adjust milk production to feed intake. The consequential NEB and mobilization rate of body tissue appear to be directly related to a prolonged post-partum interval of first ovulation and to lower conception rate (Butler and Smith, 1989).

Fertility problems are often developed in high yielding cows with more than 6,000 kg milk per lactation (Whitmor

et al., 1974; Nebel and McGilliard, 1993; Macmillan et al., 1996) and with an increased feed intake pre-partum (Kruip et al., 1998). A comparison of data on ovarian activity based on measurements of milk progesterone concentration in moderate-yielding (4,000 to 5,000 kg milk per lactation) cows fed mainly grass and conserved forage (Fagan and Roche, 1986) versus that in cows producing 7,000 to 9,000 kg milk per lactation fed high amounts of concentrates (Opsomer et al., 1998), shows an increased incidence of post-partum anoestrus, abnormal ovarian cycles and prolonged luteal phases (high progesterone for >20 days before breeding) in high yielding cows (Table 1).

However, Villa-Godoy et al. (1988) could not demonstrate an association of duration of luteal phases with EB. Consequently energy management from the late gestation period through the post-partum period has significant effects on reproductive function (Ferguson, 1996). The interval from parturition to first ovulation in dairy cattle is related to the level of milk production (Stevenson and Britt, 1979) and EB (Butler et al., 1981). The post-partum ovarian activity is more closely associated with milk production than with total digestible nutrient intake (Whitmore et al., 1974).

Body condition scoring system is a useful method for evaluating body energy reserves and is widely used for evaluating nutritional status in dairy cows (Wildman et al., 1982; Edmonson et al., 1989; Hady et al., 1994). Body condition score (BCS) represents a subjective assessment of the tissue reserves (Markusfeld et al., 1997) and nutritional status (Staufenbiel et al., 2003) of dry and lactating cows. Changes in body condition have been more useful than body weight (BW) changes because those are influenced by gut fill, growth, and frame size (Wildman et al., 1982; Nebel and McGilliard, 1993). Edmonson et al. (1989) exhibit a five-point scale, from 1 indicating lean to 5 indicating obese. The five-point body condition scoring system is a practical tool for assessment of body reserves and changes in BCS during lactation and dry periods are a pattern of body fat mobilization (Hady et al., 1994; Gallo et

Table 1. A comparison of post-partum reproduction parameters based on measurement of progesterone in milk twice weekly in two different studies using either moderate-yielding (Fagan and Roche, 1986) or modern high-yielding cows (Opsomer et al., 1998)

	Traditional moderate-yielding (Fagan and Roche, 1986)	Modern high-yielding (Opsomer et al., 1998)
Use of progesterone assay		
Number of animals	463	448
Normal cyclical patterns (%)	78	53.5[a]
Prolonged interval to 1st ovulation (%)	7	20.5[a]
Temporary cessation of ovulation (%)	3	3
Prolonged luteal phase (%)	3	20[a]
Short cycles (%)	4	0.5
Other irregular patterns (%)	4	2.5

[a] Categories with a major disparity between the two studies.

al., 1996). BCS at parturition can have a direct effect on milk yield, fertility and health of cows (Boisclair et al., 1986; Treacher et al., 1986; Markusfeld et al., 1997). Well and poorly conditioned cows respond differently to the metabolic demands of early lactation and some of these differences render obese cows more susceptible to disease (Reid et al., 1986). Management factors aim to have cows entering the dry period in good BCS, and to maintain this score during the dry period. Garnsworthy and Topps (1982) and Garnsworthy and Jones (1987) concluded that cows with lower condition scores at parturition generate a greater percentage of milk yield directly from feed rather than via body fat, reach positive EB earlier in lactation and are more efficient over the total period than cows with higher condition scores. There appear to be no benefits from feeding cows to achieve a condition score greater than 1.5 to 2.0 at parturition, where 1.0 represents a very thin animal and 4.0 an excessively fat animal, if high-energy complete diets are offered in early lactation. This was also approved by Garnsworthy and Jones (1993).

Crowe (2008) reviewed that the key to optimize resumption of ovulation is an appropriate pre-partum nutrition and management so that post-partum condition loss of cows is restricted to <0.5 BCS units.

Backfat thickness measured by ultrasound on a defined point is also an objective criterion of the quantity of existing body fat reserves (Staufenbiel, 1997). Staufenbiel (1992) located this examination site in the sacral region between the caudal one-quarter and one-fifth connection line going from the dorsal part of the tuber ischia (pins) to the tuber coxae (hooks). A phenotypical correlation of about 0.8 exists between backfat thickness and total body fat resources. A 1 mm backfat thickness relates to approximately 5 kg total body fat (Klawuhn and Staufenbiel, 1997). The lactational changes between catabolism and anabolism are demonstratively reflected by backfat thickness. Decreasing backfat thickness describes the extent of lipolysis rate, adipogenesis rate (Staufenbiel, 1997), and EB (Staufenbiel et al., 1993). The nadir of backfat thickness characterizes transition from negative to positive EB (Kanitz et al., 2003).

EFFECTS ON DRY MATTER INTAKE AND PERFORMANCE

A cow producing 35 kg of milk daily requires three times more energy for production than for body maintenance (Butler and Smith, 1989). Following parturition, dry matter intake (DMI) needs to increase in order to meet the high nutrient demands of milk production (Roche et al., 2000). A low proportion of concentrate in the diet and a slowly increasing concentrate level post-partum induces a greater NEB (Kokkonen et al., 2004). Rapid

mobilization of body fat reserves and thus circulating fatty acids (FA) may further depress appetite and increase the difference between energy intake and output (Macmillan et al., 1996). In high-lactating cows, Coulon and Rémond (1991) summarized that for 1 kg concentrate DM feeding (8.0 MJ NEL) there is a linear increase in milk production of about 0.8 to 1.2 kg. Throughout lactation an increase of milk yield is accompanied by increasing energy intake. In cows, an additional energy supply of 14 to 21 MJ NEL results in an increase of more than 2.0 kg milk per kg concentrate (DM) in NEB, of about 1.1 kg in an equalized EB, and only about 0.6 to 0.3 kg in cows maintained on a surplus of energy. Olsson et al. (1998) detected that a higher average daily concentrate intake of 3.8 kg until one month after parturition resulted in a daily yield difference of 4 kg milk. The additional energy intake of concentrate is not converted 100% into milk production, since suppression of forage intake, mobilization of body reserves in terms of undersupply and in early lactation, accumulation of body reserves at oversupply, as well as negative correlations of forage and concentrate on digestion and metabolism have to be considered (Gruber et al., 1995). Milk composition is mainly affected by genetic merit, but can be also influenced by feeding management and metabolic situation (Kraft and Dürr, 2005).

Effect of pre-partum energy supply on dry matter intake in lactation

The effects of dry period ration on DMI in lactation are well documented. Several studies regarding the effects of pre-partum energy supply on feed intake in lactation are illustrated in Table 2. The results are heterogeneous. A general statement cannot be made in summary.

Coppock et al. (1974) as well as Johnson and Otterby (1981) stated that the extent to which intake decreases in late pregnancy depends on energy status; the greater the energy content of the diet, the less is eaten. This was also affirmed by Nocek et al. (1983).

Kunz et al. (1985) reported that cows fed only 0.75 of requirements during the final 70 days pre-partum exhibited faster increases in DM and NEL intake immediately after parturition, compared with animals fed *ad libitum*. Many studies have observed a lower feed intake of well-conditioned cows followed by a greater NEB in early lactation (Land and Leaver, 1981; Garnsworthy and Topps, 1982; Bines and Morant, 1983; Treacher et al., 1986; Garnsworthy and Jones, 1993; Grummer et al., 1995; Cameron et al., 1998; Holcomb et al., 2001; Knight, 2001; Urdl et al., 2007). Trends towards higher grain consumption in early lactation were detected by Gardner (1969) for cows subjected to energy underfeeding prior to calving compared with cows fed above requirements in the dry period. In the study of Land and Leaver (1981), two groups of cows were

Table 2. Effect of pre-partum energy supply on feed intake and milk yield and composition in lactation

n	Treatments	Energy supply pre-partum			Feed intake post-partum				Milk yield					Reference
		Duration (weeks)	Concentrate (kg/d)	Roughage	DMI roughage + concentrate (kg/d)	DMI concentrate (kg/d)	BW (kg)	Duration (weeks)	Milk (kg/d)	ECM (kg/d)	Fat (%)	Protein (%)	Duration (weeks)	
13	Low energy	8	0.0	H, P	13.0	10.5	608	12	29.0	24.0	2.67	3.25	12	Davenport and Rakes (1969)
14	Moderate energy		2.3		12.7	10.0	598		27.0	22.8	2.87	3.17		
16	High energy		12.0		12.2	9.8	587		30.3	25.9	3.01	3.04		
12	Control	8	1.8	H, GS, CS	19.2	n.s.	518	9	30.4	n.s.	n.s.	n.s.	Week 2 to 9	Fronk et al. (1980)
12	Over-conditioned		6.4 to 8.2		19.6		775		31.4					
31	Hay	4	0.0	H, GS, CS	11.8	n.s.	n.s.	4	25.0	n.s.	n.s.	n.s.	week 2 to 4	Johnson and Otterby (1981)
31	Low concentrate		1.0		12.6				25.4					
31	High concentrate		4.2		11.9				24.6					
n.s.	BCS 2.5 at calving	n.s.	n.s.	H	16.3	n.s.	n.s.	16	23.6	n.s.	3.86	3.19	16	Land and Leaver (1981)
	BCS 3.5 at calving				15.9				25.7		3.95	3.06		
16	Low BCS at calving	8	n.s.	H, S	22.3	n.s.	n.s.	16	n.s.	n.s.	3.65	n.s.	16	Garnsworthy and Topps (1982)
16	Medium BCS at calving				21.2						4.05			
16	High BCS at calving				20.7						4.09			
95	Hay	7	n.s.	H, CS	16.7	n.s.	n.s.	8	33.9[a]	n.s.	3.4[a]	3.0	9	Nocek et al. (1983)
84	Hay and corn silage				16.1				32.5[b]		3.7[b]	2.9		
8	Fed to meet the requirements	10	0.0	H, GP, CC	n.s.	n.s.	n.s.	n.s.	20.1	22.8	5.10	3.50	21	Kunz et al. (1985)
17	Overfed		1.0						20.8	23.4	5.10	3.40		
11	102% of requirements	8	0.0	H, CS	18.0	n.s.	690	12	31.0	n.s.	3.38	3.17	12	Boisclair et al. (1986)
11	131% of requirements		0.0		18.0		707		32.6		3.31	3.08		
11	162% of requirements		0.5		18.0		734		32.1		3.48	3.10		
9	BCS 2.5 at drying off	22	n.s.	H	17.2	n.s	n.s.	10	30.9[a]	n.s.	4.61	2.81	6	Treacher et al. (1986)
9	BCS 4.0 at drying off				15.8				26.5[b]		4.93	2.86		
15	Fed restricted	12	0.0	GS, CS	18.2	n.s.	562	14	36.1	31.1	3.29[a]	2.75	14	Holter et al. (1990)
15	Fed to meet the requirements		2.7		18.6		586		35.6	34.3	4.10[b]	2.76		
26	Low BCS at calving	12	n.s.	H, P	18.3	n.s.	535	16	27.4	27.5	4.35	2.92	16	Garnsworthy and Jones (1993)
26	High BCS at calving				17.4		569		27.3	27.2	4.28	2.91		
38	Fed to meet the requirements	24	0.7	GS	20.3	n.s.	492	16	28.0	n.s.	3.90	3.11	23	Grummer et al. (1995)
38	Oversupplied		3.8		18.4		503		27.5		3.74	3.01		
9	Control	9	2.9	OH	17.9	n.s.	n.s.	14	35.1	n.s.	3.11	2.96	14	Grum et al. (1996)
10	High grain dry period diet		5.4		18.7				35.5		3.38	3.07		
10	Low energy	3	2.7	H, GS	14.8[a]	6.8[a]	n.s.	4	21.2	21.8	4.32	3.34	12	Olsson et al. (1998)
10	High energy		6.2		17.3[b]	7.9[b]			21.9	22.7	4.42	3.25		
8	Low energy	10	n.s.	H, GS	17.53	n.s.	599	4	n.s.	39.98	4.79	3.66	4	Agenäs et al. (2003)
8	Medium energy				15.87		586			36.87	4.71	3.49		
8	High energy				17.14		630			38.63	5.07	3.83		

Table 2. Effect of pre-partum energy supply on feed intake and milk yield and composition in lactation (Continued)

		Energy supply pre-partum				Feed intake post-partum				Milk yield					
n	Treatments	Duration (weeks)	Concentrate (kg/d)	Roughage	DMI roughage + concentrate (kg/d)	DMI concentrate (kg/d)	BW (kg)	Duration (weeks)	Milk (kg/d)	ECM (kg/d)	Fat (%)	Protein (%)	Duration (weeks)	Reference
6	Straw and grass silage	4	0.0	GS, S	13.5[a]	4.9	607	8	24.1[a]	23.2	3.86[a]	3.16	8	McNamara et al. (2003b)
6	Grass silage		0.0		13.8[ab]	5.1	626		26.2[b]	25.7	4.03[ab]	3.15		
6	Grass silage and concentrate		3.0		14.2[b]	5.1	603		28.2[b]	28.2	4.15[b]	3.23		
30	Low energy	4	2.6	GS, CS, S	20.7	n.s.	718	10	39.5	n.s.	3.55	3.03	10	Rabelo et al. (2003)
30	High energy		6.2		20.8		718		37.5		3.62	3.10		
28	Fed to meet the requirements	5	0.0	GS, S	15.2	7.0	588	8	25.5	24.0	3.69	3.14	8	Ryan et al. (2003)
28	Oversupplied		3.0		15.0	7.0	618		26.5	25.4	3.81	3.17		
5	Low energy	3	1.6	GS	16.8	8.7[a]	691	5	32.7	33.6	4.33[a]	3.41	5	Kokkonen et al. (2004)
5	Medium energy		2.9		18.5	10.1[b]	675		31.8	31.8	3.98[b]	3.32		
5	High energy		4.5		20.3	12.1[c]	682		34.4	32.6	3.63[b]	3.40		
18	80% of requirements	9	n.s.	AH, AS, CS	19.7	n.s.	630	week 3 to 6	36.7	n.s.	3.36	2.76	week 3 to 6	Dann et al. (2005)
17	*Ad libitum*				19.9		623		35.3		3.54	2.84		
19	Forage group	4	0.0	GS	16.1	5.9	n.s.	16	26.6	n.s.	4.35	3.31	16	Keady et al. (2005)
19	Concentrate group		3.4		16.5	5.9			26.8		4.42	3.31		
13	DMI 5.5 kg/d pasture	4	0	P	13.0	0	n.s.	Week 3 to 5	20.6	n.s.	4.67	3.55	Week 2 to 5	Roche et al. (2005)
13	DMI 8.0 kg/d pasture		0		13.4	0			21.8		4.82	3.57		
13	DMI 10.5 kg/d pasture		0		12.0	0			20.0		4.95	3.56		
13	DMI 13.0 kg/d pasture		0		11.5	0			21.6		5.01	3.53		
4	80% of requirements	8	n.s.	H, CS	17.5	n.s.	570	12	37.4	n.s.	4.59	2.75	12	Carlson et al. (2006)
4	Control				19.6		572		39.0		4.45	2.65		
12	80% of requirements	9	n.s.	AS, CS	22.4	n.s.	581	15	42.1	n.s.	3.27	3.04	15	Douglas et al. (2006)
12	*Ad libitum*		0.0		19.9		591		40.6		3.35	3.05		
80	Normal dry period	8	n.s.	GS, CS, S	21.1	n.s.	653	7	41.0[a]	41.0[a]	4.13	3.29[a]	7	Engelhard et al. (2007)
	Shortened dry period	4			21.1		663		45.7[b]	44.1[b]	3.91	3.10[b]		
14	Control	2	0.0	H, CS, AWS	16.2	n.s.	650	2	32.9		4.33	3.49	2	Guo et al. (2007)
14	Transition diet		4.6		16.4		698		33.4		4.54	3.70		

n.s. = Not specified; H = Hay; P = Pasture; GS = Grass silage; CS = Corn silage; S = Straw; GP = Grass pellets; CC = Corn cubes; OH = Oat hay; AH = Alfalfa hay; AS = Alfalfa silage; AWS = Alfalfa-wheat silage.
[a,b,c] Significantly different (p<0.05); no symbol p>0.05 or not specified.

individually fed on hay and concentrates in late pregnancy to achieve a condition score of 2.5 or 3.5, respectively, at parturition. During the first 16 weeks of lactation, DMI for the better-conditioned cows was lower (16.3 vs. 15.9 kg DM/d). Broster and Broster (1984) also argued that a low feed intake before calving was followed by greater intake in lactation than for cows fed generously pre-partum. Treacher et al. (1986) fed cows to achieve condition scores at parturition of 2.5 (thin) and 4.0 (fat). The mean daily intake of DM for each group of cows during the first 10 weeks of test lactation is shown in Figure 1. Although the mean daily DMI of the fat group was consistently lower than of the thin group (15.8 vs. 17.2 kg; SE 0.81), the difference was not statistically significant.

Grummer et al. (1995) fed heifers a high- or low-concentrate diet from day 170 of gestation. The concentrate-rich diet decreased the feed intake by about 1 kg/d DM in the first 20 weeks of the following lactation. In the study of Douglas et al. (2006) during the first 21 days post-partum, cows restrictively fed in the dry period (80% of NEL requirement) had higher intakes of DM and NEL compared with overfed animals (160% of NEL requirement). The decreased food intake of fat ruminants is thought to be a mechanism for regulating adipose tissue depots (Treacher et al., 1986). It is likely that short-term mechanisms controlling intake are mediated by certain
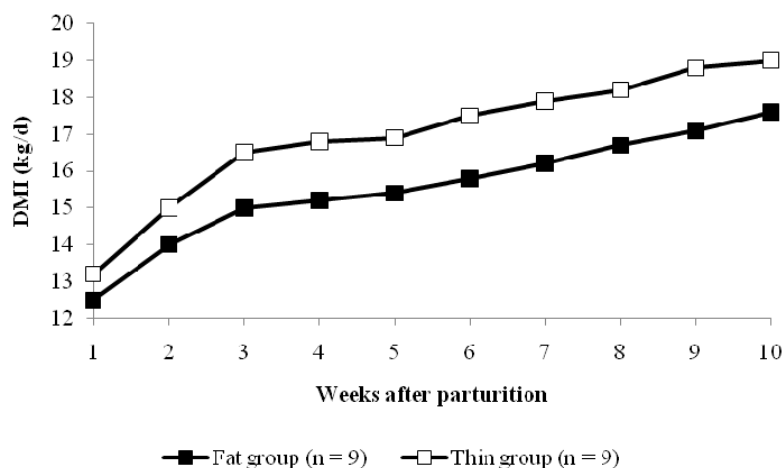
Figure 1. Mean daily DMI during the first 10 weeks post-partum (p>0.05) (adapted from Treacher et al., 1986).

short-chain FA (Bines and Morant, 1983). These authors have postulated that a more rapid rate of FA synthesis in the adipose tissue of thin cows may reduce blood levels of lipogenic precursors and so enhance their absorption from the rumen and stimulate food intake. During the dry period, rumen short-chain FA production is related to feeding intensity and stimulates rumen papilla growth, which in turn facilitates rumen absorption and may influence DMI (Agenäs et al., 2003). Long-term effects of higher serum insulin concentration in animals fed low fibre diets may account for a more pronounced decrease in DMI compared to animals fed higher fibre diets (Ingvartsen and Andersen, 2000).

However, the studies of Davenport and Rakes (1969), Fronk et al. (1980), Johnson and Otterby (1981), Johnson (1984), Boisclair et al. (1986), Holter et al. (1990), Garnsworthy and Hugget (1992) as well as Agenäs et al. (2003) showed no difference in DMI for low- and well-conditioned cows in early lactation, which implies that neither differences in adipose tissue nor the extent of adaptation to high DMI necessarily influences feed intake capacity (Agenäs et al., 2003). These authors explained that DMI is adjusted to EB by metabolic or hormonal factors. Vandehaar et al. (1999) attested that increased nutrient-density of pre-partum diets did not decrease feed intake during lactation. Ryan et al. (2003) and Kokkonen et al. (2004) concluded that the proportion of concentrate in the pre-partum diet has no effect on voluntary DMI post-partum. In the studies of Keady et al. (2005), Carlson et al. (2006), Guo et al. (2007) and Roche (2007), pre-partum energy intake also showed no effect on post-partum DMI. It may be concluded that the treatments in these studies did not create any differences in rumen absorption that influenced DMI. A 30% reduction in DMI is typical during the pre-partum transition period (Bertics et al., 1992; Grummer, 1995). In the study of Olsson et al. (1998), the DMI around calving time decreased among all cows independent of

energy level in the diet. Physical limitations, due to fetal growth, have been suggested as an explanation for decreased DMI near the time of parturition (Ingvartsen and Andersen, 2000).

Effects of pre-partum energy supply on milk yield and milk composition

At parturition, milk yield is raised by well-developed fat storages because of their metabolic and energetic utilization (Domecq et al., 1997; Markusfeld et al., 1997). Loss in milk yield can also appear in over-conditioned animals (Waltner et al., 1993; Staufenbiel, 1997), because excessive energy intake pre-partum leads to metabolic problems and decreases DMI in the following lactation (Holter et al., 1990; Garnsworthy and Jones, 1993). The effect of pre-partum level of intake is difficult to separate from BCS at calving (Roche, 2007). There are close relationships between milk yield and backfat thickness (Staufenbiel, 1997; Staufenbiel et al., 2003) and BCS (Wildman et al., 1982; Veerkamp et al., 1994). The reported effect of pre-calving DMI on milk production in the literature appears inconclusive as showed in Table 2.

Gardner (1969) investigated the influence of different pre-partum energy intake on milk production. Milk yield or milk composition was not significantly affected by pre-partum energy intake. It has been shown by Fronk et al. (1980) that an oversupply of energy in the dry period did not increase the performance when high energy rations were fed in lactation. In the experiments of Boisclair et al. (1986), the pre-partum energy intake had no effect on milk yield in the first twelve weeks after parturition. In the study of Kunz et al. (1985), the average milk yield during the first 125 days was independent of energy intake during the dry period and early lactation. The most marked difference was a considerably lower peak yield for cows on a restricted energy level in the dry period. However, the peak yield in these animals was maintained for up to 60 days, while the

yield started to decline after only 20 days in cows fed more generously in the dry period. The milk constituents were not affected. In the study of Jones and Garnsworthy (1989) neither dietary energy concentration pre-partum nor condition score at parturition significantly affected milk yield. Holter et al. (1990) observed no difference in milk yield in moderate- and low-condition cows. Grum et al. (1996) could not demonstrate an effect of high-fat diets in the dry period on milk protein in the following lactation, but a decreasing percentage and production of milk fat. Corro et al. (1999) reported that the changes in BCS during the last month of pregnancy and first month of lactation did not correlate (p>0.05) with milk yield. Holcomb et al. (2001) found no negative effects of restricted feeding in the dry period and in early lactation except lower milk fat percentage. Also Garnsworthy and Jones (1993), Grummer et al. (1995), Agenäs et al. (2003) and Rabelo et al. (2003) did not observe any effects of pre-partum energy intake on milk yield or composition in the following lactation. In the trial of Roche et al. (2005) the effect of pre-partum nutrition on milk production was small. High pre-partum DMI increased milk yield in lactation. Milk fat yield also increased with increasing DMI pre-partum and BCS at parturition until week three post-partum, after which treatment effects were not evident. Guo et al. (2007) found no effect of diet in the transition period on milk yield or milk components in the first 21 days in milk (DIM) (p> 0.05). In the trial of Carlson et al. (2006), milk yield was not affected by pre-partum treatment. Castañeda-Gutiérrez et al. (2009) studied the effect of different peri-partum dietary energy supplementations. Milk production and milk components were not affected by dietary supplementation. Reasons for the lack of responses may be variations in cow parity, BCS at calving, quality of the basal diet, or the genetic potential of the cows (McNamara et al., 2003b). Carlson et al. (2006) concluded that any milk yield response to pre-partum diet is likely due to metabolic factors rather than increased functional activity of the mammary gland. Reid et al. (1986) suggested that well-conditioned cows utilized energy with a lower efficiency which may have been due to fatty liver problems. Broster and Broster (1984) supported the idea that, although the effects of pre-partum feeding could be observed throughout lactation, moderate underfeeding before calving could be offset by more generous feeding after calving. Also, high average BCS and little differences in BCS at calving between the different treatment groups in these studies might explain the small effects of pre-calving DMI on post-calving milk production (Roche et al., 2005).

In contrast, different studies showed that energy supply in the dry period had a positive effect on milk production. Waltner et al. (1993) underlined that the amount of body fat at calving is positively related to milk production in early lactation. They hypothesized that in cows with the ability to produce more than 9,000 kg fat-corrected milk (FCM) in 305 days, a limited amount of body fat at calving may be a critical factor in meeting that potential. Under commercial dairying conditions, Frood and Croxton (1978) reported that a higher condition score at parturition resulted in higher milk yield. Similarly, Land and Leaver (1981) demonstrated during the first 16 weeks of lactation differences in milk yield and composition for cows calving with a condition score of 2.5 or 3.5 as follows: milk yield (kg/d) 23.6 and 25.7; milk fat (g/kg) 38.6 and 39.5; milk protein (g/kg) 31.9 and 30.6, respectively. The 305-day lactation yields (kg) were 5,096 and 5,718, respectively. They concluded that a high level of feeding resulting in an increased BCS pre-partum could be an effective management strategy. In the experiment of Bertics et al. (1992), eleven cows were allowed *ad libitum* intake prior to calving (control), and eleven cows were maintained at the same level of DMI recorded during days 21 to 17 prior to calving by force feeding the feed refusals via rumen cannulas. They found that the cows force-fed before parturition had a higher milk yield (46.1 vs. 41.7 kg/d) post-partum and a higher milk fat (4.22 vs. 3.88%) during the first 28 days of lactation.

Markusfeld et al. (1997) detected that cows calving with a higher BCS produced more milk with a higher fat and protein content in the first 90 days of lactation. Olsson et al. (1998) recorded a significantly smaller milk yield in the first month post-partum for cows on a low nutritional level (142 MJ ME/d) at parturition compared with cows with an energy intake of 186 MJ ME/d (24.7 vs. 28.8 kg/d, respectively). Ryan et al. (2003) showed significantly higher milk yields for the first four weeks of lactation in cows receiving concentrate in the dry period ration. In addition, cows fed concentrate were calving with a higher BCS, compared with cows receiving only roughage in the dry period (Figure 2). There were no significant differences between the treatments in the concentrations of fat, protein and lactose.

Agenäs et al. (2003) postulated that a high dry period feeding intensity may increase milk fat content in early lactation. Keady et al. (2005) investigated the effect of level of nutrients in late gestation on milk yield and composition. A high energy intake pre-partum led to an increased milk fat content and yield but had no effect on milk protein content. High milk fat in lactation as a consequence of high energy feeding in the dry period is probably an effect of increased adipose tissue mobilisation. The experiments of McNamara et al. (2003b) and Urdl et al. (2007) showed that pre-partum energy intake had significant effects on milk yield post-partum. In the experiment of Urdl et al. (2007) cows receiving 75% of energy requirement pre-partum yielded 25.3 kg/d milk in the following lactation, cows receiving 100 and 125% of energy requirements pre-partum yielded
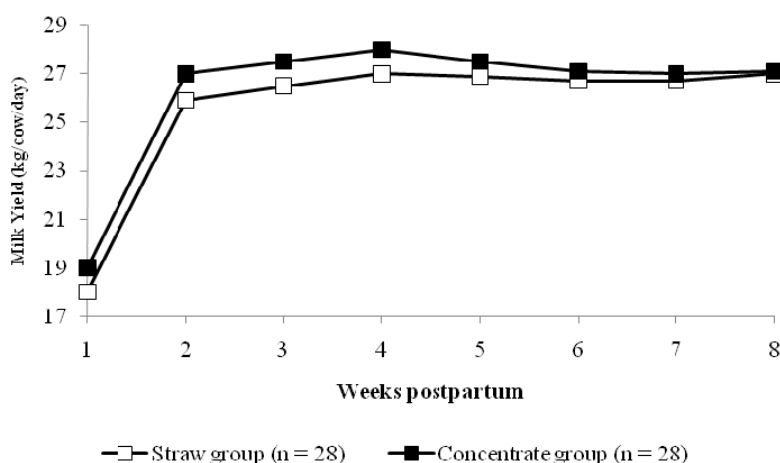
Figure 2. The effect of pre-partum diet on post-calving milk yield (p>0.05) (adapted from Ryan et al., 2003).

28.2 and 29.4 kg/d milk post-partum, respectively. However, pre-partum diet had no effects on milk constitution, only lower lactose concentrations were observed in milk of cows receiving 75% of energy requirement in the dry period. Engelhard et al. (2007) varied length and feeding of the dry period in Holstein dairy cows. Intensively-fed dry cows with a shortened dry period of 30 d exhibited a lower milk yield in the following lactation than cows with an ordinary dry period, independent of lactation number. The milk loss of the following lactation was lower than the milk gain due to a prolonged previous lactation. In the experiment of Roche (2007), pre-partum DMI restriction reduced milk fat production during the first five weeks post-partum in grazing dairy cows, but differences were not significant. Degaris et al. (2008) concluded that pre-partum transition diets increased milk and milk protein yields and decreased the milk fat percentage, but not the milk protein percentage or milk fat yield. Watters et al. (2008) investigated two dry period management strategies on milk production, milk components and milk composition. Cows were assigned to a traditional (55 d) or shortened (35 d) dry period. Post-partum, cows which passed through a traditional dry period produced more milk and tended to produce more solids-corrected milk than cows which passed through a 35 d dry period. Milk fat percentage did not differ between treatments, but milk protein percentage was greater for cows with a shortened dry period. Transition diets should improve the subsequent lactational performance because of an increase of non-fibre carbohydrate content, improved protein balance and amino acid profile and a lower dietary cation-anion difference and balanced macro- and micro-mineral content. All these factors have a positive effect on milk production. Increased energy density of the pre-partum diet, especially of increased fermentable carbohydrate concentration, lead to increased development of rumen papillae and adaptation of rumen microflora to post-partum high concentrate diets (Degaris et al., 2008). An improved rumen constitution increases the efficiency of energy utilization (Kokkonen et al., 2004).

However, many authors have reported an advantage of restricted feeding pre-partum in producing more milk in lactation. Nocek et al. (1983) described that cows fed hay while dry produced more milk with lower fat percent, and were not different for 4% FCM to cows fed additional corn silage or corn silage and liquid protein supplement. In the study of Treacher et al. (1986) obese cows (BCS 4.0 at parturition) had lower daily milk yields and less milk protein and lactose than thin cows (BCS 2.5 at parturition) in early lactation. Sørensen and Enevoldsen (1991) analyzed the effect of planned dry period lengths of 4, 7, and 10 weeks on subsequent lactational yield. Compared with a 7-week planned dry period, a 3-week decrease lowered the level of milk production by 2.8 kg of 4% FCM/d in the first 84 days of the subsequent lactation, whereas a 3-week increase raised the level of milk production by 0.5 kg/d. In the first 168 days of the subsequent lactation, the difference between 4-week and 7-week planned dry periods was 2.7 kg/d, and the difference between 7- and 10-week periods was 0.4 kg/d. Holtenius et al. (2003) suggested that cows that are fed to reduce BCS during the dry period may perform well after parturition if they are offered a high-quality total mixed ration *ad libitum* during lactation. Maybe the removal of the physiological restriction imposed on appetite by body fat allows thinner cows to maximize their food intake and milk production, particularly if a high energy diet is offered *ad libitum*. It is also possible that the greater incidence of disease in obese cows impairs milk yield.

Effects of post-partum energy supply on milk yield and composition

It is a matter of common knowledge that more generous feeding in early lactation leads to only a little direct increase in milk yield (Johnson, 1984; Kunz et al., 1985), as shown

in Table 3. Negative associative effects on digestibility and partitioning of additional nutrients to tissue gain are factors reducing responses to additional concentrate. Consequently, marginal milk yield responses to additional concentrate supply decrease considerably when the level of concentrate feeding increases (Kokkonen et al., 2004). Broster and Broster (1984) postulated that milk yield alters by about 0.1 l per MJ change of ME input in common feeding systems. Chilliard (1992) reasoned that short-term effects led to better mammogenesis and lactogenesis during the time around parturition, or better digestive adaptation, and that long-term effects led to a better availability of body reserves at calving. Fat cows generally have lower voluntary feed intake, but produce the same amount of milk, due to body lipid mobilization (Garnsworthy, 1988). These cows are more susceptible to metabolic disorders and reproductive problems (Chilliard, 1992). However, it seems that cumulative NEB correlates more with energy intake than with milk yield. Deficiencies in diet content or total DMI may result in a deficiency of energy-yielding nutrients and result in more NEB for longer periods of times (Ferguson, 1996).

Milk constituents are directly or indirectly related to the nutrient supply and the proportion of individual nutrients, respectively (Farries, 1983b). Concentrations of lactose and urea in milk are correlated positively with EB. In contrast, the concentrations of acetone, fat, protein and fat:lactose in milk are correlated negatively with EB (Kunz et al., 1985; Reist et al., 2002).

It is a fact that cows having a high loss of BW in early lactation have higher milk fat concentrations, because the mobilized body fat is taken up directly by the mammary gland (Farries, 1983a; Farries, 1983b). DeVries and Veerkamp (2000) showed that a relatively large decrease in fat percentage during early lactation was significantly correlated with a lower nadir of EB, larger energy deficits, and later return to positive EB. They concluded that a decrease in fat percentage in early lactation might serve as an indicator of EB. Underfed fat cows are able to maintain their milk and fat yields, due to a very high body lipid mobilization (Chilliard, 1992). High fibre content in the diet also increases milk fat concentration. However, feeding concentrates with a high fat content decreases milk fat (Janicek et al., 2007). Products of ruminal biohydrogenation of linoleic acid may lead to events that cause milk fat depression. Kraft and Dürr (2005) established a reference range for fat between 3.5 and 4.5%.

Milk protein is directly influenced by protein intake (Blum et al., 1985) and energy supply of rumen bacteria (Farries, 1983a; Grieve et al., 1986). In early lactation DMI is reduced. This leads to a decreased production of microbial protein, followed by a lack of amino acids for milk protein synthesis (Farries, 1983a). Decreased milk protein yield and content in underfed thin cows are probably also related to the low ability for body protein mobilization (Chilliard, 1992). Reid et al. (1986) also suggested that endogenous protein is not suitable to support high protein concentrations in milk. In well-conditioned cows the utilization of amino acids for gluconeogenesis is decreased as a result of the higher digestible energy intake (Fronk et al., 1980). Decreased milk protein yields have often been described in cows fed high amounts of fat due to

Table 3. Effects of post-partum energy supply on milk yield and composition

n	Groups' description	Duration (weeks)	Concentrate (kg/d)	Roughage	Milk (kg/d)	Fat (%)	Protein (%)	Reference
6	Low energy	week	2.7	H, CS	n.s.	4.78[a]	3.40[a]	Blum et al. (1985)
6	High energy	5	6.6			3.77[b]	3.20[ab]	
6	Supplemented with crystalline fat		4.6			3.13[b]	3.04[b]	
7	37% concentrate	12	7.2	GS	35.4	4.20	3.23	Ferris et al. (1999)
7	48% concentrate		10.2		35.6	4.10	3.30	
7	59% concentrate		13.1		37.9	4.02	3.38	
7	70% concentrate		15.4		39.2	3.94	3.35	
4	30% concentrate	12	3.4	GS	19.0	3.96	2.98	Ferris et al. (2003)
4	40% concentrate		6.0		23.1	4.13	3.09	
4	50% concentrate		8.6		25.8	3.98	3.22	
4	60% concentrate		11.2		27.5	3.95	3.36	
4	70% concentrate		13.7		28.4	4.11	3.50	
13	10% corn bran	6	n.s.	CS, AH, AL	32.7	3.58	2.99	Janicek et al. (2007)
13	17.5% corn bran				33.4	3.50	2.97	
13	25% corn bran				35.8	3.32	3.06	

H = Hay; CS = Corn silage; GS = Grass silage; AH = Alfalfa hay; AL = Alfalfa haylage.
[a,b] Significantly different (p<0.05); no symbol p>0.05 or not specified.

indirect lack of fermentable carbohydrates and stimulatory effects of fat on milk synthesis. Sørensen and Enevoldsen (1991) reported that milk protein yield was increased when cows were given a traditional dry period compared with a shortened dry period. One possible reason for the increase in protein percentage could be an improved EB, which spares amino acids and energy for protein synthesis. Kraft and Dürr (2005) established a reference range for protein in milk between 3.2 and 3.8%.

Grieve et al. (1986) proposed that the ratio of contents of milk fat and protein is a better predictor of energy status of the cow than either component by itself as it is more sensitive and consistent. In the experiment of Gruber et al. (1995) the fat:protein ratio was higher in cows which received a low energy diet at the beginning of lactation. They explained this by adipose tissue mobilization due to energy undersupply, followed by an increase of milk fat content und a decreased milk protein content caused by a decrease of microbial protein synthesis in the rumen. Kraft and Dürr (2005) established a reference range for fat:protein ratio of 1.0 to 1.5. The optimum range lies between 1.0 and 1.25. A smaller value might be an indicator of acidosis; a higher value might indicate ketosis.

The milk lactose concentration provides only little indication of energetic imbalances, because the lactose content in milk of healthy dairy cows is nearly constant (Farries, 1983b; McNamara et al., 2003b). Kraft and Dürr (2005) established a reference range for lactose between 46 and 50 g/L.

In the study of Gardner (1969), a high post-partum energy level increased production of milk, protein, and lactose without affecting percentages of milk components. In the experiment of Murdock and Hodgson (1969), mean FCM production was slightly higher in cows receiving concentrate in the diet than in cows fed only forage, differences in milk production for different levels of concentrates were not significant (p>0.10). Milk fat was significantly higher (p<0.05) for cows fed silage and hay than for those fed hay as the sole roughage. Röhrmoser and Kirchgessner (1982) investigated the consequences of a 15% undersupply in gross energy during a period of four weeks in the middle of lactation (beginning of the experiment at day 149 of lactation). The cows responded to the reduced energy intake directly with a decrease in milk yield (Figure 3). There was no significant difference in milk fat between the two groups. The milk protein percentage decreased slowly but constantly during the trial period in the experimental group.

Johnson (1984) demonstrated significant effects of feeding in the early part of lactation on the yields of milk, protein and lactose, but not on milk fat or BW change. Kunz et al. (1985) reported a decrease of milk production during the first week of lactation in cows fed only 0.75 of
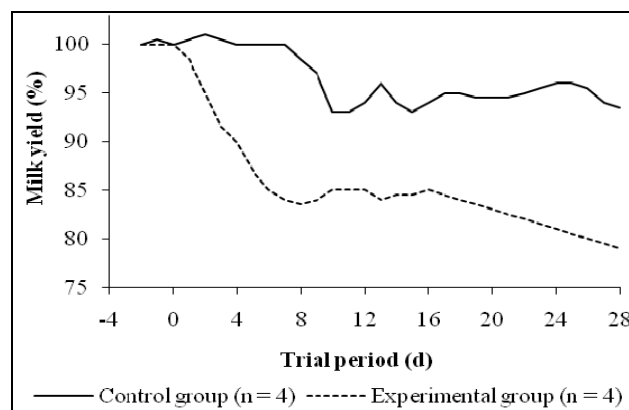

Figure 3. Average daily milk yield for control (adequate energy intake) and experimental (15% undersupply in gross energy) cows (Mean of group in the beginning of the experiment = 100%) (p<0.01) (adapted from Röhrmoser and Kirchgessner, 1982).

requirements compared to animals whose energy intake was planned to cover energy requirements. McNamara and Hillers (1986a) observed that heifers receiving a low energy diet (60% hay and 40% concentrate) ingested 19% less net energy and produced 7% less milk of 28% higher milk fat percent compared with heifers fed a high energy diet (40% hay and 60% concentrate). In the study of Kaufmann et al. (1987) a 11% surplus of gross energy intake in lactation resulted in a 0.9 MJ/d higher average excretion of milk energy. Broster et al. (1989) fed a high and a moderate energy ration in lactation. The high energy ration contained 150 MJ/d (heifers' diet) and 180 MJ/d (cows' diet). The moderate energy ration contained 125 MJ/d (heifers' diet) and 150 MJ/d (cows' diet). Milk yield of the high energy supplied animals was 4693 kg per lactation, the yield of animals supplied with moderate energy was only 3,797 kg per lactation. There was no statistically significant effect on the fat or protein contents in milk. Chilliard (1992) reported decreased milk protein yields in lean underfed cows. Garnsworthy and Hugget (1992) observed an increasing milk fat concentration but decreased protein concentration in cows receiving a fat-supplemented diet. Increasing milk yield with increasing concentrate level in total mixed diets were monitored by Friggens et al. (1998). Ferris et al. (2003) demonstrated significant increases in milk yield, milk protein content and milk energy output with increasing level of concentrate inclusion. Kokkonen et al. (2004) also found that rapid increases of concentrate tended to increase (p<0.10 or better) milk yield, during lactation weeks 1 to 5, but an increased proportion of concentrate in the pre-partum diet tended to decrease (p<0.10 or better) fat content in milk. The average response of ECM yield to rapid increase of concentrate was 1.68 kg per kg increase of concentrate DM (Kokkonen et al., 2004). In the study of McNamara et al. (2003b) a greater amount of concentrate supplement post-partum increased fat and protein yields. In the trial of Patton

et al. (2006) cows milked once daily had lower milk yield and higher milk fat and milk protein concentrations compared with cows milked three times daily, probably due to less NEB caused by lower milk yield. Staufenbiel et al. (2003) concluded that a lower backfat thickness lead to negligibly higher milk yield, but a nadir below 10 mm of back fat thickness resulted in decreased milk production. Burke and Roche (2007) found that the yield of FCM during the first 35 days of lactation was reduced by 23% among cows on a restricted feed intake. In the experiment of Roche (2007), post-partum feed restriction reduced yield of FCM, fat and protein during the first five weeks post-partum in grazing dairy cows. Decreased (p<0.05) yields of FCM, fat and protein were also evident for 10 weeks after the end of feed restriction. Urdl et al. (2007) demonstrated significant differences in milk yield and composition for 75, 100 and 125% post-partum energy intakes. Cows receiving 75% of energy requirement yielded an average of 20.9 kg/d milk in lactation, cows receiving 100 and 125% of energy requirements post-partum yielded 29.6 and 32.3 kg/d milk, respectively. The milk fat percent decreased in cows on the high energy level (4.41 and 4.07% for the 75 and 125% animals, respectively), but milk protein percent increased (3.00 and 3.40% for the 75 and 125% animals, respectively).

EFFECTS OF ENERGY SUPPLY ON REPRODUCTION

Reproductive performance has declined in modern dairy systems concurrently with strong genetic progress for high milk yield (Nebel and McGilliard, 1993). This low fertility is related to a multitude of health, physiological, and management factors, themselves a result of modifications to a number of physiological processes, including gluconeogenesis, nutrient partitioning, insulin resistance, and appetite signalling (Lucy, 2003). Infertility is the main culling factor in dairy herds (Farries, 1983a). The study of McGowan et al. (1996) demonstrated that when high genetic merit cows are appropriately fed and managed, high milk production and satisfactory reproductive performance can be achieved. Roche et al. (2000) reasoned that nutritional management of the dairy cow in the transition period about three weeks before calving to about three weeks after calving has significant carry-over effects on reproductive performance. A high NEB in the periparturient and early post-partum period decreases luteinizing hormone (LH) pulse frequency, growth rate and diameter of the dominant follicle, insulin-like growth factor I (IGF-I), glucose and insulin concentrations and increases growth hormone (GH) and certain blood metabolites; these effects result in greater loss of BCS and a higher percent of anoestrus cows in the herd. Loss of body condition during the breeding period is thought to result in lower conception rates and more open days (days from calving to conception) (Fronk et al., 1980; Butler et al., 1981). Butler et al. (1981) found that EB during the first 20 days of lactation was inversely related to days to normal ovulation. Resumption of ovarian cyclicity is largely dependent on LH pulse frequency.

Pregnancy occurs ordinarily as recently as finishing fat mobilization (Kanitz et al., 2003). Patton et al. (2006) reasoned for dairy cows that once-daily milking in early lactation may promote earlier resumption of ovarian cyclicity, mediated through improved nutritional status. High serum cholesterol concentrations induced by the supplementation of fat in the diet is associated with an increase in serum and follicular progesterone concentrations, a decrease in serum estradiol concentrations (Hawkins et al., 1995), and an increase in prostaglandin F2α (PGF$_{2\alpha}$) (Lucy et al., 1991), which leads to a delayed resumption of ovarian cyclicity. In the study of Staples et al. (1990), cows in a more negative energy status ate less, produced less milk, and lost more BW, resulting in an abnormal oestrous cycle.

Plasma progesterone concentrations are normally used to indicate when the cow has returned to normal oestrous cycle, but the secretion of progesterone is reduced by spontaneous caloric deficit and is modulated by timing and magnitude of maximal caloric deficit (Villa-Godoy et al., 1988). Staples et al. (1990) defined evidence of corpus luteum activity as either i) plasma progesterone concentrations greater than 1 ng/ml for more than two consecutive sample days (short cycle) and followed by subsequent sustained rises in progesterone concentrations, or ii) sustained rises in progesterone concentrations without a prior short cycle.

Figure 4 shows how energy deficiency influences ovarian function. Insulin and IGF-I act directly on the follicles (pathway 1). The decreased insulin and IGF-I concentrations in high yielding dairy cows cannot sufficiently stimulate follicular growth (Nebel and McGilliard, 1993). If there are decreased insulin and glucose concentrations, structures and messengers of the central nervous system (CNS) signal metabolic stress to the hypothalamus (pathway 2). The result is reduced synthesis and secretion of gonadotropin releasing hormone (GnRH), and subsequently the synthesis and secretion of follicle stimulating hormone (FSH) and LH. Leptin, released from adipocytes during lipolysis, also acts as a messenger of energy deficiency to the hypothalamus (pathway 3) (Kanitz et al., 2003).

Milk production is stimulated by prolactin and GH. Prolactin and GH inhibit the synthesis and secretion of GnRH and consequently the synthesis and secretion of FSH and LH (Kanitz et al., 2003). In high-yielding cows prolactin and GH concentrations in blood are increased (Nebel and McGilliard, 1993). Blum et al. (1985) showed
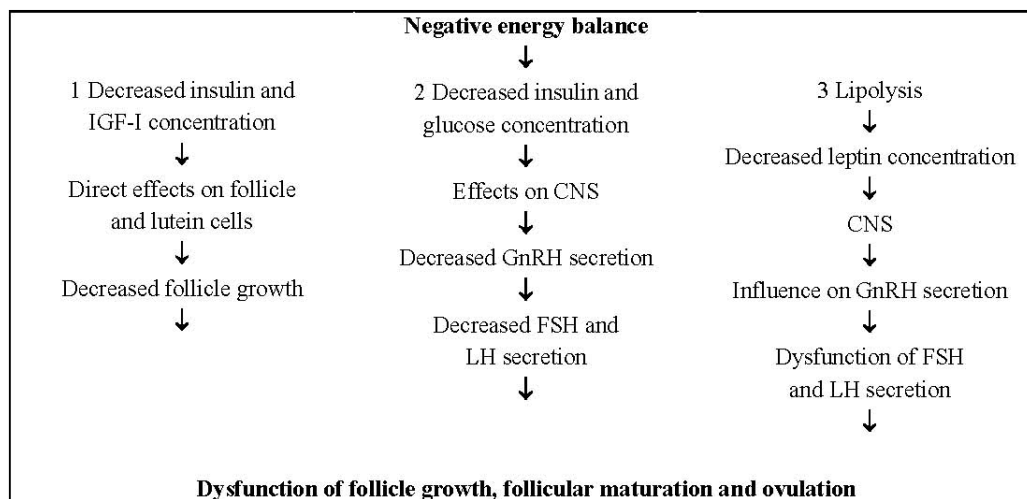
Figure 4. Relationships between energy deficiency and ovarian functions (scheme) (adapted from Kanitz et al., 2003).

higher values of GH in cows receiving a low energy diet compared with cows on a high energy intake (6.82 vs. 2.43 µg/L). Kunz et al. (1985) also measured higher GH levels during the dry period in animals fed energy restricted to requirements compared to those fed *ad libitum*. In the study of Roche et al. (2005), increasing energy intake in late gestation was associated with pre-partum plasma concentrations of GH that declined linearly (6.03, 4.03, 3.94, and 3.80 ng GH/ml for 56, 84, 103, and 112 MJ of ME/d per cow, respectively). The post-partum GH concentrations were not affected by the pre-partum treatment. This was confirmed by Burke and Roche (2007) and Roche et al. (2007). However, in the study of Grum et al. (1996) cows fed a high-fat diet during the dry period had higher GH concentrations pre-partum.

It is important to decrease the incidence of metabolic disease by achieving high DMI and minimising the period of NEB after parturition (Roche et al., 2000). Dairy cows tolerate slight under-nutrition during early post-partum and weight loss, and resume reproductive function by 15 to 40 days after calving despite being in NEB (Villa-Godoy et al., 1988; Butler and Smith, 1989; Staples et al., 1990). In the experiment of Butler et al. (1981), the magnitude of NEB during the first 20 days of lactation was inversely related to days to normal ovulation (r = -0.60) and to milk production (r = -0.80). Milk yield was not closely related to days to ovulation (r = 0.30) and also not significantly related to serum prolactin concentrations over the first three months of lactation (r = 0.27). Butler et al. (1981) concluded that EB during the first 20 days of lactation is important in determining the onset of ovarian function following parturition. Beam and Butler (1999) proposed that the day of EB nadir is more important than the degree of NEB in suppressing LH pulse frequency. Delayed resumption of ovulation was related to the degree of NEB.

The conditional nadir of backfat thickness should not decline below 13 mm on herd average, otherwise increasing incidence of fertility problems are suspected (Staufenbiel et al., 2003).

It is well documented that energy stores during late gestation, parturition, and early lactation affect the length of the post-partum anoestrous interval and the likelihood of a successful pregnancy (Markusfeld et al., 1997; Beam and Butler, 1999; Engelhard et al., 2007; Roche et al., 2007).

Houghton et al. (1990a) showed an interaction between pre- and post-partum energy intake affected post-partum anoestrous interval (d) and cycling activity (%), respectively: low energy pre-partum - low energy post-partum = 72.6 and 33.3; low energy pre-partum - high energy post-partum = 54.3 and 56.3; maintenance energy pre-partum - low energy post-partum = 65.7 and 52.9; maintenance energy pre-partum - high energy post-partum = 68.4and 54.3). Under-conditioned cows generally had a longer post-partum anoestrous interval but a higher first service conception rate than moderate or over-conditioned cows. This observation was also recorded by Markusfeld et al. (1997). Forage to concentrate ratio can have an effect on fertility in cows. Allrich et al. (1987) reported a tendency for longer intervals from calving to second ovulation (7.5 days, nonsignificant) when the percentage of concentrate was increased from 50 to 70%, and this occurred despite a tendency for improved EB by this change. The results of Andersson et al. (1991) showed that increasing total energy intake in early lactation reduced the period from parturition to last service. Only one MJ of ME can shorten the interval by about 0.3 days in primiparous cows and by 0.1 days in multiparous cows. However, feeding 2 kg more concentrate per day at calving to multiparous cows, and 15 days after calving to primiparous cows, causes longer intervals from calving to first insemination and from calving to last

insemination, respectively. Concentrates often contain a higher percentage of fat than forage. A high level of fat in the diet is related to an increase in luteal lifespan and function of the corpus luteum. This means that increased post-partum energy intake and weight gain are essential for under-conditioned cows if they are to have acceptable fertility parameters (Houghton et al., 1990a).

Nocek et al. (1983) monitored reproductive performance during the lactation subsequent to dry period treatments. Results are shown in Table 4. Days to first observed oestrus were identical among treatments, averaging 47 d. The dry period feeding did not influence services per conception rate, as confirmed by Ruegg et al. (1992).

Wildman et al. (1982) reported that average BCS in groups of cows varying in days open were different (p< 0.05). Days open increased as BCS increased. The average BCS was 2.66, 2.92 and 3.22 for cows <60, 60 to 100, and >100 days open, respectively. In the study of Houghton et al. (1990a), a high energy diet post-partum increased (p<0.10) pregnancy rate by 22.7%. McGowan et al. (1996) observed that BCS of cows during the first 26 weeks of lactation was negatively related to number of services per conception and inter-calving interval. However, milk yield was positively related to number of services per pregnancy and calving interval. Huszenicza et al. (1987) found that cows calving in a medium body condition resumed cyclic ovarian activity about ten days earlier than those calving in a body condition poorer than average (60.1±19.4 vs. 70.6±14.4 d, respectively). No difference was found between the two groups in the incidence of cyclicity disorders, conception rate, and time of conception. Cows only maintaining their body condition, or showing a decline in body condition, required a much longer time after calving to resume cycling (66.1±19.4 vs. 46.0±13.3 d, respectively, showed a higher incidence of cyclicity disorders, conceived in a lower proportion and later than cows exhibiting an improvement of body condition. Holtenius et al. (2003) demonstrated that cows fed at a high level during the dry period had a long

interval, 52 days, from parturition to normal cyclicity according to milk progesterone profiles. Burke and Roche (2007) described that when pasture is the sole dietary source during the calving transition period, postartum anovulatory intervals may be influenced negatively by low pre-partum energy intake levels. Colazo et al. (2009) summarized that animals which were feed-restricted pre-partum were less fertile as reflected by a lower percent pregnancy to first-time artificial insemination and had increased days open, indicating that the carryover effect on fertility was probably through an impairment of oocyte competence. Houghton et al. (1990a) suggested that cows must be in moderate to nearly moderate body condition at parturition to maintain acceptable fertility parameters.

The degree of change in body condition is in a close negative correlation with the duration of post-partum acyclia and with the intervals from calving to first ovulation and from calving to conception (Huszenicza et al., 1987). Huszenicza et al. (1987) observed, for an energy intake which met only 76% of the actual energy requirement, a prolongation of the post-partum acyclia (71.2±21.4 vs. 50.7±13.6 d), a higher incidence of cyclicity disorders, and a reduction in the conception rate (6 of 12 vs. 11 of 13), compared with cows provided with sufficient energy. The results of Houghton et al. (1990a) and Ruegg et al. (1992) suggest that cows must be fed to obtain nearly moderate body condition by time of breeding to obtain optimal pregnancy rates.

Milk yield and services per conception are phenotypically positively correlated (r = 0.12) and, because of that, in high-yielding cows the rate of insemination is higher than in extensively kept cows (Badinga et al., 1985). However, Burke and Roche (2007) found no relationship between post-partum anovulatory intervals and milk production characteristics in dry period pasture-fed cows. Ferguson (1996) presented data from 531 Holstein cows showing the change in body condition, as a reflection of NEB, and conception rate at first insemination (Table 5). Cows losing more than -0.5 BCS unit had significantly lower conception rates. Cows appear to tolerate a body condition loss up to -0.67 units before fertility declines.

Table 4. Reproductive performance during the lactation subsequent to dry period treatments (adapted from Nocek et al., 1983)

	Dry period treatment	
	100% hay	50% hay, 50% corn silage
Number of cows	94	82
Days to first observed oestrus	47	47
Pregnant by 100 days (%)	60	59
Days open	94[a]	85[b]
Services/conception	2.2	2.0

[a,b] Means within rows with different superscripts differ (p<0.10) differ by pair-wise multiple F comparison, as described by author.

Table 5. The influence of rate of post-partum body condition loss on first service conception rate (adapted from Ferguson, 1996)

Range	Body condition loss (Mean)	Conception rate[a] (calving-breeding)
0.51 to 1.0	(0.75)	55.9
0.01 to 0.50	(0.25)	49.5
	(0)	46.3
-0.01 to 0.50	(-0.25)	43.2
-0.51 to 1.0	(-0.75)	37.0
>-1.0	(-1.5)	28.6

[a] n = 531 cows. Scale of Condition Score 1 to 5 (Wildmann et al., 1982).

Extreme loss (greater than one unit of body condition on a five-unit scale) of body condition after parturition results in lower fertility (Table 6) (Nebel and McGilliard, 1993), but, within the moderate range (one scoring unit), body condition and fertility are not related (Butler and Smith, 1989). Ruegg et al. (1992) observed longer days of conception for cows losing >0.75 points of condition in lactation.

Ultimately, cows that lose more body condition soon after parturition have pregnancy rates that are similar to those of cows that lose little condition, so infertility associated with body tissue loss is temporary (Nebel and McGilliard, 1993). In the study of McGowan (1996), the degree of body condition loss in primiparous and multiparous cows between parturition and week 10 of lactation was negatively related to the number of days to first observed oestrus. In the study of Kim and Suh (2003), the number of days to first breeding after calving was longer ($p<0.05$) in cows with a high loss of body condition (103 ± 7.8 day) than in the group with moderate condition loss (87 ± 5.3 day).

However, Treacher et al. (1986) and Olsson et al. (1998) found no significant differences in any of the fertility traits in cows receiving different concentrate levels in late gestation and early lactation. Richards et al. (1986) could not detect an effect of post-partum nutritional management on interval to oestrus or interval to pregnancy in beef cows. Keady et al. (2005) found no effect of pre-partum energy intake on post-partum onset of cyclicity. In the trial of Castañeda-Gutiérrez et al. (2009), feeding different dietary supplementations peri-partum (different FA supplements or propylene glycol) showed no effect on days to ovulation compared with control animals. Colazo et al. (2009) postulated that the negative consequences on fertility in cows subjected to pre-partum feed restriction abated with time.

EFFECTS OF ENERGY SUPPLY ON HEALTH

Inability of the cow to cope with the metabolic demands of high production is manifest in several production diseases followed by economic loss and an animal welfare concern (Mulligan and Doherty, 2008). Several early studies suggested that certain disorders in early lactation may be associated with diet (Coppock et al., 1974; Morrow, 1976), while other studies with different diets suggested little effect on health (Davenport and Rakes, 1969; Gardner, 1969). Nocek et al. (1983), Chilliard (1992), and Olsson et al. (1998) observed no effects of dry period diet on clinical or subclinical manifestation of diseases in the subsequent lactation. Mulligan and Doherty (2008) concluded that the manifestation of production diseases is caused by the complex relationship of imbalances in inputs and outputs.

Table 6. Relationship between body condition loss during first five weeks post-partum and reproductive performance (adapted from Butler and Smith, 1989)

	Body condition loss		
	< 0,5	0,5 to 1,0	>1,0
n	17	64	12
Days to first ovulation	27[a]	31[a]	42[b]
Days to first observed oestrus	48[ab]	41[a]	62[b]
Days to first service	68[a]	67[a]	79[b]
First service conception rate (%)	65[a]	53[a]	17[b]
Services per conception	1.8	2.3	2.3
Pregnancy rate (%)	94	95	100

[a,b] Significantly different ($p<0.05$); no symbol $p>0.05$.

Grummer (1995) and Drackley (1999) described the transition period as the period from three weeks pre-partum until three weeks post-partum. This period is characterised by marked changes in endocrine status, a reduction in feed intake and a rising nutrient demand for the developing foetus and the impending lactogenesis. Most of the metabolic diseases of dairy cows, such as milk fever, ketosis, retained placenta and displaced abomasum, occur within the first two weeks of lactation because the rumen microbes are mostly not adapted to the high energy density of the lactation diet. There is a risk of developing rumen acidosis because the lactate producers respond rapidly to the higher starch diet and produce high amounts of lactate. The bacterial population that converts lactate responds only slowly to a change in diet (Goff and Horst, 1997). Vandehaar et al. (1999) concluded that increasing the energy density up to 6.7 MJ of NEL/kg in diets during the last month of gestation improves nutrient balance of cattle pre-partum and decreases hepatic lipid content at parturition. Staufenbiel et al. (2003) proposed a conditional nadir that should not decline below 13 mm backfat thickness on herd average in order to maintain a high production level without an increasing incidence of health disorders.

The incidence of periparturient diseases, for example, milk fever, ketosis and mastitis, is higher in over-conditioned cows (Morrow, 1976; Fronk et al., 1980; Treacher et al., 1986) and resistance to infection is decreased (Morrow, 1976). Excessive lipid mobilization from adipose tissue is linked with greater incidence of health problems in the transition period (Drackley, 1999). The mobilisation of FA from adipose tissue to support the nutrient demands of lactation is a natural biological phenomenon but increasing NEFA in blood results in the accumulation of TG in hepatocytes and the impairment of liver function. A fatty liver is not able to derive an adequate amount of glucose for metabolism, which also plays a central role in feed intake regulation, fertility and immunity (Mulligan and Doherty, 2008). Morrow (1976) described fat cow syndrome as a disorder resulting from excessive energy

consumption and nutrient imbalances in dry cow diets.

Coppock (1974) concluded that dry period diets high in grain or corn silage predisposed cows to displaced abomasum. Morrow (1976) and Boisclair et al. (1987) reported a higher rate of displaced abomasum postpartum in dairy cows energy-oversupplied in dry period. Cameron et al. (1998) found a significant association between NEB pre-partum, as reflected by elevated NEFA concentration, and the occurrence of displaced abomasum. Different authors have reported that an increased plasma NEFA concentration may cause hepatic lipidosis and ketosis. Hepatic lipidosis affects insulin level. Insulin reduces the rate of abomasal emptying, and cows with abomasal displacement exhibit a resistance to insulin. Ketosis decreases DMI, followed by reduced rumen fill and forestomach motility, and potentially abomasal motility (Cameron et al., 1998).

Johnson and Otterby (1981) fed three different diets: all hay; corn silage, alfalfa silage, and 1.0 kg grain/d; or silage plus 4.1 kg grain/d for the last 30 days post-partum. There was no incidence of displaced abomasum in any treatment group. Nocek et al. (1983) assigned 289 cows to all hay, 50:50 hay:corn, or limited corn silage plus liquid protein supplement at drying-off. The non-significant trend was for more frequent displaced abomasum as the diet moved further from all hay with 3.0, 4.3, and 6.3% lactational incidence rate, respectively.

Excessive body condition at parturition (Morrow, 1976; Markusfeld et al., 1997; Knight, 2001) and NEB post-partum (Baird, 1982) lead to ketosis. The lactational incidence rate of clinical ketosis among Holstein Friesian cows is 1.1 to 9.2% (Erb and Gröhn, 1988). Markusfeld (1985) investigated the association between overfeeding pre-partum, metritis and ketosis. In the second week after parturition the overall rate of incidence of ketone bodies in urine (ketonuria) was 18% and that of parturient uterine diseases was 56.5% in the overfed group. 80% of all cows with ketonuria concurrently suffered from post-parturient uterine diseases. Shirley (1994) reported that primiparous cows fed to a BCS of 4.0, and maintained in that condition for the last 60 d before calving, experienced a high incidence of sub-clinical ketosis and a 50% incidence of displaced abomasum within the first 30 d post-partum. In the experiment of Olsson et al. (1998), no cases of ketosis occurred in cows on a low dietary energy level in the first month of lactation. Noro et al. (2006) observed a prevalence of 44% subclinical ketosis in lactating cows when only grazing, and no cases in grazing cows supplemented with concentrate. Clinical ketosis can cause fertility problems (Baird, 1982). However, Johnson and Otterby (1981) observed only a small effect of dry period ration on post-partum ketosis risk.

Kim and Suh (2003) described the occurrence of metritis and metabolic diseases (including abomasal displacement, milk fever, and ketosis) which was greater (p<0.01) in cows losing 1.0 to 1.5 BCS points in the first four months in lactation than in cows losing only 0.00 to 0.75 points BCS (23% and 2%, respectively).

NEB at the beginning of lactation can cause fatty liver syndrome (Morrow, 1976). Bertics et al. (1992) suggested that some fat infiltration occurs prior to and during calving. This infiltration may result from elevated NEFA caused by endocrine changes that are associated with calving and by reduced feed intake during the final weeks preceding parturition. Lipid accumulation in liver may contribute to health disorders and decreased milk production (Drackley, 1999).

Retained foetal membranes can also be a consequence of overfeeding in the dry period (Morrow, 1976). However Markusfeld et al. (1997) observed that the risk of retained placenta was greater for cows that were under-conditioned at drying off, whereas cows that lost more body condition during the dry period suffered additionally from metritis.

In contrast, Watters et al. (2008) concluded that dry period length had no influence on incidence of mastitis or metabolic disorders like ketosis, retained placenta, displaced abomasum, and metritis.

Nocek et al. (1983) summarized that varying forage:concentrate ratio in lactational diets has only a small effect on health. A variety of forage types can be used successfully during the dry period as long as the ration is nutritionally balanced and fed in amounts to achieve or maintain adequate body condition.

It can be concluded that individual production diseases of the dairy cow are best not considered in isolation. For example ketosis, fatty liver, retained placenta, hypocalcaemia, metritis and displaced abomasum may be all interrelated (Mulligan and Doherty, 2008).

EFFECTS OF ENERGY SUPPLY ON CHANGES OF BODY RESERVES

Lipid mobilized from body reserves makes a substantial contribution to the energetic cost of milk production in early lactation (Friggens et al., 2004). Gardner (1969) postulated that an average of 7.9 MJ of digestible energy was required per kilogram of solids-corrected milk to maintain a relatively constant BW through a complete lactation. During a lactation cycle, dairy cows are successively mobilizing and storing body reserves (Chilliard et al., 1991; Friggens et al., 2004), independent of the requirement for milk production (Farries, 1983a; Friggens et al., 1993). During pregnancy and lactation, adipose tissue undergoes specific metabolic alterations (McNamara and Hillers, 1986a). McNamara and Hillers (1986b) demonstrated that genetic potential for milk production is linked with adipose tissue metabolic rates and

adipose tissue lipolysis is not greatly affected by a large decrease in NEB due to decreased energy intake in early lactation. Adipose tissue provides energy in the form of FA and glycerol to other organs, especially when the dietary intake does not meet requirements (McNamara, 1991). These adaptations consist of mid-pregnancy anabolism followed by a significant shift to catabolism in late pregnancy and a dramatic catabolic shift in early lactation (Baumann and Currie, 1980; McNamara, 1991). In late lactation and the dry period, there are two reasons for building body reserves. On the one hand, mobilization in early lactation represents an extra energy source to compensate for the NEB as a consequence of reduced feed intake; on the other hand, high pre-partum BW gains lead to health and metabolic problems (Fronk et al., 1980; Garnsworthy and Topps, 1982). The duration and magnitude of these adaptations depend on milk energy secretion, net energy intake, genotype, and endocrine regulation (McNamara, 1991).

At parturition, the amount of body fat is an indicator of the energy available to supply the difference between dietary energy intake and the requirements for maintenance and milk production during early lactation (Garnsworthy and Topps, 1982; Boisclair et al., 1986; Treacher et al., 1986). The post-partum delay in hyperphagia is associated with body tissue reserves being mobilized to support milk production (Baumann and Currie, 1980). The physical and physiological regulators of feed intake are not able to avoid nutritional oversupply; therefore, mainly adipose tissue is synthesized (Davenport and Rakes, 1969; Fronk et al., 1980; Boisclair et al., 1986).

However, BW changes at parturition can be used only with restriction as an indicator of rate of body mass mobilization and retention post-partum (Boisclair et al., 1986). Wildman et al. (1982) could not correlate BW and frame size measurements with BCS. In the study of Hattan et al. (2001), the EB and BCS measurements indicated that cows achieved positive EB between weeks 12 and 18 of lactation, whilst BW measurements showed gains from week 6. This means that BW is not a reliable index of energy status in high-yielding dairy cows during early lactation, whilst the extent of energy mobilization in such cows may be substantial and prolonged. Increases of BW during lactation are largely a result of increased gut fill, gut tissue mass and water retention due to degradation of adipose tissue, besides the development of foetus and mammary gland which superimpose on the effect of BW changes (Davenport and Rakes, 1969; Fronk et al., 1980; Boisclair et al., 1986; Hattan et al., 2001). Change in body condition in cows during early lactation indicates to a higher extent how much body tissue is mobilized for milk yield (Nebel and McGilliard, 1993). Ryan et al. (2003) fed cows a grass silage/concentrate or a grass silage/straw diet

pre-partum and found that average BCS at parturition was significantly higher in the grass silage/concentrate group (3.00) than in the grass silage/straw group (2.73), but there was no difference in BW. Treatment had no significant effect on BCS loss and BW loss post-partum.

McNamara et al. (2003b) concluded that, due to the exponential rise of foetal development in late gestation, the target BW gain should be 0.6 kg/d in the final four weeks of gestation. Chilliard (1992) postulated that when milk yield exceeds 20 kg/d, cows eat more but not enough to meet the mammary needs for nutrients. Consequently, BW loss increases. Imakawa et al. (1987) observed that high-yielding dairy cows lose 20 to 25% of BW in early lactation.

Oldenbroek (1988) observed that cows receiving 50% concentrate (DM) in the diet were already increasing their BW soon after parturition, while cows receiving a complete roughage diet increased their BW much later in lactation. Probably, in the concentrate group the rumen microbes are better adapted on the high concentrate lactation diet. The study of Holter et al. (1990) confirmed that underfed cows in late gestation mobilize body tissue at a lower rate in the following lactation. Despite the small BW loss in early lactation the pre-partum underfed cows could not reach their former BW at parturition until lactation week 14. Garnsworthy (2007) postulated that well-conditioned cows at parturition lose more body fat than low-conditioned cows (-65 vs. -37 kg BW, respectively), because it seems that cows have a physiological target level for body reserves in early lactation (Garnsworthy and Topps, 1982). Davenport and Rakes (1969) varied energy intake pre-partum, achieving different BW at parturition. The cows on a low pre-partum energy level mobilized least body mass in the following lactation compared to moderate-supplied and overfed animals. In consequence, the moderate-fed cows already achieved their parturition BW 16 weeks post-partum, whereas the better-supplied cows mobilized body reserves for a longer period. The degree of body tissue mobilization in lactation depends on feed intake post-partum and on the amounts of mobilizable adipose and protein tissue (Davenport and Rakes, 1969).

However, in the experiment of Olsson et al. (1998) pre-partum energy intake did not influence BW at parturition, but cows underfed in the dry period showed a significantly higher body mass gain in the first three months of lactation. Colazo et al. (2009) suggested that lipid mobilization did not differ between restricted- and *ad libitum* fed cows, although the former lost more BW and entered a state of NEB during the pre-partum period.

Wildman et al. (1982) measured different BCS for each persistency of lactation. At the beginning of lactation, a part of the energy necessary for milk production is derived from body reserves and not from feed, and at the end of lactation part of the feed energy is apportioned to body tissue
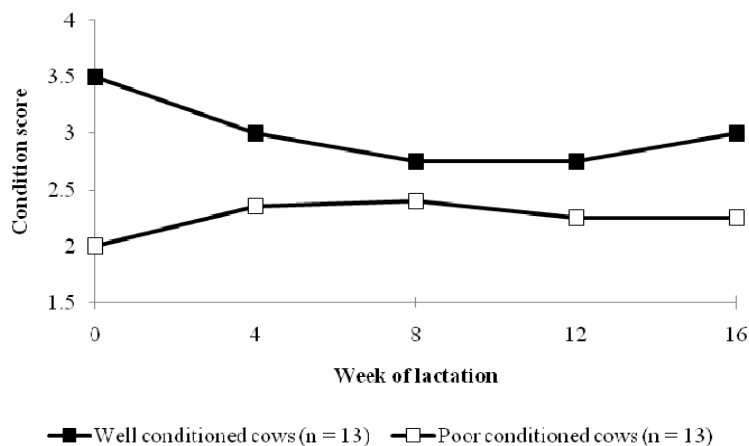
Figure 5. Mean condition score during the first 16 weeks of lactation (p<0.05) (adapted from Garnsworthy and Jones, 1993).

(Gruber et al., 2003). High- yielding cows cannot maintain a positive EB during early lactation and have to mobilize body reserves, and cows in the later stages of lactation do not regulate their feed intake to the physiological requirements for milk production (Coppock et al., 1974; Villa-Godoy et al., 1988; Roche et al., 2000; McNamara, 2003a). Jones and Garnsworthy (1989) stated that with diets of lower energy concentration, intake is limited by rumen capacity and thin cows eat the same as fat cows. This results in increased fat mobilization and a slight decrease in milk yield by cows which are fat at calving, but the limited fat reserves of cows which are thin at calving are insufficient to compensate for reduced energy intake leading to large reductions in milk yield. Nutritional manipulation of cows to be fatter, or leaner, than normal at parturition provokes a change in subsequent body lipid mobilization such that normal levels of body fatness are regained approximately three to four month after calving (Garnsworthy and Topps, 1982; Broster and Broster, 1998). High-producing cows should lose not more than -0.5 BCS units by 30 days after calving and begin to increase BCS by 12 to 14 weeks post-calving (Ferguson, 1996). In the experiment of Waltner et al.

(1993), a moderate loss of 0.5 to 1.5 BCS units by 120 DIM was associated with higher milk production. High rates of loss (more than 1.5 or 2.0 BCS units) have been associated with reduced milk production compared with potential production. Better-conditioned cows lose more BCS than lean cows regardless of dietary energy intake post-partum (Fronk et al., 1980; Treacher et al., 1986; Ferguson and Sniffen, 1991). This was also confirmed by Kunz et al. (1985) and Houghton et al. (1990b). During the first 16 weeks of lactation, Land and Leaver (1981) demonstrated differences in condition change (-0.41 vs. -1.03) and BW change (-0.04 vs. -0.10 kg/d) for cows calving with a condition score of 2.5 or 3.5. In the study of Treacher et al. (1986), cows calved with a BCS of 2.5 (thin) or 4.0 (obese). The obese cows lost 48 kg BW and 1.20 units condition score during early lactation compared with 27 kg BW and 0.52 units condition score in the thin cows. Garnsworthy and Jones (1993) found a significant effect of condition score at parturition on condition score and BW losses in early lactation, with well-conditioned cows losing considerably more reserves than thin cows (Figures 5 and 6).
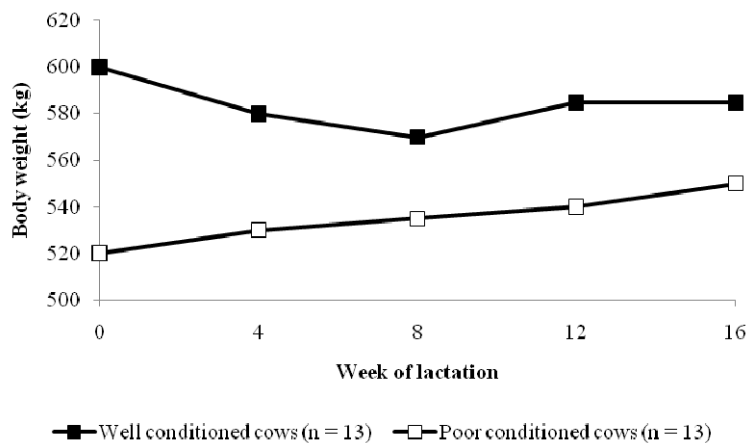
Agenäs et al. (2003) and Holtenius et al. (2003)

Figure 6. Mean BW during the first 16 weeks of lactation (p<0.05) (adapted from Garnsworthy and Jones, 1993).

assumed that well-conditioned cows are less efficient in energy utilization than thinner animals. In the experiment of Holtenius et al. (2003), well-conditioned cows lost more body condition than cows in a low or moderate condition post-partum, although there was no significant difference in EB. The relationship between BCS at parturition and loss of BCS in early lactation is genetically determined and very strong (r^2 = 0.82). This was also confirmed by Chilliard (1992). Douglas et al. (2006) attested to a lower BW and BCS for pre-partum feed-restricted cows, but they converged to similar nadirs post-partum compared with cows supplied feed *ad libitum* in the dry period.

Dietary fat does not suppress body lipid mobilization during the early post-partum period (Grummer et al., 1995; Grum et al., 1996). Chilliard (1992) summarized the relationship of protein feeding and body fat mobilization. An increased supply of limiting amino acids to the mammary gland can indeed increase milk yield, followed by an increased energy requirement of the cow. This can lead, on the one hand, to increased DMI or, on the other hand, to increased degradation of fat tissue that will supply FA for fat synthesis and oxidative energy in the mammary gland. In an earlier study, Garnsworthy (1988) observed similar results. In his trial, milk response to an increased protein supply was higher in fat than in lean cows.

However, Nocek et al. (1983) found no differences in BCS at termination of the dry period, although cows were fed different diets containing 100% hay, 50% hay and 50% corn silage during the dry period, or limit-fed corn silage plus 1.1 kg liquid protein supplement. Reid et al. (1986) performed an experiment with two groups of cows to compare the effect of calving in good or poor condition on the mobilization of adipose tissue. There were no differences between groups in the amount of adipose tissue mobilized between 4 weeks before and 26 weeks after parturition. Subcutaneous fat depth over the shoulder reached minimum values in both groups at twelve weeks after parturition, when energy deficit became zero.

The studies of Garnsworthy and Topps (1982) and Douglas et al. (2006) showed that BCS converges post-partum, despite different pre-partum diets or BCS. In the trial of Holcomb et al. (2001), pre-partum diets did not affect post-partum means for BW and BCS. Engelhard et al. (2007) found no significant effects of length and feeding in the dry period on changes in BW and backfat thickness in the following lactation. Guo et al. (2007) detected no special effects of dry period energy intake on changes of BW and BCS in lactation. The observed changes of BCS and BW were the genetically determined changes described by Garnsworthy and Topps (1982).

Chilliard (1992) underlined that the extent and duration of body fat and protein mobilization after parturition depend on milk potential, feeding level and quality, and initial body condition. Body fat ranges from 80 to 120 kg and body proteins comprise 80 to 90 kg at parturition in Holstein Friesian cows (Chilliard, 1992). In early lactation, dairy cows can mobilize up to 90 kg body fat and more than 20 kg body protein, depending on energy intake pre-partum and milk yield. In advancing lactation these nutrients are restored (Bell, 1995). Chilliard et al. (1998) concluded that, in a period of under-nutrition, the cow is able to mobilize 80% of adipose and 15 to 20% of protein reserves. Most of the body protein is structural components, thus a large amount of protein tissue cannot be mobilized (Chilliard, 1992). Bauman and Currie (1980) demonstrated the importance of lipid mobilization. In high-yielding dairy cows the estimated amount of body fat mobilized to meet the energy deficit was equivalent to over 50% of the milk fat output over the first five weeks of lactation. During the first 16 weeks of lactation, when the cows were in negative NEB, they mobilized 50 to 60 kg of fat - about 10% of their BW and probably at least 50% of their total adipose lipid reserves. Tissue mobilization during the first 2 months of lactation is from 15 to 60 kg of lipids (Martin and Ehle, 1986) and from 0 to 15 kg of protein (Chilliard, 1987). In the study of Tamminga et al. (1997), energy balance in early lactation resulted in mobilisation of 42 kg empty body weight (EBW), 31 kg fat and 5 kg protein. Cows mobilized an average of 0.70 kg EBW, 0.56 kg fat and 0.04 kg protein per day; the largest part of this mobilization took place in the first week after parturition with 37% of EBW, 12% of total fat and 58% of total protein being mobilized. Johnson (1984) fed adult British Friesian cows on a moderate energy level for 20 weeks after calving. The cows were unable to compensate for the dietary energy deficit and produced about 450 kg milk from body energy reserves.

Houghton et al. (1990b) offered a low energy ration pre-partum to beef cows. On day 30 post-partum, the cows were slaughtered to measure body composition. The low energy diet reduced (p<0.01) BCS, cow weight, total empty body lipid, body energy and daily predicted maintenance energy per $W^{0.75}$ after parturition. The decreased daily energy requirement for under-conditioned cows could be due to decreased $W^{0.75}$. As $W^{0.75}$ decreases, it influences daily fasting heat production and can result in a decreased maintenance energy requirement. Some results of this study are shown in Table 7.

In their study, Holter et al. (1990) divided the dairy herd into thin condition and normal condition groups. When compared with the normal group, cows in the thin condition group exhibited less body fat mobilisation (-206 vs. -507 g/d). Chilliard et al. (1991) determined BW, BCS, deuteriated water dilution space, estimated body lipids and proteins, and calculated energy balance in 24 multiparous Holstein cows at week 1, 7, 20, and 39 post-partum. Cows received two levels of energy concentrate. They concluded

Table 7. Effects of pre-partum energy intake on cow body weight and energy reserves (n = 128) (adapted from Houghton et al., 1990b)

	Pre-partum energy intake	
	Low energy	Maintenance energy
Gestation, d 190		
BCS	3.12	3.12
BW (kg)	521.7	525.3
TEBL[1] (%)	15.8	15.9
BE[2] (MJ)	3,555.4	3,593.1
Parturition		
BCS	2.61[a]	3.27[b]
BW (kg)	476.2[a]	535.0[b]
TEBL[1] (%)	12.4[a]	16.8[b]
BE[2] (MJ)	2,907.7[a]	4,149.1[b]

[1] Total empty body lipid.
[2] Total MJ of body energy (based on TEBL and total empty body protein).
[a,b] Significantly different (p<0.01); no symbol p>0.01.

that 1 unit change in BCS corresponded to changes of 35 to 44 kg in BW, 21 to 29 kg in body lipids, and 837 to 1,256 MJ in body energy. One kilogram of BW change corresponded to a change of 18 or 23 to 25 MJ in body energy when calculated from cumulative EB or body components, respectively.

The body components of dairy cows at several physiological stages were well documented by Andrew et al. (1994). The physiological stage had no effect on BW and all empty body constituents, except fat. Empty body fat was reduced by 42.3 kg for early lactation cows compared with pre-partum cows. The protein content did not change over the reproductive cycle, except for protein expressed as a percentage of fat-free matter. Then, for cows in early lactation the tissue protein was lower.

The energy value of BW gain in dairy cows was quoted as 25 MJ/kg by the NRC (2001). In the short term, in common feeding systems 1 MJ change in ME intake is accompanied by 0.01 kg change in BW (Broster and Broster, 1984). An 11% surplus of gross energy intake in lactation induces a gain in energy retention by body tissue of about 14.6 MJ/d (Kaufmann et al., 1987).

EFFECTS OF ENERGY SUPPLY ON METABOLIC PARAMETERS

The effects of pre-partum feeding intensity on several plasma metabolites are shown in Table 9.

Fat metabolism

Baumann and Currie (1980) reviewed the details of biochemical pathways in adipose tissue. Body energy reserves are predominantly stored in the form of lipids in adipose tissue. Lipid synthesis includes *de novo* synthesis of

FA from acetate, uptake of FA from circulating lipoproteins via the enzyme lipoprotein lipase, and esterification of these FA into triglycerides (TG) (the storage form of lipid). They summarized several studies of the temporal relationship between metabolism of adipose tissue and onset of lactation in rats. At about day 19 of pregnancy, lipoprotein lipase activity in adipose tissue decreased, and both flux rates and activities of key enzymes in the regulation of *de novo* FA synthesis started to decrease rapidly. The effect is that energy storage in adipose tissue is diminished and the concentration of free FA in blood is increased. Extraction of NEFA by the liver is proportional to the concentrations present in blood (Bell, 1979). FA utilization in liver and muscles involves both oxidation to ketone bodies or esterification to TG and secretion into the blood bound to a transport protein (Reid et al., 1986). Thus, measuring blood NEFA can indirectly indicate the amount of NEFA taken up by the liver and potentially esterified to TG (Carlson et al., 2006). Elevated NEFA and ketone body concentrations in blood and high hepatic TG concentrations post-partum indicate increased mobilization of FA from adipose tissue of cows fed a high energy diet pre-partum to accumulate extra body condition (Grummer et al., 1995; Drackley, 1999). This may predispose cows to a higher incidence of metabolic disorders (Baird, 1982).

FA oxidation in the brain and liver has been suggested as a signal in intake regulation (Ingvartsen and Andersen, 2000). In the adipose regulatory cycle, insulin depresses lipolysis while it increases lipid synthesis in adipose tissue as a result of high energy feeding. High energy diets should provide more glucose for conversion to α-glycerol phosphate in adipose tissue and provide more NADPH via the pentose phosphate cycle for FA synthesis (Fronk et al., 1980). If cows were able to utilize lipogenic substrates more rapidly when thin than when fat, it would be expected that concentrations of these substrates in blood and rumen fluid would be lower in thin cows than in well-conditioned cows when both are fed at the same level (Bines and Morant, 1983). Holtenius et al. (2003) suggested that well-conditioned cows had a greater degree of insulin resistance in early lactation which gave rise to more pronounced net lipolysis from adipocytes. This also offers a possible explanation for the higher concentration of NEFA and the more pronounced BCS loss.

NEFA concentration

Increased adipose tissue mobilization post-partum is correlated with increased NEB and higher levels of plasma NEFA mobilized from adipose tissue (Ferguson, 1996; Drackley, 1999). Cows in NEB mobilize more body fat reserves and produce glycerol for energy resources, which leads to increased NEFA concentrations in blood (DeVries and Veerkamp, 2000). These NEFA are taken up by the liver

and can be oxidized for additional energy supply or esterified into TG, which can result in hepatic lipidosis and ketosis (Van den TOP et al., 1995; DeVries and Veerkamp, 2000). Plasma NEFA is an important parameter to help evaluate EB of the cow because they are elevated in energetic stress (Burke and Roche, 2007) and stored fat is mobilized (Holcomb et al., 2001). In fasting cows, plasma NEFA concentration increases until reaching a plateau (about 1 mM) after circa one week (Chilliard et al., 2000). The desirable concentration of NEFA for lactating cows is below 0.62 mmol/L in early lactation and below 0.10 mmol/l for cows in late gestation (Kraft and Dürr, 2005). According to Whitaker et al. (1983), the desired plasma concentration for NEFA is below 0.7 mmol/L for cows in early lactation and below 0.4 mmol/L towards the end of pregnancy. Bines and Morant (1983) concluded that FA synthesis in adipose tissue happens faster in under-conditioned cows than in cows in good condition. This results in lower blood values of precursors of FA and so their carry-over from the rumen. This stimulates voluntary feed intake, before rapid chemical regulators act.

However, in the experiment of Blum et al. (1985) cows receiving a low energy diet were characterized by the highest level of NEFA compared with cows receiving high amounts of starch. The NEFA concentrations were 0.27 and 0.12 mmol/L, respectively. In the study of Kunz et al. (1985), cows fed 75% of energy requirements during the first 60 days of lactation had higher NEFA levels during the first two months of lactation, compared with cows whose energy intake covered their energy requirements. Roche et al. (2005) showed that, with increasing DMI in the dry period, NEFA concentrations declined dramatically (0.90, 0.45, 0.23, and 0.24 mmol/L of NEFA for 5.4, 8.2, 10.0, and 11.0 kg/d DMI, respectively). In the trial of Rabelo et al. (2005), during the dry period cows fed a high-energy density diet had lower concentrations of plasma NEFA compared with cows fed a low-energy density diet. In the study of Douglas et al. (2006), restricted-fed cows had increased concentrations of NEFA in plasma during the dry period compared with cows receiving feed *ad libitum*.

In contrast, Morrow (1976) observed that in obese dry cows NEFA are elevated above the normal of 7 mg/dL. Kunz et al. (1985) demonstrated that cows fed at a restricted level in the dry period had lower NEFA concentrations in the following lactation compared with cows fed *ad libitum* in the dry period. In the experiment of Engelhard et al. (2007), NEFA concentration in blood of dairy cows with a normal or shortened dry period was near the physiological limit of 0.4 mmol/L during the first 50 days of lactation. After day 50 of lactation, the values were in the standard range. In obese cows, with low milk yield and a long dry period, NEFA values were elevated at every lactational stage. Fronk et al. (1980) showed that obese cows mobilize more body fat than cows with a moderate body condition as indicated by higher plasma NEFA post-partum. McNamara et al. (2008) found lower NEFA concentrations due to lower milk production in cows milking only once daily compared to cows milking two or three times daily.

Bertics et al. (1992) observed that as parturition approached, plasma concentrations of NEFA increased from <0.5 to 2.0 mmol/L. Reid et al. (1986) described the development of NEFA concentrations in plasma for obese and lean calving cows (BCS 4.0 and 2.5, respectively) around parturition (Figure 7). Plasma concentrations of NEFA began to rise in both BCS groups before parturition, reaching a maximum one week after calving with BCS group 4.0 being higher than BCS group 2.5 (p = 0.08). NEFA concentrations remained significantly higher in BCS group 4.0 during weeks 2 to 6 (p<0.01) and until the end of lactation (p<0.05).

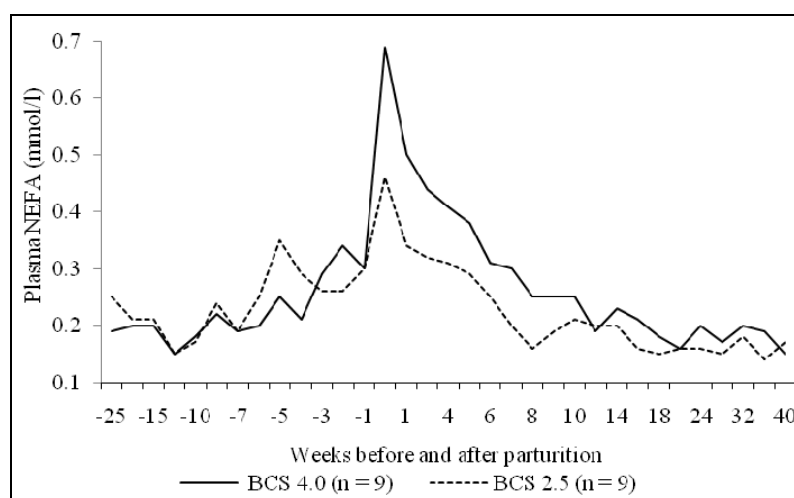Increasing NEFA concentrations as parturition approached were also described by Guo et al. (2007).

Figure 7. Plasma NEFA concentrations before and after parturition (adapted from Reid et al., 1986).

Increased NEFA is a result of decreased DMI before parturition, hormonal changes before and at parturition that stimulate mobilization of NEFA from adipose tissue to provide energy for lactogenesis (McNamara, 1991), and stress of calving (Ryan et al., 2003). Less NEFA in plasma after parturition probably reflect greater utilization of circulating FA by mammary tissue (Lake et al., 2007).

Fronk et al. (1980) and Bines and Morant (1983) showed that NEFA concentration was higher in well-conditioned cows before intake of feed, but after feeding there was no difference in the NEFA concentrations in blood of poor- or well-conditioned cows. Rukkwamsuk et al. (2000) observed significantly higher NEFA concentrations in cows that were overfed during the dry period (Figure 8). This was also observed by Holtenius et al. (2003).

In the trial of Douglas et al. (2006), peri-partum NEFA rose markedly, independent of dry period feed supply, but was also higher for cows previously fed *ad libitum*. In the first 21 days of lactation, plasma concentrations of NEFA remained lower in cows restrictively fed during the dry period. Guo et al. (2007) described a greater area under the curve for post-partum NEFA concentration in cows fed a high energy transition diet compared with control animals. Higher levels of NEFA in well-conditioned cows imply a greater rate of lipolysis in these animals in response to energy deficit (Bines and Morant, 1983; Douglas et al., 2006). The degree and duration of fat mobilization also depend on the quantity of fat accumulated during the dry period (Kunz et al., 1985). In the experiment of Watters et al. (2008), cows with a shortened dry period had significantly lower NEFA concentrations than those assigned to a traditional dry period.

NEFA concentrations usually increase when cows are fed supplemental fat in diet (Grum et al., 1996). Lake et al.

(2007) observed that cows fed supplements with cracked, high-linoleate or cracked, high-oleate safflower seeds in the first 3 month of lactation had greater (p<0.001) NEFA concentrations in plasma than control cows fed a low-fat supplement. An enhanced release of FA after hydrolysis by lipoprotein lipase and an elevated basal lipolysis could in part account for the relatively high basal NEFA in cows receiving supplemental fat (Blum et al., 1985). In the trial of Castañeda-Gutiérrez et al. (2009), feeding different peri-partum dietary supplementations (different FA supplements or propylene glycol) showed no effect on plasma concentration of NEFA compared with control animals.

However, in the study of Kokkonen et al. (2003), cows receiving a diet with 20% concentrate had higher (p<0.05) plasma NEFA than cows receiving 40 or 60% concentrate in the ration one week pre-partum. Holcomb et al. (2001) observed that cows fed a high energy diet in the dry period had lower mean NEFA in the following lactation than cows fed a low energy diet pre-partum. This suggests that cows fed high concentrate diets were not mobilizing as much energy from their adipose tissue. This was also observed by Olsson et al. (1998). In the experiment of Vandehaar et al. (1999), increased nutrient supply in the dry period (84 MJ NEL/d) led to lower NEFA concentrations in plasma compared with cows offered 57 MJ NEL/d (0.176 vs. 0.233 mmol/L) around parturition. In the trial of Roche (2007), plasma concentrations of NEFA were elevated in DMI-restricted cows independent of the lactational stage.

Increased NEFA mobilization during the period of NEB in early lactation and during under-nutrition is due to a decrease in FA re-esterification, together with lipolysis (Chilliard et al., 2000).

Ryan et al. (2003) and Roche et al. (2005) could not find significant effects of pre-partum diet on post-partum NEFA concentration. Rabelo et al. (2005) detected no differences in NEFA concentrations for cows consuming diets differing in energy density in lactation. They could not detect any effects possibly because the dietary effect was overwhelmed by the change in endocrine status.

Effects on liver values

In liver, lipid accumulation may contribute to health disorders and decreased milk production (Drackley, 1999). The pre-partum DMI (Bertics et al., 1992) and BCS (Engelhard et al., 2007) have an effect on the lipid percentage in liver. Poor EB and elevated NEFA would be expected to increase liver lipid content, which typically peaks at or near the day of calving (Grummer, 1995; Grum et al., 1996). Extreme rates of lipid mobilization lead to increased uptake of NEFA by liver and increased TG content (Drackley, 1999). Olsson et al. (1998) suggested that TG synthesis is affected not only by NEFA supply but obesity, stress, and high levels of insulin and glucose are
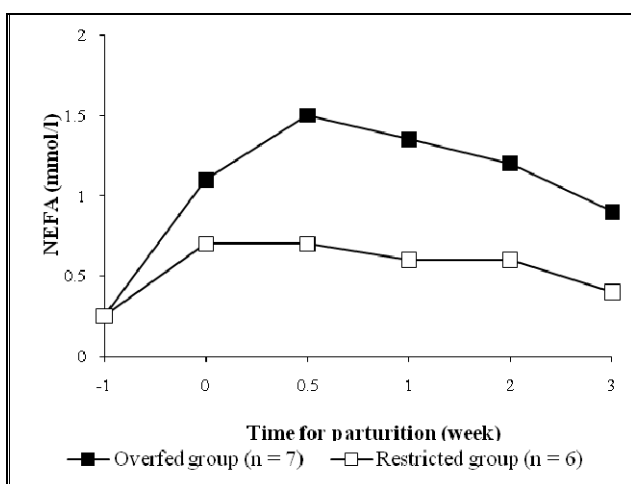

Figure 8. Serum NEFA concentrations before and after parturition in cows that were either fed a restricted energy intake or were overfed during the dry period (p<0.05) (adapted from Rukkwamsuk et al., 2000).

also important factors in the development of fatty liver. Grum et al. (1996) suggested that chronically increased NEFA and low insulin during the dry period led to increased esterification activity for NEFA, which could lead to decreased TG accumulation. Hepatic lipid contents of less than 12% are in the physiological range (Engelhard et al., 2007). Fronk et al. (1980) detected that an over-condition in the dry period resulted in significantly higher hepatic lipid content (12.5%) than in control cows (9.8%). Similar observations were made by Rukkwamsuk et al. (2000); in the dry period overfed cows had higher concentrations of serum NEFA and consequently accumulated greater amounts of TG in the liver than did cows given a restricted energy intake (Figure 9).

In the experiment of Reid et al. (1986), well-conditioned cows at calving had greater infiltration of fat in the liver at one and four weeks of lactation than lean cows. In the study of Fronk et al. (1980), the TG concentration in liver of fat cows was 2-fold greater than in controls. The increased deposition of NEFA in liver reflects a relative inability of obese cows to utilize the mobilized FA (Reid et al., 1986), possibly because of reduced synthesis of the transport proteins (Fronk et al., 1980).

Grum et al. (1996) found that cows fed high fat diets during the dry period had decreased TG accumulation in the liver at 1 d post-partum, which was accompanied by lowered plasma NEFA, increased peroxisomal β-oxidation of palmitate by liver homogenates, and decreased esterification of palmitate by liver slices. The hepatic lipid accumulation observed in the study was predominantly caused by decreased energy and nutrient intakes pre-partum for cows fed the high fat diet rather than by fat supplementation *per se* (Douglas et al., 2006). Vandehaar et

al. (1999) suggested that liver enzymes were perhaps altered to increase oxidation and decrease esterification of FA. However, Douglas et al. (2006) indicated no increased hepatic lipid accumulation due to dietary fat. Castañeda-Gutiérrez et al. (2009) observed no differences in hepatic TG content for cows fed different FA supplements or propylene glycol three weeks post-partum compared with control animals. This indicates that diet has a smaller impact on TG accumulation in liver peri-partum.

Bertics et al. (1992) found a negative correlation (r = 0.80) between DMI pre-partum and liver TG directly after calving. In their study, the liver TG increased by 227% for control cows versus 75% for those kept on feed during the final three weeks pre-partum. This indicates that factors additional to feed intake also may contribute to the development of fatty liver. In the experiment of Vandehaar et al. (1999), increased nutrient intake in the dry period (83 MJ NEL/d) led to less TG in liver compared with cows offered 59 MJ NEL/d (0.9 vs. 1.5%, wet tissue basis) at parturition. These findings support the idea of Bertics et al. (1992) that FA mobilization at the end of gestation is a determinant. In contrast, Drackley et al. (1991) indicated that restriction of feed to approximately 80% of *ad libitum* consumption did not result in fatty liver in early lactation, even though plasma NEFA concentrations were greatly increased. However, liver TG probably was elevated already when feed restriction was introduced at 14 days after parturition. Rabelo et al. (2005) observed that liver TG content at parturition was not affected by energy intake in late gestation. However, liver TG content in lactation declined in cows on a high energy level compared with cows on a low energy level. Douglas et al. (2006) reported lower post-partum concentrations of total lipid and TG in liver of cows previously fed a restricted ration.

These studies indicate that perhaps there is an optimal time before calving to start cows on higher energy diets, but further research is needed.

Ketone body concentration

Ketone body concentration in blood can also indicate energetic stress and rate of lipid mobilization in the animal. Increased mobilization of body tissues in early lactation is generally associated with an increased production and concentration of ketones (Ingvartsen and Andersen, 2000). There is a limit to the amount of mobilized FA that can be oxidized in liver. When this limit is reached, TG accumulates within the hepatocytes, and acetyl-coenzyme A is converted to ketone bodies (Goff and Horst, 1997). Fronk et al. (1980) and Carlson et al. (2006) described β-hydoxybutyrate (BHB) as a key indicator of hepatic ketogenesis as a result of influx of NEFA into the liver. The desirable concentration of BHB for lactating cows is below
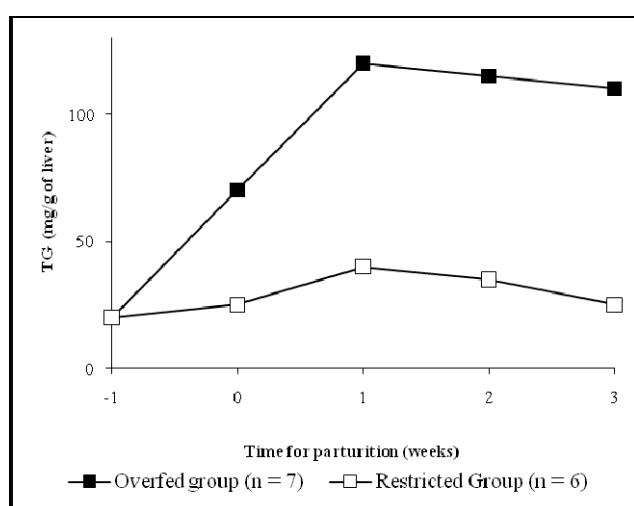

Figure 9. TG accumulation in liver before and after parturition in cows that were either fed a restricted energy intake or were overfed during the dry period (p<0.05) (adapted from Rukkwamsuk et al., 2000).

1.00 mmol/L in early lactation and below 0.60 mmol/L in late gestation (Whitaker et al., 1983). Kraft and Dürr (2005) established a reference range of BHB for lactating cows as below 0.85 mmol/L and below 0.60 mmol/L for cows one week pre-partum. Increasing ketone body production reduces DMI (Farries, 1983b) and consequently milk production (Goff and Horst, 1997). The appearance of ketone bodies in blood, milk and urine enable diagnosis of ketosis which usually becomes clinically evident from ten days to three weeks after parturition (Goff and Horst, 1997). McNamara et al. (2003a) suggested that BHB may be a more useful indicator of EB and also of BCS and BW loss than either glucose or NEFA.

Kunz et al. (1985) demonstrated that cows fed at a restricted level in the dry period had lower ketone body concentrations in the following lactation compared with cows fed *ad libitum* in the dry period. This contrasted with the study of Kokkonen et al. (2004) which found that a low proportion of concentrate in the diet and a slow increase in concentrate level after calving induced high blood ketone values during the first weeks of lactation. This was confirmed by Blum et al. (1985). Five weeks after parturition, cows with a high energy intake had lower acetoacetate and BHB concentrations in plasma than cows on a low energy intake (0.08 vs. 0.18 and 0.86 vs. 1.71 mmol/L, respectively). Kunz et al. (1985) concluded that during the first two months of lactation ketone body levels were higher in cows fed only 0.75 of requirements during the first 60 days of lactation compared with cows given an adequate energy intake. Roche et al. (2005) showed that, with increasing DMI BHB concentrations declined in the dry period (0.71, 0.40, 0.40, and 0.38 mmol/L of BHB for 5.4, 8.2, 10.0, and 11.0 kg/d DMI, respectively). In the experiment of Rabelo et al. (2005), animals on a high energy density level in early lactation had lower plasma BHB concentrations compared with cows on a low energy density level. Noro et al. (2006) observed lower BHB levels in grazing cows offered supplementary concentrate compared with animals without concentrate supplementation. In the trial of Roche (2007), the plasma concentrations of BHB were elevated in DMI-restricted cows independent of the lactational stage. In the trial of Castañeda-Gutiérrez et al. (2009), periparturient cows fed different FA supplements or propylene glycol showed a decrease in BHB concentrations compared with control animals. Farries (1983b) proved a dependency between the amount of BW loss post-partum and the concentration of ketone bodies. There was also a dependency between weight loss post-partum and energy intake in the dry period and the duration and intensity of acetone reaction - summarized as an index (Table 8).

In contrast, in the study of Gardner (1969) cows offered a high energy level in their pre-partum diet had elevated blood ketones in lactation. McNamara (2003a) demonstrated higher plasma BHB concentrations two weeks after parturition in cows fed more generously in the dry period. In the study of Douglas et al. (2006), plasma concentrations of BHB remained lower in cows fed restrictively in the dry period. Guo et al. (2007) showed that higher energy intake in the dry period led to higher aceto-acetate levels in early lactation. This would be consistent with the greater loss of BW and BCS post-partum observed in well-conditioned cows (Houghton et al., 1990b; Ferguson and Sniffen, 1991), as well as higher NEFA levels in these treatments. The increase of ketone body concentration in well-conditioned cows is probably related to adipose mobilization and elevated hepatic metabolism when DMI is depressed (Guo et al., 2007). McNamara et al. (2008) found lower BHB concentrations in cows milking only once daily than in cows milking two or three times daily, probably due to less NEB caused by lower milk yield.

However, there are some studies in which the authors could not detect any alterations of blood or liver values in cows caused by their ration. Fronk et al. (1980) showed that the BCS has no effect on plasma BHB in dairy cows. This was also affirmed by Holtenius et al. (2003). Hepatic lipid metabolism is normally able to keep pace with the influx of NEFA (Fronk et al., 1980). In the study of Zanartu et al. (1983), ketone bodies were not influenced by the diet of the cow. The BCS of cows has no influence on the lipogenic substrates in blood after feeding. Bines and Morant (1983) reported that the acetate and BHB concentrations after feed ingestion do not differ between cows in a low or good condition. Roche et al. (2005) also could not observe any effects of pre-partum energy intake on post-partum BHB concentrations in plasma. These results indicated that esterification of FA to TG was not affected.

Table 8. Variation in BW and ketones in blood and milk of dairy cows (adapted from Farries, 1983b)

n	BW change (kg)	Ketone bodies in blood (mg/100 ml)	Acetone reaction in milk		
			% of cows	Reaction time (days)	Index (intensity×time)
16	-64	20,5	54	32	41
16	-47	15,5	53	26	32
16	-18	15,0	27	17	18
16	+ 6	10,1	35	10	12

Table 9. Effects of pre-partum feeding intensity on metabolic parameters in blood plasma

	Energy supply pre-partum				Metabolic parameter					Reference
n	Groups' description	Concentrate (kg/d)	Roughage	Time (weeks)	Parameter	Prepartum	1 d after calving	Postpartum	Time (weeks)	
11	102% of requirements	0.0	H, CS	8	NEFA (mmol/L)	n.s.	n.s.	0.220	week	Boisclair et al.
11	131% of requirements	0.0						0.216	4	(1987)
11	162% of requirements	0.5						0.258		
					BHB (mmol/L)	n.s.	n.s.	1.098		
								1.177		
								1.474		
					Glucose (mmol/L)	n.s.	n.s.	3.38		
								3.24		
								2.94		
11	Normal fed	n.s.	n.s.	3	NEFA (mmol/L)	n.s.	0.802	n.s.	n.s.	Bertics et al.
11	Forced feeding via rumen canula						0.645			(1991)
					Liver lipid (%)	n.s.	30.8	n.s.		
							23.6			
					Glucose (mmol/L)	n.s.	3.39[a]	n.s.		
							4.20[b]			
10	Control	2.9	OH	9	NEFA (mmol/L)	0.13	0.70	0.10	11	Grum et al.
10	High grain dry period diet	5.4				0.10	0.65	0.10		(1996)
					Liver lipid (%)	5.5	12.0	4.5		
						5.5	11.0	5.5		
					BHB (mmol/L)	0.02	1.34	0.01		
						0.05	1.36	0.02		
					Glucose (mmol/L)	4.09	3.25	4.09		
						4.48	3.53	3.81		
					Insulin (μIU/ml)	6.23	2.49	10.79		
						10.38	4.15	5.81		
8	75% of requirements	n.s.	n.s.	8	NEFA (mmol/L)	0.20	n.s.	0.37	8	Holtenius et al.
8	110% of requirements					0.14		0.51		(2003)
8	178% of requirements					0.13		0.59		
					BHB (mmol/L)	1.00	n.s.	1.09		
						1.31		1.49		
						1.09		1.43		
					Glucose (mmol/L)	2.80	n.s.	2.46		
						2.95		2.57		
						3.16		2.89		
					Insulin (μIU/ml)	7.33	n.s.	4.50		
						10.41		4.59		
						18.52		5.23		
6	Straw and grass silage	0.0	GS, S	4	NEFA (mmol/L)	n.s.	0.38	0.10[a]	8	McNamara et al.
6	Grass silage	0.0					0.36	0.10[a]		(2003a)
6	Grass silage and concentrate	3.0					0.44	0.17[b]		
					BHB (mmol/L)	n.s.	0.35	0.43		
							0.34	0.48		
							0.35	0.42		
					Glucose (mmol/L)	n.s.	5.40	4.02		
							5.23	3.97		
							5.30	4.03		
28	Fed to meet the requirements	0.0	GS, S	5	NEFA (mmol/L)	0.04	0.18	0.21	8	Ryan et al.
28	oversupplied	3.0				0.07	0.14	0.16		(2003)
					Glucose (mmol/L)	3.12	3.76	3.65		
						3.09	3.69	3.73		
5	Low energy	1.6	GS	3	NEFA (mmol/L)	0.26[a]	n.s.	0.37	5	Kokkonen et al.
5	Medium energy	2.9				0.21[b]		0.26		(2004)
5	High energy	4.5				0.21[b]		0.34		
					TG (mmol/L)	0.32	n.s.	0.20		
						0.31		0.26		
						0.31		0.26		
					BHB (mmol/L)	0.42[a]	n.s.	0.71[a]		
						0.49[b]		1.04[b]		
						0.52[b]		0.83[b]		
					Glucose (mmol/L)	3.77[a]	n.s.	3.50		
						4.23[b]		3.47		
						4.01[b]		3.75		
					Insulin (μIU/ml)	5.5[a]	n.s.	9.7		
						10.3[b]		8.6		
						17.4[c]		12.2		

Table 9. Effects of pre-partum feeding intensity on metabolic parameters in blood plasma (Continued)

n	Groups' description	Concentrate (kg/d)	Roughage	Time (weeks)	Parameter	Prepartum	1 d after calving	Postpartum	Time (weeks)	Reference
						Energy supply pre-partum → Metabolic parameter				
18	80% of requirements	n.s.	AH, AS, CS	9	NEFA (mmol/L)	0.292	1.091	0.263	15	Dann et al. (2005)
17	*Ad libitum*					0.167	1.118	0.307		
					Liver lipid (%)	4.25	6.01	4.56		
						4.52	7.71	4.50		
					BHB (mmol/L)	0.40	0.87	0.40		
						0.34	0.85	0.45		
					Glucose (mmol/L)	3.22	2.90	3.27		
						3.39	2.94	3.11		
					Insulin (µIU/ml)	4.84	2.52	4.36		
						8.19	2.76	5.28		
30	Low energy	2.6	GS, CS, S	4	NEFA (mmol/L)	0.254[a]		n.s.	1	Rabelo et al. (2005)
30	High energy	6.2				0.190[b]				
					BHB (mmol/L)	0.40		n.s.	1	
						0.40				
					Glucose (mmol/L)	2.92	2.85	n.s.	1	
						3.03	2.74			
					Insulin (µIU/ml)	13.4[a]	10.2	n.s.	1	
						16.9[b]	10.3			
13	DMI 5.5 kg/d pasture	0.0	P	4	NEFA (mmol/L)	0.90	0.53	0.86	6	Roche et al. (2005)
13	DMI 8.0 kg/d pasture	0.0				0.45	0.48	0.85		
13	DMI 10.5 kg/d pasture	0.0				0.23	0.68	0.85		
13	DMI 13.0 kg/d pasture	0.0				0.24	0.62	0.91		
					BHB (mmol/L)	0.71	0.46	0.64		
						0.40	0.53	0.86		
						0.40	0.51	0.99		
						0.38	0.51	1.11		
					Glucose (mmol/L)	3.20	3.37	3.15		
						3.38	3.40	3.40		
						3.53	3.45	3.28		
						3.53	3.52	3.11		
					Insulin (µIU/ml)	0.21	0.29	0.15		
						0.32	0.26	0.17		
						0.26	0.29	0.17		
						0.31	0.23	0.15		
4	80 % of requirements	n.s.	H, CS	8	NEFA (mmol/L)	0.1	0.8	0.1	16	Carlson et al. (2006)
4	Control					0.2	0.6	0.1		
					BHB (mmol/L)	0.48	0.58	2.11	6	
						0.48	0.58	1.44		
					Insulin (µIU/ml)	10[a]	1	6	12	
						3[b]	2	7		
12	80% of requirements	n.s.	AS, CS	9	NEFA (mmol/L)	0.307	n.s.	0.273	24	Douglas et al. (2006)
12	*Ad libitum*					0.165		0.441		
					BHB (mmol/L)	0.413	n.s.	0.475		
						0.378		0.536		
					Cholesterol (mg/dl)	115.5	n.s	174.9		
						99.9		159.9		
					Glucose (mg/dl)	3.46	n.s	3.54		
						3.77		3.54		
					Insulin (µIU/ml)	7.2	n.s	8.1		
						9.7		7.4		
40	Normal dry period	0.0	GS, CS, S	8	NEFA (mmol/L)	n.s.	0.69	0.23	7	Engelhard et al. (2007)
40	Shortened dry period	n.s.					0.53	0.22		
				4	BHB (mmol/L)	n.s.	0.819	0.616[a]		
							0.738	0.750[b]		
14	Control	0.0	H, CS, AWS	2	NEFA (mmol/L)	0.25	n.s.	0.43	2	Guo et al. (2007)
14	Transition diet	4.6				0.23		0.53		
					BHB (mmol/L)	0.32	n.s.	0.45		
						0.39		0.54		
					Glucose (mmol/L)	2.96	n.s.	3.25		
						3.86		3.31		

n.s. = Not specified; H = Hay; P = Pasture; GS = Grass silage; CS= Corn silage; S = Straw; GP = Grass pellets; CC = Corn cubes; OH = Oat hay; AH = Alfalfa hay; AS = Alfalfa silage; AWS = Alfalfa-wheat silage.
[a,b,c] Significantly different (p<0.05); no symbol p>0.05 or not specified.

Cholesterol concentration

Normally cholesterol concentration in the blood plasma ranges from 120 to 220 mg/dl (McDonald et al., 2002). Cholesterol is mostly produced in the small intestinal epithelium to transport dietary lipid; therefore, lower concentrations in feed-restricted animals might be expected because of lower DMI (Douglas et al., 2006). It is also the precursor of steroid hormones (McDonald et al., 2002). Kappel et al. (1984) and Douglas et al. (2006) described a decrease of serum cholesterol before calving and then the cholesterol concentration increased for 88 days after calving (Kappel et al., 1984). Possible explanations for the pre-partum decrease in serum cholesterol concentrations include the fetal utilization of cholesterol and the utilization of cholesterol for progesterone synthesis (Guédon et al., 1999). Cholesterol concentrations are directly related to milk production (Kappel et al., 1984; Guédon et al., 1999). In the experiment of Blum et al. (1985), cows receiving a low energy diet were characterized by lower cholesterol concentrations in blood compared with cows on a high energy level in early lactation (108.5 vs. 130.1 mg/dl, respectively). In the study of Kim and Suh (2003), the total cholesterol concentration was lower at month 1 of lactation in cows with a high loss of body condition (165±5.3 mg/dl) than in the group with moderate condition loss (183±5.8 mg/dl); however, cholesterol levels in the other periods were not different between the two groups. Lower cholesterol concentrations in severe body condition loss may reflect the increased availability of body reserves during the early post-partum period. In the trial of Douglas et al. (2006), supplementing fat in the dry period diet increased pre-partum concentrations of cholesterol in plasma regardless of intake.

Carbohydrate metabolism

Lower concentrations of glucose and insulin in plasma resulting from feed restriction throughout the dry period are associated with moderately higher rates of adipose tissue TG mobilization to support energy needs, and are reflected in the sustained loss of BCS throughout the dry period (Douglas et al., 2006). Elevated concentrations of plasma glucose and insulin suggest that nutrient EB is positive (Rabelo et al., 2005).

Glucose concentration

Glucose is used as an energy source (McDonald et al., 2002). Glucose is needed to provide reducing equivalents and as a source of glycerol for the production of TG (Bines and Morant, 1983). Glucose stimulates FA re-esterification in adipose tissue (Chilliard et al., 2000). Kappel et al. (1984) described an increase of plasma glucose before calving and then the glucose concentration declined to a minimum value between 11 and 25 days post-partum,

probably because of high glucose requirements for lactose synthesis. Grum et al. (1996) and Douglas et al. (2006) also described decreasing plasma glucose concentrations for all treatment groups as calving approached. The decrease in glucose concentration during late gestation may result from fetal growth, mammary gland development (Guo et al., 2007) and natal stress (Kunz et al., 1985). Glucose concentration should remain above 3 mmol/L according to Whitaker et al. (1983). Kraft and Dürr (2005) established a reference range for glucose concentration between 2.2 and 3.3 mmol/L. In well-conditioned parturient cows, blood glucose is below 2.2 mmol/L accompanied by ketonemia and ketonuria in many cows due to ketosis; the glucose level can reach 5.6 mmol/L at the time of parturition, during parturient paresis, or at other times when the cow is severely stressed (Morrow, 1976).

However, Reid et al. (1986) and Grummer et al. (1995) could not show significant differences in blood glucose in lactation, if different diets were fed in the dry period before parturition.

Bines and Morant (1983) proved that plasma glucose concentrations were always lower in thin cows. Holtenius et al. (2003) reported higher plasma glucose levels in cows offered a high energy diet in late gestation. After parturition, the glucose concentration fell markedly in all experimental animals, independently of dry period diet, and reached a nadir about two weeks post-partum. This was also described by Roche et al. (2005) and Guo et al. (2007). In the trial of Rabelo et al. (2005), cows fed a high energy density diet during the dry period had higher plasma concentrations of glucose compared with cows fed a low energy density diet.

Blum et al. (1985) reported that glucose levels were elevated on day 37±3 of lactation in cows receiving a high concentrate diet compared with cows on a low energy level (3.46 and 3.18 mmol/L, respectively). In the study of McNamara et al. (2003a), plasma glucose concentrations two weeks post-partum were significantly higher in cows receiving 8 kg/d concentrate in their ration compared with cows receiving only 4 kg/d (3.77 vs. 3.56 mmol/L, respectively). In the experiment of Rabelo et al. (2005), animals on a high energy density level had higher plasma glucose concentrations in early lactation compared with cows on a low energy density level. Noro et al. (2006) also observed higher glucose levels for grazing cows offered supplementary concentrate during lactation. In cows milking once daily, plasma glucose concentrations tended to be higher than in cows milking two or three times daily (McNamara et al., 2008). An increase of serum glucose with energy intake probably represents the effect of greater energy (as propionate) availability (Boisclair et al., 1987). Kunz et al. (1985) demonstrated that cows fed in the dry period at a restricted level had higher blood glucose concentrations in the following lactation compared with

cows fed *ad libitum*. This study suggested a higher rate of utilization of energy sources in low-conditioned cows.

However Zanartu et al. (1983), Olsson et al. (1998), Holcomb et al. (2001) as well as Kim and Suh (2003) found no differences in plasma glucose concentration in late gestation and early lactation for cows on different nutritional energy levels. In the trial of Castañeda-Gutiérrez et al. (2009), feeding different dietary supplements peri-partum (differnt FA supplements or propylene glycol) showed no effect on plasma concentration of glucose compared with control animals. Maybe these authers could not find any difference in glucose concentrations because all of the cows studied were fed to meet their energy requirements. Differences among studies may reflect differences in peripartuml DMI.

Insulin concentration

Insulin is an essential peptide hormone and a product of the pancreas (Kraft and Dürr, 2005). Insulin encourages the uptake of glucose and the synthesis of steroid hormones (McDonald et al., 2002). Measuring insulin levels can help to quantify the metabolic and physiological responses to different feeding levels (Carlson et al., 2006). Insulin secretion and tissue responses to insulin decrease in early-lactating animals (Chilliard, 1992). This favours liver glucose production and adipose tissue mobilization (Chilliard, 1987). Insulin has been shown to affect appetite (Agenäs et al., 2003). Andersson et al. (1991) suggested that increased concentrate feeding increases the propionate:acetate ratio in the rumen. Propionate regulates the concentration of insulin in the plasma. Insulin reduces the rate of abomasal emptying, and cows with a displaced abomasum exhibit a resistance to insulin, which can lead to higher serum insulin concentrations (Cameron et al., 1998). In the trial of Douglas et al. (2006), concentration of insulin in plasma decreased for all treatment groups as parturition approached. This is consistent with previous observations (Kunz et al., 1985; Grum et al., 1996; Dann et al., 2005) and is part of the adaptation of energy metabolism to the onset of lactation, allowing the cow to mobilize its tissue deposits (Holtenius et al., 2003; Kokkonen et al., 2004). Feeding a high concentrate diet in the dry period apparently interferes with this mechanism (Kokkonen et al., 2004). The results of Olsson et al. (1998) indicated that the feeding level pre-partum does influence the serum insulin level. Early lactation is characterized by a moderate degree of insulin resistance in adipose tissue and muscles, thereby promoting the mobilization of NEFA and amino acids and the sparing of glucose (Bell, 1995).

Reid et al. (1986) showed that well-conditioned cows had significantly higher plasma insulin concentrations (p< 0.05) than lean cows during the dry period. Blum et al.

(1985) described lower insulin concentrations in cows fed a low energy diet compared with cows on a high nutritional energy level in early lactation. Kunz et al. (1985) concluded that during the first two months of lactation insulin levels were lower in cows fed only 0.75 of requirements during the first 60 days of lactation compared with cows on a moderate energy intake. Grum et al. (1996) found that cows fed a high fat diet in the dry period had higher concentrations of insulin in plasma than cows fed a high grain diet during the last three weeks pre-partum. In the experiment of Olsson et al. (1998), the serum insulin level in the last three weeks of gestation was significantly higher in cows receiving additional concentrate in the dry period than in roughage-fed cows. There were no treatment differences after parturition. Holcomb et al. (2001) found higher plasma insulin concentrations in cows fed more concentrates in the dry period. Holtenius et al. (2003) offered different dry period diets varying in energy content. Cows receiving 177 MJ ME/d (high energy diet) had higher insulin concentrations in their plasma during the dry period than the low or moderate energy group. This is consistent with other studies reviewed by Grummer et al. (1995) and Rabelo et al. (2005). McNamara et al. (2008) showed lower plasma insulin concentrations in cows milking twice or three times daily than in cows milking only once a day. High plasma insulin concentration reflects a positive EB (Holtenius et al., 2003). Feeding excessive amounts of concentrate during the dry period may result in insulin resistance in over-conditioned cows. This phenomenon is characterized by increased plasma NEFA despite a high insulin level and impaired capacity to utilize glucose (Kokkonen et al., 2004).

CONCLUSION

Over the past decades, numerous studies have been performed to investigate potential effects of energy intake on milk production, development of metabolic diseases, fertility, changes of body tissue and metabolic parameters. The results reported in the literature are heterogenous. A general statement cannot be made in summary. The effects of dry period ration on DMI and milk yield in lactation are well documented. A lot of studies have pointed out a lower feed intake of well-conditioned cows at parturition followed by a greater NEB and loss of milk yield in early lactation. Dairy cows are able to compensate partly for the genetically determined NEB at the beginning of lactation. In contrast, more generous feeding in lactation leads to little direct increase in milk yield. In the last decades, genetic progress for high milk yield led to decreased reproductive performance and a greater risk of production diseases in high-yielding dairy cows. Malnutrition potentiates the

decrease in reproductive performance. Temporary underfeeding and increased mobilization of fat tissue can have negative implications on resumption of ovarian activity after parturition, conception rate and fertility. The results of the studies evaluated suggest that feed restrictions during the dry period have carryover effects on post-partum reproductive performance of high-yielding dairy cows. The post-partum anoestrous interval depends, on the one hand, on the energy reserves stored before calving and, on the other hand, on the magnitude and duration of NEB after parturition. In early lactation many metabolic diseases could occur mostly due to the fact that the rumen microbes are not adapted to the high energy density of lactation diets. The transition diet plays a major role in development of rumen conditions. Overconsumption in the dry period promotes metabolic diseases. Optimization of feeding by the use of well-balanced diets appears to be a key factor for avoiding disorders in early lactation. The results of the studies evaluated show that underfeeding in the dry period to achieve proper fatness at calving does not cause health problems. During a lactation cycle, changes in body reserves are genetically determined and independent of the requirement for milk production and pregnancy. However, the duration and magnitude of mobilization and storage of adipose tissue depend on milk energy secretion, feeding level and feed quality, body condition, genotype, and endocrine regulation. Energy input and output also affect metabolic parameters in blood and liver. Pre-partum intake results in changes in serum metabolites according to plane of nutrition and energy balance. Helpful parameters to make a statement of fat metabolism are NEFA in blood and liver, liver TG, and ketone bodies in blood. Changes in carbohydrate metabolism can be shown by glucose and insulin concentration in blood.

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