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Effects of dietary energy level and source on foetal development and energy balance in concurrently pregnant and lactating primiparous rabbit does

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Abstract

The aim of this experiment was to study the effects of dietary energy level and source on foetal growth and survival and mobilization of body stores in concurrently pregnant and lactating primiparous rabbit does. Does were given a moderate-energy diet (≈ 9.9 MJ digestible energy (DE) per kg dry matter (DM); group M, no. = 23) or a high-energy diet (≈ 12.2 MJ DE per kg DM). In this latter case, additional energy came from starch (group S, no. = 23) or starch and fat (group F, no. = 22). Primiparous rabbit does were mated within 12 h after parturition and were slaughtered on day 28 of gestation-lactation. During the first 21 days, the DE intake and milk production were higher in the group F than in the groups S and M ($P < 0.05$). On day 28 of pregnancy, the weight of adipose tissues and liver, as well as the lipid content of the carcass, were higher in the groups S and F than in the group M ($P < 0.05$). Foetal survival and weight were similar in the three groups. These results indicate that increased energy level of the diet did not improve foetal survival or growth in concurrently pregnant and lactating primiparous does. On the contrary, it could reduce the mobilization of fat stores, especially if the energy source is starch.

Keywords: dietary fat, energy intake, foetal growth, milk production, rabbits.

Introduction

In primiparous rabbit does mated shortly after parturition, lactation led to lower foetal survival (-10.4%) and growth (-19.6% ; Fortun, Prunier and Lebas, 1993). When pregnancy and lactation are concurrent, voluntary food intake of primiparous rabbit does seems to be insufficient to supply all the nutritional requirements: maternal tissue growth, foetal development, and milk production (Maertens and de Groote, 1988). Therefore, protein and lipid mobilization are necessary to meet the nutritional deficit. Parigi-Bini, Xiccato, Cinetto and Dalle Zotte (1992) have shown that proportionately 0.06 and 0.46% of initial protein and lipid body content respectively were mobilized during concurrent pregnancy and lactation in primiparous does. The nutritional deficit led to competition between uterus and mammary gland for nutrient supply, and seemed responsible for the lower foetal growth (Fortun, Prunier, Etienne and Lebas, 1994). Influence of this competition on embryonic and foetal survival remains unclear.

Several studies have shown that an increase in digestible energy (DE) content of the diet increases

the DE intake of the doe, particularly with a fat-enriched diet (Maertens and de Groote, 1988; Fraga, Lorente, Carabaño and de Blas, 1989; Barreto and de Blas, 1993). Theoretically, this should decrease the nutritional deficit of the doe, the depletion of body stores and the competition between uterus and mammary gland. Fraga *et al.* (1989) and Xiccato, Parigi-Bini, Dalle Zotte, Carazzolo and Cossu (1995) have shown a higher milk production in does given high-energy diets. However, little information is available about the influence of energy intake on foetal development and mobilization of maternal body tissues.

The aim of this experiment was to determine the influence of dietary energy level and source on foetal survival and growth and body composition of primiparous rabbit does.

Material and methods

Diets

Three diets were formulated with 860 g/kg of a common base containing wheat, alfalfa, beet pulp,

Table 1 *Ingredients, composition and digestible energy of the diets*

	Diet		
	S	F	M
Ingredients (g/kg)			
Wheat	190	190	199
Alfalfa 17LP	208	208	208
Soya-bean meal	168	168	159
Sunflower meal	150	150	150
Beet pulp	114	114	114
Maize starch	140	74	
Wheat straw			140
Wood fibre		36	
Sunflower oil		30	
Salts and vitamins	30	30	30
Composition (g/kg)			
Dry matter (DM)	882	888	890
Ash	87	87	93
Crude fibre	142	177	193
Crude protein	207	203	207
Digestible crude protein	148	146	136
Energy (MJ/kg DM)			
Gross energy	17.80	18.47	18.24
Digestible energy	12.22	12.12	9.88

soya-bean and sunflower meal (Table 1). The M diet was formulated by adding 140 g wheat straw per kg to the common base and had a moderate DE content (9.88 MJ DE per kg dry matter (DM)). On the contrary, the two other diets were high-energy diets (≈ 12.2 MJ DE per kg DM). In the S diet, the supplement of energy come from maize starch (140 g/kg), while in the F diet energy came from fat (30 g sunflower oil per kg) and maize starch (74 g/kg; Table 1).

Apparent digestibility of the diets was measured with 23 females during their 3rd week of gestation-lactation (eight, eight and seven females in M, F and S respectively) according to the method of Perez, Lebas, Gidenne, Maertens, Xiccato, Parigi-Bini, Dalle Zotte, Cossu, Carazzolo, Villamide, Carabaño, Fraga, Ramos, Cervera, Blas, Fernandez, Falcao e Cunha and Bengala Freire (1995). As expected, DE contents of the S and F diets were similar (Table 1).

Animals

One-hundred and thirty primiparous 22-week-old Californian \times New Zealand does (A1066 σ \times A2077 ϕ) were presented to the male within 12 h after parturition (day 0). Females were assigned at parturition to one of the three experimental groups, corresponding to the distribution of one of the three experimental diets. Diets were given from day 0 until slaughter. Does were allocated to the experimental groups according to their litter size and their live weight. Females were caged individually with a

controlled light/dark cycle (16 h/8 h) and had free access to water and to experimental diet.

At parturition, litters were equalized at 10 young rabbits, after crossfostering. Does and their young were weighed weekly, and food intake was determined at that time. Young rabbits had free access to their dam's diet until weaning which occurred on day 28 of lactation. All does were slaughtered on day 28 of gestation-lactation in order to study reproductive performance and body composition.

Reproductive performance

The genital tract was removed and dissected immediately after slaughter. Foetuses were divided into live foetuses (L) and dead foetuses (D). Ovulation rate was determined by counting the number of corpora lutea (CL) after the ovarian dissection. Foetal mortality was defined as follows: early mortality EM = $(CL - (L + D)) \times 100/CL$; and late mortality LM = $(D \times 100)/(L + D)$. Early mortality probably occurs during the first half of pregnancy and includes fertilization and implantation failures. Late mortality probably occurs during the second half of pregnancy. Live foetuses and their placentas were weighed. Foetuses were then frozen until determination of chemical composition.

Body composition

Does were dissected and carcass (muscles and bones), skin, empty digestive tract (without gut fill), adipose tissue (perirenal and interscapular), liver, kidneys, heart + lungs and uterine horns (without uterus content) were weighed. Empty body was defined as carcass + skin + empty digestive tract + liver + adipose tissue + uterine horns + heart + lungs + kidneys. Maternal carcasses were then frozen until analysis.

Representative samples of ground matter (foetuses or carcasses) were freeze dried and analysed for DM (24 h at 103°C), protein (N \times 6.25), ash (incineration for 6 h at 550°C) and energy (adiabatic calorimeter). Lipid content was estimated as follows: lipids (g/kg) = $1000 - (g \text{ water per kg} + g \text{ protein per kg} + g \text{ ash per kg})$.

Statistical analyses

Data were analysed by analysis of variance, using the general linear procedure (GLM; Statistical Analysis Systems Institute (SAS), 1987), except for the number of dead or resorbed foetuses which were analysed using the non-parametric test (Conover, 1980; SAS, 1987). For ovulation rate, number of foetuses, and body characteristics at slaughter, the main effect was treatment. For foetal mortality the

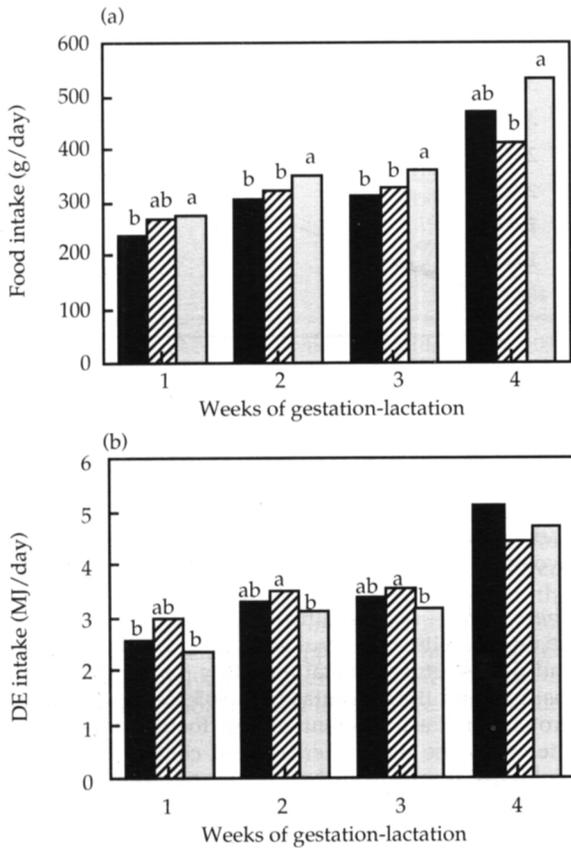


Figure 1 (a) Food and (b) digestible energy (DE) intake during gestation-lactation in the S (■), F (▨) and M (□) groups.

main effect was treatment, and the number of CL was added as a covariate. Analyses of mortality were not based on percentage but on actual numbers (e.g. CL-L for total mortality). For foetal, placental, uterine horns, litter and newborn weights, the main effect was treatment and litter size was added as a covariate. Live weight and food intake were analysed according to a split-plot design including the effect of treatment, the effect of rabbit doe within treatment (error to test the treatment effect), the effect of stage of gestation and the treatment \times stage of gestation interaction. If the treatment \times stage of gestation interaction was significant, comparisons between treatments were made for each stage of gestation. When treatments differed, comparisons of the means were tested using the Student-Newmann-Keuls' procedure. For all the variables analysed, the effect of energy content of the diet (S + F *v.* M) and the effect of energy source (S *v.* F) were also tested with the contrasts' method of GLM.

Results

All the does were receptive to the male and were mated within 12 h after parturition. The percentage of pregnant does was 70% and was similar in the three groups. Sixty-eight of the 91 pregnant does continued the experiment (no. = 23, 22 and 23 in groups S, F and M respectively), and the 23 other does were used to determine the digestibility of the diets (see **Material and methods**).

During the first 3 weeks of gestation-lactation, daily food intake of the does was lower in group S (287 (s.e. 7) g/day) than in groups F and M (311 (s.e. 8) and 328 (s.e. 8) g/day, respectively; $P < 0.01$). On the contrary, during the last week of pregnancy (does + litters), the lowest food intake was in group F (Figure 1a). Food intake during overall gestation-lactation was higher in M group than in groups F and S (10.6 (s.e. 0.2) kg *v.* 9.5 (s.e. 0.2) and 9.3 (s.e. 0.3) kg, respectively; $P < 0.01$).

From days 0 to 21, DE intake was higher in group F than in group S (3.34 (s.e. 0.08) *v.* 3.09 (s.e. 0.07) MJ/day; $P < 0.05$), and the lowest DE intake was observed in group M (2.88 (s.e. 0.07) MJ/day). During the last week of lactation, energy intake was lower in group F than in group S ($P > 0.05$; Figure 1b).

Table 2 Effects of origin and energy content of the diet on body composition (g) and chemical composition of body on day 28 of pregnancy

	Group			Contrast	
	S	F	M	S + F <i>v.</i> M	S <i>v.</i> F
No. of does	23	22	23		
Live weight	3923	3891	3859	35.7	
Body composition					
Empty body†	2985	2915	2820	37	
Carcass	1960	1907	1858	19.2	
Skin	521	524	504	7.0	
Digestive tract	222	224	220	2.9	
Liver	136 ^a	132 ^a	116 ^b	2.6	**
Adipose tissues	52 ^a	38 ^b	28 ^b	2.5	**
Uterine horns	45	43	46	1.0	
Heart + lungs	30	28	28	0.6	
Kidneys	19	19	20	0.2	
Chemical composition					
Water (g/kg)	630 ^a	643 ^a	668 ^b	4	
Ash (g/kg)	48	48	48	1	
Protein (g/kg)	211	210	211	3	
Lipid (g/kg)	111 ^a	99 ^a	73 ^b	6	***
Energy (MJ/kg)	9.22 ^a	8.76 ^a	7.85 ^b	0.2	***

^{a,b} Groups with different superscripts differ at $P < 0.05$.

† Empty body = carcass + skin + digestive tract + liver + adipose tissue + uterine horns + heart + lungs + kidneys.

Table 3 Effects of origin and energy content of the diet on litter size, litter weight and milk production

	Group			Contrast	
	S	F	M	s.e.	S v. F
No. of does	23	22	23		
Litter size					
Born alive	10.5	10.1	10.7	0.2	
Born dead	0.3	0.7	0.4	0.1	
Equalization	10	10	10		
21 days	9.0	9.4	9.2	0.1	
28 days	8.8	9.3	8.8	0.1	
Litter weight (g)					
Equalization	520	551	539	7.6	
21 days	2490 ^b	2847 ^a	2625 ^{ab}	40.4	**
28 days	3800 ^b	4477 ^a	3930 ^b	81.9	**
Milk production (g)					
0-21 days	3580 ^b	4180 ^a	3800 ^{ab}	69.4	**

^{a,b} Groups with different superscripts differ at $P < 0.05$.

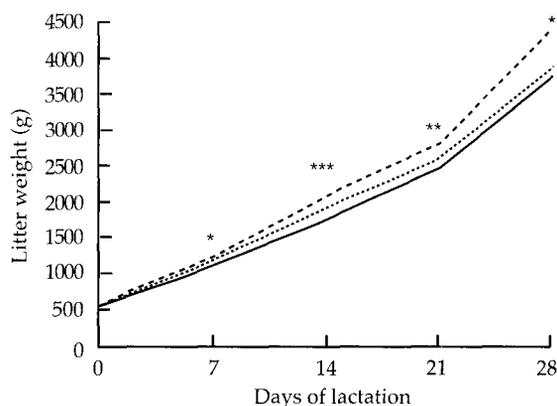
† Contrasts S + F v. M were not significant ($P > 0.05$).

Live weight of the does was similar in the three groups from mating (3605 (s.e. 42) g) to day 28 of pregnancy (3891 (s.e. 44) g). Does in the three groups gained weight during the first half of pregnancy (+461 (s.e. 21) g) and lost weight during the second half of pregnancy (-175 (s.e. 18) g).

On day 28 of pregnancy, the weights of carcass, skin, digestive tract, uterine horns, kidneys and heart + lungs were similar in the three groups ($P > 0.05$; Table 2). The weight of adipose tissue was higher in group S than in the two other groups ($P < 0.01$), while the weight of liver was lower in group M than in the two other groups ($P < 0.05$). Empty body weight tended to be higher for the does eating high-energy diets (S + F v. M; $P > 0.05$).

Lipid and energy contents of does bodies were lower, whereas water content was higher, in group M than in the two other groups ($P < 0.001$). Protein and ash contents were similar in the three groups (Table 2).

At the first parturition, the numbers of live (10.5 (s.e. 0.3)) and dead young rabbits (0.4 (s.e. 0.1)) were similar in the three groups. Then litters were equalized to 10 young rabbits. Litter size at weaning (9.0 (s.e. 0.2)) did not differ between treatments (Table 3). Milk production between birth and 21 days was estimated by litter growth: the conversion index of rabbit milk to litter weight gain was about 1.82 (Lebas, 1969). Milk production was higher in group F (4.18 (s.e. 0.1) kg) than in group S (3.58 (s.e. 0.2) kg; $P < 0.05$; Table 3). At weaning (day 28 of lactation),

**Figure 2** Evolution of litter weight during lactation in the S (—), F (---) and M groups (.....).

young rabbits were heavier in group F than in the two other groups ($P < 0.05$; Figure 2).

There was no significant difference between treatments either in ovulation rate, number of live and dead foetuses, foetal mortality, or weight of the foetuses and the placentas ($P > 0.05$; Table 4). Water, protein and ash content of the foetuses were not altered by the diet, whereas lipid content tended to be higher in group F than in the two other groups ($P > 0.05$; Table 5).

Discussion

The effects of dietary energy level or fat inclusion in the diet on reproductive performance have been the subject of several experiments. However, in many

Table 4 Effects of origin and energy content of the diet on reproductive performance during concurrent pregnancy and lactation†

	Group			s.e.
	S	F	M	
No. of does	23	22	23	
Corpora lutea	11.0	11.1	11.4	0.2
No. of foetuses				
Total	10.2	9.8	10.2	0.3
Alive	9.3	9.1	9.5	0.3
Dead	0.9	0.7	0.7	0.1
Early mortality (%)	6.4	12.7	10.9	1.7
Late mortality (%)	8.7	6.7	5.8	1.1
Mean foetus weight (g)	31.2	32.3	33.4	0.5
Mean placenta weight (g)	6.9	6.7	7.0	0.1

† There were no significant effects of treatment, origin or energy content of the diet ($P > 0.05$).

Table 5 Effects of origin and energy content of the diet on chemical composition of the foetuses on day 28 of pregnancy†

	Group			s.e.
	S	F	M	
No. of does	23	22	23	
Water (g/kg)	851	849	850	1
Ash (g/kg)	19	19	19	0.1
Protein (g/kg)	96	96	97	1
Lipid (g/kg)	34	36	34	1
Energy (MJ/kg)	3.4	3.4	3.4	0.04

† Contrasts S + F v. M and S v. F were not significant ($P > 0.05$).

studies, interpretation of these effects could be difficult because diets were formulated with very different proportions of each ingredient. Therefore, effects of dietary energy level could be confounded with effects of dietary energy source. Moreover, it was not always possible to keep a constant digestible protein level in each diet and thus effects of protein level could add to those of energy level. In the present work, diets were formulated with a common basis, and the energy supplement had a single (starch) or a dual source (starch and fat). Moreover, crude and digestible protein levels were very similar in the three diets.

Increased dietary energy content led to decreased DM intake, and the decrease was lower when the diet contained fat. However, daily DE intake was higher with high-energy diets. This is in agreement with the results of Partridge, Lobley and Fordyce (1986), Fraga *et al.* (1989) and Xiccato *et al.* (1995). Therefore, in contrast with a previous view (Lebas, 1986), it seems obvious now that highly productive intensively reared primiparous does could not adjust their voluntary food intake of a moderate-energy diet, to eat a constant amount of DE (Maertens and de Groote, 1988).

During the last week of lactation, food intake was lower for the 'litters + does' eating the diet containing fat. This could be explained by a low intake of the litter component of this grouping since litters had free access to the dam's diet. This could have been due to a lower palatability of F diet for young rabbits and/or higher milk production of the F does.

Source of energy (starch *v.* fat) influences milk production. According to the results of Fraga *et al.* (1989), and Cervera, Fernandez-Carmona, Viudes and Blas (1993), diets containing fat led to higher milk production and to higher weaning weight. The results of Xiccato *et al.* (1995) indicated that the addition of fat could improve the utilization of DE

for milk production. Otherwise, milk production was positively correlated with DE intake ($r = +0.50$; $P < 0.001$). Influence of the diet on young rabbit growth could have been mediated by modifications in the milk composition. Nevertheless, Xiccato *et al.* (1995) as well as Fraga *et al.* (1989) found no influence either of dietary energy level or the addition of fat in the diet on the chemical composition and the energy content of doe's milk. However, Fraga *et al.* (1989) observed a higher proportion of long-chain fatty acids in the milk of does given a diet supplemented with 35 g pork lard per kg. In the present experiment, no effect of dietary energy level or source on young rabbit mortality during lactation was found, in agreement with Castellini and Battaglini (1991) and Barreto and de Blas (1993).

Xiccato *et al.* (1995) found that high-energy diets were not able to reduce energy deficit and body mobilization because they stimulate milk production. On the contrary, the results here indicated that high-energy diets led to slightly decreased maternal body mobilization. Indeed, empty body was positively correlated with DE intake ($r = +0.42$; $P < 0.001$). Moreover, the lipid concentration in the body and the weight of adipose tissue were higher for does receiving the high-energy diet than for does which were given the moderate-energy diet. Nevertheless, the lipid content of the maternal body was negatively correlated with milk production ($r = -0.24$; $P < 0.05$). Therefore, the lower adipose tissue weight observed in the F group than in the S group, in spite of the higher DE intake, could be explained by the higher milk production.

Viudes de Castro, Santacreu and Vicente (1991) found that a lower number of pups were born alive when does received a fat-enriched diet. On the contrary, Maertens and de Groote (1988) observed a higher number of pups born alive per litter in does given high-energy diets. The results here showed no effect of dietary energy level or source on the number of live foetuses or foetal mortality. Therefore, this question remains to be answered.

To our knowledge, little information is available about the effect of dietary energy on foetal growth and composition in concurrently pregnant and lactating rabbit does. We could not demonstrate any effect of dietary energy level or source on foetal or placental weight on day 28 of pregnancy. However, the lipid content in the foetuses tended to increase when the does received a fat-enriched diet. The permeability of the rabbit placenta to fatty acids could explain this result (Elphick and Hull, 1977). Its implications for subsequent foetal survival remain to be elucidated.

Conclusion

It appears from the results of this experiment that concurrently pregnant and lactating primiparous rabbit does cannot adjust their voluntary food intake to eat a constant amount of DE. High-energy diets lead to increased DE intake and higher milk production. However, the depletion of body stores could also be slightly reduced, more especially if energy comes from starch instead of fat. On the contrary, energy supplementation seems to have little effect on foetal development in primiparous does that are simultaneously pregnant and lactating.

Voluntary food intake of multiparous does is higher than that of primiparous does, but milk production is also increased in multiparous does. Therefore, if such an intensive reproductive rhythm is maintained, the does will probably never be able to make up large amounts of body reserves. However, the distribution of a diet with a high-starch content could increase the lipid reserves. Nevertheless, a longer kindling to remating interval, should permit the females to replete body reserves lost during lactation. Effects of such a better body condition on long-term reproductive performance remain to be elucidated.

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