

Influence of the nutritional deficit of foetal survival and growth and plasma metabolites in rabbit does

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Summary — Two experiments were conducted in order to determine the influence of nutritional deficit on foetal survival and growth in rabbits does. All females were mated within 12 h of parturition and all the young were removed at that time. In experiment 1, females were fed close to *ad libitum* (C1, $n = 20$), or restricted to 100% (M1, $n = 20$) or 75% (R1, $n = 19$) of the maintenance energy requirement. On d 28 of gestation, foetal mortality was similar in the 3 groups, whereas foetal weight and protein content of the litters were reduced in feed-restricted groups ($P < 0.001$). In experiment 2, females were fed *ad libitum* (C2, $n = 12$) or were restricted to the same level as in R1 (R2, $n = 13$). Blood samples were collected on d 17 and 28 of gestation before and after (1 and 3 h) a standardized meal. Pre- and postprandial concentrations of non-esterified fatty acids and urea were lower in the R2 than in the C2 females ($P < 0.01$). Preprandial concentrations of glucose were similar in both groups at d 17, and higher in the R2 group than in the C2 group at d 28. The postprandial concentration of glucose was higher 1 h after the meal and lower 3 h after the meal in the R2 group ($P < 0.01$). Progesterone was significantly higher in the R2 females at d 17 ($P < 0.001$). These results suggest that nutrient deficit may be responsible for reduced foetal growth in concurrently pregnant and lactating does.

rabbit / gestation / foetal mortality / foetal weight / plasma metabolite

Résumé — Influence du déficit nutritionnel sur la survie et la croissance fœtales, et sur la concentration des métabolites plasmatiques chez la lapine. Deux expériences ont été mises en place afin de déterminer l'influence d'un déficit nutritionnel sur la survie et la croissance fœtales chez la lapine. Toutes les femelles ont été saillies au cours des 12 h suivant la mise bas, et tous les lapereaux nouveaux-nés ont été retirés à ce moment. Dans la première expérience, les femelles sont nourries à un niveau proche de l'*ad libitum* (lot C1, $n = 20$), ou restreint à 100% (lot M1, $n = 20$) ou 75% (lot R1, $n = 19$) du besoin énergétique d'entretien. Au 28^e jour de gestation, la mortalité fœtale est similaire dans les 3 lots tandis que le poids des fœtus et la teneur en protéines des portées sont réduits chez les femelles ayant une alimentation restreinte ($P < 0,001$). Dans la seconde expérience, les femelles du lot C2 ($n = 12$) sont alimentées à volonté, et celles du lot R2 ($n = 13$) subissent une restriction alimentaire identique à celle des lapines du lot R1. Des prises de sang sont effectuées aux 17 et 28^e jours de gestation, avant, 1 h et 3 h après un repas standard.

Les concentrations pré- et postprandiales d'acides gras non estérifiés et d'urée sont plus faibles chez les femelles du lot R2 ($P < 0,01$). La concentration préprandiale de glucose est similaire dans les 2 lots au jour 17 et plus élevée dans le lot R2 que dans le lot C2 au jour 28. La concentration postprandiale de glucose est supérieure, 1 h après le repas et inférieure, 3 h après le repas, dans le lot R2 que dans le lot C2 ($P < 0,01$). La concentration en progestérone est supérieure dans le lot R2 au jour 17 ($P < 0,001$). Les résultats suggèrent que le déficit nutritionnel est responsable de la diminution de la croissance des fœtus chez les lapines simultanément gravides et allaitantes.

lapin / gestation / mortalité fœtale / croissance fœtale / métabolites plasmatiques

INTRODUCTION

In rabbit does that are mated immediately after parturition, foetal survival and growth are impaired in lactating animals (established by comparison with non-lactating animals) and the increase in foetal mortality seems to occur when milk production is maximal (Fortun *et al*, 1993). In pregnant and lactating females, the energy and protein requirements are very high and despite an increase in feed intake, the energetic balance is negative and body reserves are mobilized to a great extent (Parigi-Bini *et al*, 1991). It has therefore been suggested that nutritional deficit plays a role in the altered reproductive performance of pregnant and lactating does. This hypothesis is also supported by the observation of lower birth weights in both the rabbit (Lebas, 1975) and other species (sow: Henry and Étienne, 1978; ewe: Robinson, 1990) when the energy supply of the dam is diminished. The effects of feed restriction on foetal mortality have not been thoroughly studied in the rabbit and the results are controversial, as in other species. Some authors have reported a detrimental effect of feed restriction on litter size (guinea pig: Young and Widdowson, 1975; rabbit: Coudert and Lebas, 1985; rat: Abel, 1990), whereas others observed no effect (rabbit: Lebas, 1975; pig: Henry and Étienne, 1978).

The aim of the present study was to assess the role of nutritional deficit in the impairment of late foetal survival and growth occurring in pregnant and lactating does

mated shortly after parturition. This was done by reducing the feed intake of non-lactating does, in order to imitate the nutritional deficit due to milk production. Two experiments were conducted in order to compare the reproductive performance and body composition in pregnant does with different levels of feed intake.

The blood concentrations of glucose, non-esterified fatty acids (NEFA) and urea in the dam's blood reflect maternal nutritional status and can affect foetal nutrition (Battaglia and Meschia, 1988). Therefore, the concentrations of these metabolites were measured in plasma taken from does at 2 stages of gestation (d 17 and 28, experiment 2). The concentration of progesterone was found to be significantly lower in pregnant and lactating does than in non-lactating does (Fortun *et al*, 1993). The influence of the blood concentration of progesterone on embryo/foetal survival has been demonstrated in several species (ewe: Wilmut *et al*, 1986; hamster: Huck *et al*, 1988; pig: Ashworth, 1991). Thus, the plasma concentration of this hormone was also measured in the second experiment.

MATERIALS AND METHODS

Animals

Primiparous 22-week-old crossbred does (from a mating between A2066 bucks and A1077 does) were mated within 12 h of parturition (d 0). All

the young born were removed from their mother immediately after birth. Females were allocated to homogeneous experimental groups according to their litter size and their individual live weight so that means and the repartition of litter size and live weight at mating were similar in the different groups in each experiment. All does were fed a standard diet containing 17.5% protein and 9.7 MJ DE per kilogram of feed. Does were weighed weekly. For all groups in experiment 1 and the feed-restricted group in experiment 2, the total amount of feed was given each morning after the collection of the left-overs. When does were fed *ad libitum*, left-overs were collected once a week. For all animals, left-overs were weighed and feed intake per week was calculated from mating to d 28 of gestation.

Experiment 1

Animals in the control group (C1, $n = 20$) were fed 190 g/d of feed during the first week of gestation and 210 g/d thereafter. The feeding level in this group was close to the feed intake of primiparous pregnant does fed *ad libitum* (Fortun *et al*, 1993). The animals in the M1 group ($n = 20$) were fed 120 g/d throughout pregnancy. This feed intake was close to the maintenance requirement (421 kJ/d/kg^{0.75} during pregnancy; Parigi-Bini *et al*, 1990). The animals in the severely restricted group (R1, $n = 19$) were fed 120 g/d during the first week of gestation and 80 g/d thereafter. This feed intake corresponded to 75% of the maintenance requirement for overall pregnancy.

All does were slaughtered on d 28 of gestation before the morning meal. The genital tract was immediately removed and dissected. Placentas and foetuses were weighed. According to Adams (1960), foetuses were divided into 3 classes: 1) live (L), when foetuses were well developed and still moving; 2) dead (D), when the foetus was recognizable, but unmoving and showing marked developmental delay; and 3) resorbed (R), when the foetus was not recognizable and only the placenta was present. Ovulation rate was determined by counting the number of corpora lutea (CL) after the ovarian dissection. Foetal mortality was defined as previously described (Fortun *et al*, 1993). The following equations were used: total mortality $TM = (CL - L)100/CL$; early mortality $EM = (CL - (L + R + D))100/CL$; and late mortality $LM = ((R + D)100)/(L + R + D)$. Early

mortality probably occurs during the first half of pregnancy and late mortality thereafter (Adams, 1960).

Does were dissected and carcass (muscles, lungs, heart and bones), skin, full digestive tract (with gut fill), adipose tissues (perirenal and interscapular), liver, kidneys and uterine horns were weighed. Maternal carcasses with adipose tissues, and litters (foetuses with placentas) were then frozen until analysis. Representative samples of ground matter were freeze-dried and analysed for dry matter (24 h at 103°C), protein (N x 6.25), ash (incineration for 6 h at 550°C) and energy (adiabatic calorimeter). Lipid percentage was estimated according to Hulot *et al* (1992); lipids (%) = $(100E \text{ (MJ/100 g)} - (2.385 \times \text{protein \%})) / 3.766$.

Experiment 2

Animals were fed *ad libitum* in the control group (C2, $n = 12$). In the restricted group (R2, $n = 13$), animals were fed 120 g/d during the first week of gestation and 80 g/d thereafter.

Blood samples were collected by puncture in an auricular artery at d 17 and 28 of gestation. Preprandial samples were collected between 08:30 and 09:30 am after 18 h of fasting. A meal was distributed between 12:00 am and 01:00 pm and postprandial samples were collected 1 and 3 h after the beginning of the meal. The amount of feed was 20 g in all groups since does cannot eat more than this in one go (Père, 1987). All the feed was eaten within 20 min. Blood samples (3 ml) were collected in heparinized tubes and centrifuged immediately. Plasma was stored at -20°C until it was assayed.

Concentrations of metabolites were measured by automated enzymatic methods with a Cobas Mira Roche (Hoffman Laroche, Basel, Switzerland). Non-esterified fatty acids, glucose and urea were measured by colorimetric methods using kits containing acyl-CoA synthetase (NEFA; Unipath SA), glucose oxidase (Biomérieux), and urease (Biomérieux), respectively. The concentration of progesterone was quantified on preprandial blood samples by radioimmunoassay as described by Thibier and Saumande (1975). The sensitivity of the assay was 0.2 ng/ml and intra- and interassay coefficients of variation were 12 and 14%, respectively.

At the second parturition, the newborn were counted and weighed within 12 h.

Statistical analyses

For each experiment, data were analysed by analysis of variance, using the general linear procedure (GLM; SAS, 1987), except for the number of dead or resorbed foetuses which were analysed using non-parametric tests (Conover, 1980; SAS, 1987). For ovulation rate, number of foetuses, and body characteristics at slaughter, the main effect was treatment. For foetal mortality the main effect was treatment, and the number of corpora lutea was added as a covariate. Analyses of mortality were not based on percentage but on actual numbers (eg CL-L for total mortality). For foetal, placental, uterine horns, litter and newborn weights, the main effect was treatment and the number of live foetuses was added as a covariate. Live weight and progesterone 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 x stage of gestation interaction. For blood metabolites, time of sampling was added in the model. If the treatment x stage of gestation interaction or the treatment x time of sampling was significant, comparisons between treatments were made for each stage of gestation, or each time of sampling. When treatments differed, comparisons of the means were tested using the Student–Newman–Keuls' procedure.

RESULTS

Experiment 1

In the C1 group, the feed intake was 171 g/d, 206 g/d, 202 g/d and 170 g/d during the 1st, the 2nd, the 3rd and the 4th week, respectively. In the M1 and R1 groups, the feed intake during the 1st week was 117 g/d and 106 g/d, respectively ($P > 0.05$). During the following weeks, all the feed given to the M1 and R1 females was eaten. The live weight of does at mating was similar in the 3 groups ($3\ 605 \pm 35$ g). All females were heavier at the end than at the beginning of gestation (fig 1). The weight gain until d 28 depended on the feed level

($P < 0.001$), and R1 and M1 females were 12 and 9.5% lighter, respectively, than C1 females at the end of gestation (table I).

The weights of carcass, skin, adipose tissues, liver, and uterine horns were lower in the restricted (R1 and M1) than in the C1 group ($P < 0.001$; table I). All these values were lower in the R1 than in the M1 group, but the difference was significant only for skin, liver, and kidneys. The lipid percentage and energy content per 100 g of maternal body increased with feed level, whereas body water decreased ($P < 0.001$). Protein and ash percentage were similar in the 3 groups (table I).

There was no significant difference between treatments either in the ovulation rate, number of live, dead, and resorbed foetuses, or foetal mortality (table II). However, the weights of placentas and foetuses increased significantly with the feeding level of the doe ($P < 0.001$; table I). Percentage of protein in the foetuses increased with the feed level of the doe, whereas that of water decreased ($P < 0.001$). Energy content, ash

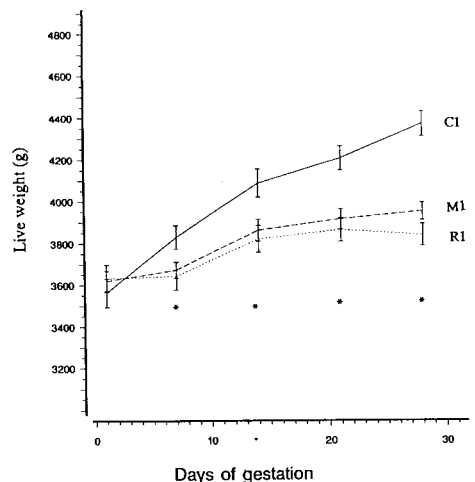


Fig 1. Experiment 1. Influence of feed level on live weight of does. * Differences between treatment groups occurred at d 7, 14, 21 and 28 ($P < 0.001$).

Table I. Experiment 1. Traits of litter and body composition of does slaughtered at d 28 of gestation.

	<i>Treatment group</i>		
	<i>C1</i>	<i>M1</i>	<i>R1</i>
<i>Dams</i>			
Number of pregnant does	20	20	19
Live weight (g)	4 371 ± 59 ^a	3 952 ± 42 ^b	3 838 ± 53 ^b
Carcass weight (g)	2 369 ± 32 ^a	2 219 ± 26 ^b	2 172 ± 34 ^b
Skin weight (g)	641 ± 11 ^a	573 ± 16 ^b	515 ± 14 ^c
Digestive tract weight (g)	448 ± 9	458 ± 14	477 ± 9
Adipose tissues weight (g)	121 ± 9 ^a	85 ± 6 ^b	71 ± 8 ^b
Uterine weight (g)	51 ± 2 ^a	40 ± 2 ^b	39 ± 2 ^b
Liver weight (g)	98 ± 3 ^a	81 ± 2 ^b	71 ± 2 ^c
Kidney weight (g)	19 ± 0.3 ^a	18 ± 0.6 ^a	16 ± 0.4 ^b
Water (%)	59 ± 0.6 ^c	62 ± 0.7 ^b	64 ± 0.9 ^a
Ash (%)	3.6 ± 0.1	3.7 ± 0.1	3.8 ± 0.1
Protein (%)	18.9 ± 0.3	19.2 ± 0.2	18.9 ± 0.2
Lipid (%)	19.3 ± 0.9 ^a	15.6 ± 0.9 ^b	13.4 ± 1.0 ^b
Energy (MJ/100 g)	1.18 ± 0.01 ^a	1.05 ± 0.01 ^b	0.96 ± 0.01 ^c
<i>Litters</i>			
Foetal weight (g)	40.2 ± 1.0 ^a	36.1 ± 1.1 ^b	30.5 ± 1.0 ^c
Placental weight (g)	7.1 ± 0.2 ^a	6.6 ± 0.3 ^a	5.5 ± 0.2 ^b
Water (%)	84 ± 0.1 ^a	85 ± 0.2 ^b	86 ± 0.2 ^c
Ash (%)	1.9 ± 0.01	1.8 ± 0.03	1.8 ± 0.03
Protein (%)	10.3 ± 0.1 ^a	9.6 ± 0.2 ^b	9.1 ± 0.1 ^c
Lipid (%)	2.9 ± 0.5	3.3 ± 0.1	3.1 ± 0.1
Energy (MJ/100 g)	0.36 ± 0.01	0.35 ± 0.01	0.34 ± 0.01

^{a,b,c} Values with different superscripts on the same line differ at $P < 0.05$.

and lipid percentage were similar in the 3 groups (table I).

Experiment 2

Feed intake over pregnancy was 52% lower in the R2 group (88 ± 0.5 g) than in the C2 group (184 ± 6 g; $P < 0.001$). Live weight of the does was similar in the 2 groups at mating ($3\ 604 \pm 47$ g). Between mating and d 28 of pregnancy, both R2 and C2 females

gained weight, but the gain was higher in the C2 group (C2: 653 ± 62 g, R2: 121 ± 49 g, $P < 0.01$). Between the first and the second parturition, does in the R2 group lost live weight (-201 ± 36 g) whereas those in the C2 group gained weight (247 ± 4 g; $P < 0.001$).

The number of live newborn at the second parturition was similar in the 2 groups. The weights of litters and newborn were lower in the R2 than in the C2 group ($P < 0.01$; table III).

Table II. Experiment 1. Reproductive characteristics of does slaughtered at d 28 of gestation.

	<i>Treatment group</i>		
	<i>C1</i>	<i>M1</i>	<i>R1</i>
Number of pregnant does	20	20	19
Number of corpora lutea	11.8 ± 0.4	10.8 ± 0.5	11.9 ± 0.5
Number of foetuses			
Live	9.5 ± 0.5	8.2 ± 0.7	8.6 ± 0.6
Resorbed	0.65 ± 0.2	0.15 ± 0.1	0.68 ± 0.2
Dead	0.20 ± 0.1	0.30 ± 0.1	0.32 ± 0.2
Total mortality (%)	19.5 ± 3.4	25.4 ± 5.3	27.1 ± 4.7
Early mortality (%)	12.4 ± 3.3	21.3 ± 5.9	19.2 ± 5.4
Late mortality (%)	7.6 ± 2.3	4.2 ± 1.6	8.5 ± 2.3

Before the meal, concentration of glucose was similar in the 2 groups at d 17, whereas it was significantly higher in the R2 group at d 28. After the meal, glucose was first higher (1 h after the meal) and then lower (3 h after the meal) in the R2 than in the C2 group (fig 2). In both groups, preprandial concentration of glucose was significantly lower, and that of NEFA was significantly higher on d 28 than on d 17 ($P < 0.01$). Pre- and postprandial concentration of

urea and NEFA were higher in the C2 than in the R2 group at both stages of gestation (d 17 and 28), but the difference was not always significant (fig 2). Whatever the group and the stage of gestation, NEFA concentration was higher before the meal than after, whereas that of urea was lower.

Plasma concentration of progesterone was significantly higher in the R2 than in the C2 group on d 17 ($P < 0.001$) whereas it was similar in both groups on d 28 (fig 3).

Table III. Experiment 2. Reproductive performance of does which were fed *ad libitum* (C2) or restricted (R2) during gestation.

	<i>Treatment group</i>	
	<i>C2</i>	<i>R2</i>
Number of pregnant does	12	13
Number of born alive	10.0 ± 0.6	9.4 ± 0.5
Number of stillborn	0	0
Newborn weight (g)	55.5 ± 3.0 *	44.4 ± 1.4
Litter weight (g)	538.2 ± 22 *	407.6 ± 17

* Means differ at $P < 0.01$.

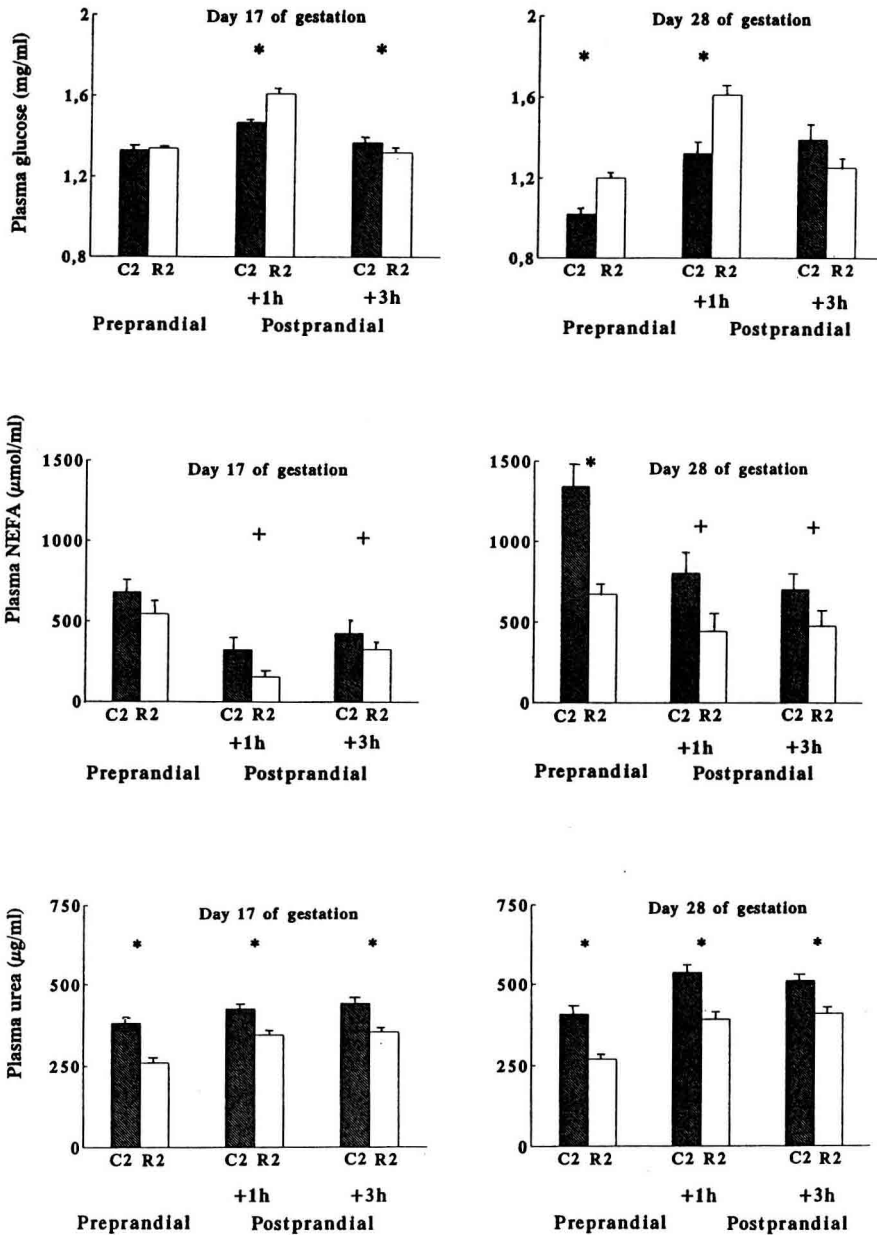


Fig 2. Experiment 2. Pre- and postprandial (+ 1 h and + 3 h) concentrations of glucose, NEFA and urea in the C2 and in the R2 females at d 17 and 28 of gestation (means and standard error of the mean). +, *Means differ significantly within a day of gestation and a time-schedule sample, (+) $P < 0.1$ and (*) $P < 0.05$.

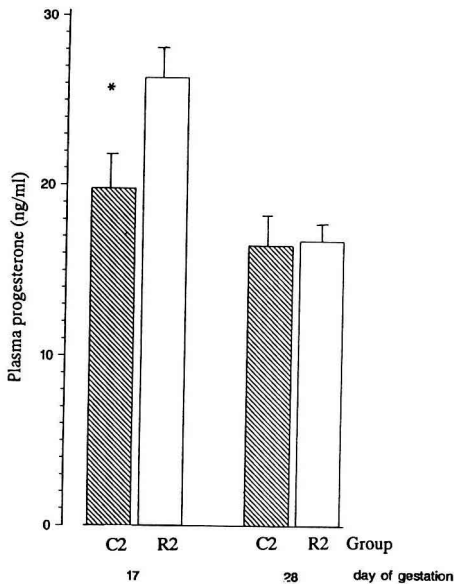


Fig 3. Experiment 2. Concentrations of progesterone in the C2 and the R2 females at d 17 and 28 of gestation (means and standard error of the mean). *Progesterone concentration was higher in the R2 group at d 17 ($P < 0.001$).

DISCUSSION

Feed intake and variation in the live weight of does throughout gestation were very similar in the C1 and C2 groups, which confirms that the level of feeding in the control group from the first experiment was close to *ad libitum*. Previous observations in the doe (Lebas, 1975) and in the sow (Henry and Étienne, 1978) have shown that feed restriction induces lower live weight at the end of gestation. Our results show that the decrease in live weight was accompanied by a decrease in the lipid percentage and energy content in the carcass analyzed with the adipose tissues. These decreases were related to the level of feed restriction. Even though the percentage of protein in the body was not modified, the protein content of the carcass was slightly decreased by feed

restriction (470 g vs 442 g and 424 g of protein in the C1, M1 and R1 groups, respectively). The reduction in lipid percentage and energy content was accompanied by an increased water percentage, in agreement with previous work (Lebas, 1973; Sadurskis *et al*, 1991).

In a previous experiment with the same line of rabbits (Fortun *et al*, 1993), pregnant and lactating does were 10% lighter than fully fed non-lactating does on d 28 of gestation. In the present experiments, a similar difference in live weight was obtained between severely restricted and fully fed does. However, the pattern of variation in live weight differed between the fully fed lactating does and the restricted non-lactating does. It increased up to d 14 and thereafter decreased in the lactating does whereas it hardly varied in the severely restricted does. The nutritional deficit probably occurred later and was more severe in the lactating than in the feed-restricted non-lactating does.

A decrease in preprandial glucose concentration throughout pregnancy has been observed in the rabbit (Gilbert *et al*, 1984) and in other species (Leturque *et al*, 1986, 1987; Kühl, 1991), and could be explained either by an increase in the rate of utilization (Hay *et al*, 1984) or in the distribution space as observed in other species (man: Kalhan *et al*, 1979; rat: Leturque *et al*, 1981). In contrast, NEFA concentration increased between d 17 and 28, as reported by Gilbert *et al* (1984). In the rabbit, the last days of pregnancy correspond to the phase of maximal growth of the foetuses (Hudson and Hull, 1975), whereas the appetite of the doe decreases. The maternal tissue's spare glucose which is preferentially used by pregnant uterus (Hauguel *et al*, 1987; Battaglia and Meschia, 1988) and the females mobilize their body reserves (Parigi-Bini *et al*, 1990) in order to satisfy the needs of their own tissues and for foetal growth. Such a phenomenon might explain the increase in NEFA concentration between d 17 and 28.

On d 17, preprandial concentrations of glucose and NEFA were similar in restricted and *ad libitum* does. In contrast, on d 28, pre- and the postprandial NEFA concentrations were lower and the preprandial glucose concentration was higher in restricted than in *ad libitum* does. These results contrast with others observed after 96 h fasting (rat: Girard *et al*, 1977; rabbit: Hauguel *et al*, 1988). Our results seem paradoxical since NEFA are indicators of body fat mobilization which might have been greater in restricted than control does as shown by lower weight of adipose tissues and lipid percentage in the carcass at the end of gestation in the first experiment. However, it must be recalled that preprandial concentrations of NEFA were measured 18 h after the previous meal and, in both groups, does had to use fat as a source of energy and synthesize glucose for essential purposes. In growing gilts and in lactating sows, 15–17 h after the previous meal, glucose levels are not modified or are increased whereas NEFA levels are not modified or are decreased in females with the lower level of feeding (Prunier *et al*, 1993a, 1993b). Thus, in agreement with Prunier *et al* (1993a), it can be hypothesized that feed-restricted animals, which are in a negative energetic balance most of the time, adapt to this state and modifications in regulation of the metabolism allow them to reduce variations in circulating levels of glucose and NEFA. A reduction in the plasma concentration of urea in the restricted group had already been observed in restricted as compared to fully fed lactating sows (Prunier *et al*, 1993a) and this could be due to a decrease in amino-acid catabolism, in relation to the lower amount of protein absorbed (Gilbert *et al*, 1984).

The observation of lower weights for placentas, foetuses and newborns in restricted rather than fully fed does is in accordance with previous results (Young and Widdowson, 1975; Lederman and Rosso, 1980; Rosso and Kava, 1980). This observation

suggests that a nutrient deficit could be involved in the impairment of foetal growth observed in pregnant and lactating does. When maternal feed intake was reduced, foetal protein and dry matter percentage decreased, whereas the lipid percentage was not modified. These results contrast with those of Hafez *et al* (1967), who reported a lower lipid percentage in newborn from feed-restricted does. In mammalian species, glucose constitutes the major energetic substrate for foetuses. However, in the rabbit species, NEFA cross the placental barrier (Elphick and Hull, 1977) and may provide a substantial fraction of the carbon requirements (Battaglia and Meschia, 1988). Thus, in restricted females, the reduction in foetal or newborn weight might be explained by a reduction in NEFA supply and placental blood flow as previously observed (Moriss *et al*, 1980; Rosso and Kava, 1980). Such phenomena might occur in lactating females due to competition between the uterus and the mammary gland for both blood flow and nutrients.

The number of foetuses that died in late gestation (resorbed + dead foetuses) was relatively high in the present control group compared with previous experimental results (0.85 vs 0.38 foetuses; Fortun *et al*, 1993). However, the ovulation rate was slightly higher (11.8 vs 11.1), whereas the number of early foetuses lost (EM) was similar in both studies (1.45 vs 1.32). Thus, the measured foetal mortality during late gestation in the present control group could result from a phenomenon involving a limitation of the litter size in order to stay below an upper limit equal to the uterine capacity as defined in the pig by Bennet and Leymaster (1989). Our results did not show any effect of feed level on early foetal mortality or on the number of dead and resorbed foetuses on d 28. Thus, the nutritional deficiency may not be responsible for the increased foetal mortality observed in lactating does. Alternatively, an eventual influence of feed restriction on

late foetal mortality could have been biased by the fact that late foetal mortality was relatively high in the control group. Moreover, it should be noted that total mortality was similar in feed-restricted does (M1: 2.6 foetuses, R1: 3.3 foetuses) and in lactating females (2.64 foetuses, Fortun *et al*, 1993), with more foetuses lost in early gestation and less in late gestation in restricted females. Therefore, the influence of a greater nutrient deficit, as it may occur around the peak of lactation in lactating females, remains to be studied.

Progesterone was increased in restricted females on d 17. A decrease in the metabolic turnover rate of progesterone has been found in restricted sows (Symonds and Prime, 1989) and this could explain the present differences. On the contrary, an increase in the metabolic turnover rate of progesterone caused by high feed intake during lactation could explain the lower progesterone concentration previously observed in lactating does (Fortun *et al*, 1993). The influence of feeding level on the circulating concentration of progesterone did not seem to modify foetal survival since the number of live, dead or resorbed foetuses, and the number of live newborns were similar in the fully fed group and the feed-restricted group. These results contrast with others showing lower embryo/foetal mortality when the concentration of progesterone is higher (ewe: Wilmut *et al*, 1986; hamster: Huck *et al*, 1988; pig: Ashworth, 1991).

CONCLUSION

Present results suggest that impairment of foetal growth in concurrently pregnant and lactating does can be explained by nutrient deficit. These experiments could not demonstrate any influence of feeding level on foetal mortality and the origin of its increase in pregnant and lactating does remains to be elucidated.

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