

Influence of the number of suckling young and the feed level on foetal survival and growth in rabbit does

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Summary — This study was undertaken to determine the influence of various degrees of nutritional deficit on foetal survival and growth in pregnant and lactating does. All females were mated within 12 h of parturition (d 0) and slaughtered at d 28. For around half of them, lactation was terminated at parturition and does were fed *ad libitum* throughout gestation (CNL group, $n = 28$) or feeding was restricted from d 15–28 (RNL group, $n = 27$). Other females were allowed to nurse 4 (FL group, $n = 27$) or 10 young (TL group, $n = 27$), and were fed *ad libitum*. Live-weight variation between d 14 and 28 ($\delta p1428$) varied highly between groups (CNL: +194 g; RNL: +112 g; FL: -113 g; TL: -197 g; $P < 0.01$). Late foetal mortality ($> d 15$) was significantly increased in lactating groups (FL: 10.4%, TL: 15.5%) compared with non-lactating groups (CNL: 5.4%; RNL: 3.6%) without any influence of $\delta p1428$. The weight of the foetuses was significantly lower in the lactating groups (CNL: 39.7 g; RNL: 39.3 g; FL: 37.5 g; TL: 34.9 g; $P < 0.001$) and was negatively related to $\delta p1428$ ($r = 0.47$; $P < 0.001$). The concentrations of progesterone were lower in lactating than in non-lactating does (TL + FL vs CNL + RNL; $P < 0.01$) on d 7 and 17, but similar on d 28. These results suggest that the detrimental effect of lactation on foetal survival and growth can be decreased by reducing the number of suckling young.

rabbit / lactation / foetal mortality / foetal growth / feed restriction

Résumé — Influence du nombre de lapereaux allaités et du niveau alimentaire sur la viabilité et la croissance foetale chez la lapine. L'objectif de cette expérience est de déterminer l'influence de l'intensité d'un déficit énergétique sur la viabilité et la croissance foetales chez la lapine. Toutes les femelles expérimentales ont été saillies et fécondées dans les 12 h qui suivent la parturition (j0) et abattues à j28. Dans les 2 premiers groupes de femelles, la lactation est arrêtée aussitôt après la mise bas par retrait des lapereaux, puis les lapines sont alimentées à volonté (lot CNL, $n = 28$) ou rationnées de j15 à j28 (lot RNL, $n = 27$). Dans les 2 autres lots, les femelles sont alimentées à volonté et allaitent une portée de 4 lapereaux (lot FL, $n = 27$) ou de 10 (lot TL, $n = 25$). Des prises de sang sont effectuées à 0, 7, 17 et 28 j de gestation. La variation de poids vif des lapines durant la seconde moitié de la gestation ($\delta p1428$) est différente entre les lots (CNL : +194 g, RNL : +112 g, FL : -113 g, TL : -197 g ; $P < 0,01$). Au 28^e jour de gestation, les poids de la carcasse et surtout de tissus adipeux sont significativement réduits dans les 2 lots de lapines allaitantes ($P < 0,001$). La production laitière (estimée) est légèrement plus faible dans le lot FL que dans le lot TL (-12,6%, $P < 0,05$). La mortalité foetale tardive ($> j15$) est plus élevée chez les lapines allaitantes (FL :

10,4%, TL : 15,5%) comparées aux lapines non allaitantes (CNL : 5,4%, RNL : 3,6% ; $P < 0,05$) sans relation avec $\delta p1428$. La concentration en progestérone plasmatique est moins élevée chez les femelles allaitantes ($P < 0,01$) à j7 et 17, mais similaire dans les 4 lots à j28. À l'abattage, les fœtus des lapines allaitantes sont plus légers (FL : 37,5 g, TL : 34,9 g) que ceux des lapines non allaitantes (CNL : 39,7 g, RNL : 39,3 g ; $P < 0,001$) et leur poids augmente linéairement avec $\delta p1428$ ($r = 0,47$; $P < 0,001$). Ces résultats suggèrent que l'effet défavorable de la lactation sur la mortalité et la croissance fœtales peut être diminué par une réduction de la taille de la portée allaitée.

lapin / lactation / mortalité fœtale / croissance fœtale / rationnement

INTRODUCTION

Rabbit does can be mated soon after parturition and are able to sustain pregnancy throughout lactation. However, when mating occurs within 12 h of parturition, foetal survival and growth are altered in lactating compared with non-lactating females (Fortun *et al*, 1993). Nutritional deficiency and/or hormonal disturbance may explain this phenomenon. The influence of energy supply on foetal growth has been poorly investigated in the rabbit species. In the sow, and particularly for the gilt, the birth weight of the piglets increases with the energy supply to the mother (Henry and Etienne, 1978). Similarly, in the ewe, restriction of food intake in early (Vincent *et al*, 1985) or in late (Robinson and Mac Donald, 1989) pregnancy depresses foetal growth. The effects of nutritional deficiency on foetal survival are more controversial (Robinson, 1986).

The energetic balance of rabbit does is negative during lactation (Parigi-Bini *et al*, 1990a) and the second half of gestation (Jean Blain and Durix, 1985; Parigi-Bini *et al*, 1990b). Consequently, the energy deficit is very high in pregnant-lactating females (Parigi-Bini *et al*, 1992) and can play a role in their altered reproductive efficiency.

The objective of the present study was to determine the influence of various degrees of energy deficit on foetal survival and growth by modulating the level of feeding in pregnant does or the number of suckling young in pregnant-lactating females.

MATERIALS AND METHODS

One hundred and thirty-nine primiparous 22-week-old crossbred does (from a mating between an A2066 buck and a A1077 doe) were mated within 12 h of parturition (d 0). The experiment was replicated twice. The first replicate was carried out in the spring ($n = 68$), the second in the autumn ($n = 71$). The females were allocated to 4 experimental groups. In the CNL ($n = 36$) and the RNL groups ($n = 35$), all young were removed immediately after birth (non-lactating does). The does in the TL group were lactating ($n = 33$) and their litters were equalized at 10 young by fostering rabbits from other groups because the mean litter size was 8.8 rabbits born. The does in the FL group were lactating ($n = 35$), and the litters were reduced to 4 young rabbits. From d 21, the young had free access to their own diet, which was different from mother's feed. The feed intake of the young was determined at d 28 (weaning).

All does were offered a standard diet containing 17.5% protein and 2 330 kcal of digestible energy per kg. Digestible energy was measured with 8 seven-week-old rabbits, according to the method of Colin and Lebas (1976). Females in the TL, FL and CNL groups were given *ad libitum* access to feed and intake was measured weekly from mating to d 28 of gestation. Females in the RNL group were fed *ad libitum* from d 0–14 of pregnancy while feed intake was restricted from d 15–28 of gestation. The individual feed intake between d 7–14 was taken as a reference. RNL females received daily a quantity corresponding to 75 and 47% of the reference feed intake during the third and fourth weeks, respectively. The does and their young were weighed weekly. Milk production between d 0–21 was estimated by litter growth (Lebas, 1969), the conversion index of rabbit milk is about 1.52 during the first week, 1.75 during the second

week, and 2.18 during the third week of lactation.

Blood samples (4 ml) were collected in heparinized tubes on d 0, 7 and 17 by puncture in an auricular artery. The does were slaughtered on d 28, and a blood sample was collected at that time. The samples were immediately centrifuged and the plasma was stored at -20°C until it was assayed for progesterone. Plasma progesterone levels were quantified by radioimmunoassay as described by Thibier and Saumande (1975). The sensitivity of the assay was 0.2 ng/ml, and the intra- and interassay coefficients of variation were 9 and 12%, respectively.

Immediately after slaughter on d 28, the pregnant uterus was removed, weighed, and dissected. Placentas and foetuses were counted and weighed. Three classes of foetuses were defined: (i) live (L) when foetuses were well developed and already moving or breathing; (ii) dead (D) when foetuses were recognizable, but immobile and showing an evident and strong developmental delay, this mortality probably occurred between d 20 and 27; and (iii) resorbed (R) when only the implantation site was recognizable. This mortality may have occurred between d 15 and 20.

Uterine horns and ovaries were weighed, and ovulation rate was determined by counting the number of corpora lutea (CL). Foetal mortality was defined as follows:

Total mortality $TM = (CL - L) \times 100/CL$

Early mortality $EM = (CL - (L + D + R)) \times 100/CL$

Late mortality $LM = (D + R) \times 100/CL$

Early mortality included fertilization failure, embryonic and early foetal mortality. Late mortality included resorbed or dead foetuses and might have occurred after d 15.

The does were dissected and carcass (muscles + bones + heart + lung + liver), skin, digestive tract with content, and adipose tissues (perirenal + interscapular tissues) were weighed.

Nonpregnant does were excluded from the analyses. The data on pregnant does (107 of 139 mated) were analyzed using the GLM procedure (SAS, 1987). For reproductive performance and characteristics at slaughter the linear model was as follows: $Y_{ij} = \mu + T_i + R_j + (TR)_{ij} + e_{ij}$ (model 1), where Y = the individual variable; μ = the mean; T = the effect of treatment; R = the effect of replicate; TR = the interaction between treatment and replicate; and e = the residual error. Additional analyses of reproductive performance were made

including the variation in live weight between d 14 and 28 ($\delta p1428$) as a covariate: $Y_{ij} = \mu + T_i + R_j + (TR)_{ij} + \delta p1428 + e_{ij}$ (model 2). In both models foetal, placental and uterine-horn weights were analyzed with litter size as a covariate. Live weight of the does and the young, feed intake and hormone concentrations were analyzed according to a split-plot design as follows: $Y_{ijk} = \mu + T_i + R_j + (TR)_{ij} + A_{(ij)} + S_k + (TS)_{jk} + e_{ijk}$, where A = the effect of animal within treatment \times replicate (error to test the treatment effect); S = the effects of stage of gestation; and TS = the interaction between treatment and stage of gestation. When the TS interaction was significant then the comparisons between treatments were made for each stage of gestation. When the treatments differed, comparisons of the means were tested using the Student–Newman–Keuls' procedure. For progesterone concentrations, lactating does (TL + FL) were also compared with non-lactating does (CNL + RNL) with the method of contrasts of the GLM.

RESULTS

The results are presented in the following order: gestation rate; growth of litters; feed intake; live-weight variations; body composition and reproductive performance of the does; and progesterone concentrations. All females were receptive to the male and the percentage of pregnant does was similar in all treatments (77%). Thus, 25, 27, 28 and 27 females were pregnant in the TL, FL, CNL and RNL groups, respectively.

The replicate had no effect on litter growth, and there was no replicate \times treatment interaction. The mortality of the young during lactation was 8.8 and 0% in the TL and FL groups, respectively. Young rabbits were heavier in the FL group than the TL group, on d 21 and 28 ($P < 0.001$; table I). Milk production was estimated at 3 650 g in the TL group and 3 190 g in the FL group ($P < 0.01$). Feed intake of litters between d 21 and 28 was 741 g and 1 327 g in the FL and TL groups, respectively ($P < 0.001$).

The feed intake of lactating females was greater than that of non-lactating females

Table I. Growth and mortality of young suckling during lactation.

	Treatment		SEM *
	FL	TL	
No of litters	27	25	—
Litter size			
At birth	8.6	8.8	0.32
After equalization	4 ^a	10 ^b	—
On d 28	4 ^a	9.1 ^b	—
Individual weight (g)			
After equalization	57.5	53.2	1.1
On d 21	493.3 ^a	277.1 ^b	16.4
On d 28	617.7 ^a	454.9 ^b	18.3

^{ab} Values with different superscripts within the same row differ by $P < 0.01$; females were lactating with 10 (TL) or 4 (FL) suckling rabbits; * standard error of the mean.

(table II, $P < 0.001$). The females in the TL and FL groups had similar feed intake throughout gestation except during the third week, when the females in the FL group had a lower feed intake (-10% , $P < 0.05$). Before restriction, feed intake was similar in the CNL and RNL groups. Between d 15 and 28, the feed intake of RNL females was 25% lower than that of the CNL females ($P < 0.001$).

Although the females were heavier in the first (spring) than in the second replicate (autumn, $P < 0.01$), there was no replicate \times treatment interaction. The live weight of does was similar in the 4 groups at mating ($3\,540\text{ g} \pm 334$, mean \pm sd) and at d 14 ($4\,086\text{ g} \pm 345$). In the second half of gestation, lactating females lost weight whereas non-lactating females gained weight. The weight loss was higher in the TL group than in the FL group, and the weight gain was higher in the CNL group than in the RNL group (table II; $P < 0.05$).

Table II. Feed intake and evolution of live-weight of the does during pregnancy.

	Treatment				SEM *	R ² **
	CNL	RNL	FL	TL		
No of does	28	27	27	25	—	—
Feed intake (g/d)						
1st week	208 ^b	212 ^b	265 ^a	290 ^a	6.9	0.26
2nd week	238 ^b	249 ^b	340 ^a	351 ^a	7.2	0.49
3rd week	230 ^c	178 ^d	321 ^b	358 ^a	8.5	0.65
4th week	157 ^b	116 ^c	251 ^a	254 ^a	7.6	0.60
Live weight (g)						
Weight at mating (g)	3 582	3 606	3 481	3 481	32	0.36
δp_{028} (g)	746.6	651.1	461.0	335.6	24	0.46
δp_{014} (g)	552	539	564	533	19	0.06
δp_{1428} (g)	194 ^a	112 ^b	-103 ^c	-197 ^d	20	0.57
Weight at slaughter (g)	4 329 ^a	4 257 ^a	3 943 ^b	3 817 ^b	37	0.36

^{abcd} Values with different superscripts within the same row differ by $P < 0.05$; females were non-lactating and fed *ad libitum* (CNL) or restricted (RNL), or pregnant and lactating with 10 (TL) or 4 (FL) young. δp_{028} , δp_{014} and δp_{1428} are variations of weight between d 0 and 28, between d 0 and 14, and between d 14 and 28 of gestation, respectively; * standard error of the mean; ** variance explained with the statistical model.

Although females in replicate 1 have higher weight of carcass, skin and adipose tissues ($P < 0.01$), there was no replicate \times treatment interaction. The weights of carcass, skin and adipose tissues differed significantly between groups (table III, $P < 0.001$). However, there was no significant difference between CNL and RNL females and only carcass and skin weights differed significantly between FL and TL females. The weight of the digestive tract was lower in the non-lactating than in the lactating groups ($P < 0.01$).

The replicate had no effect on reproductive performance. The ovulation rate was similar in the 4 groups (table IV). The total mortality tended to differ between groups of females, but early mortality was similar in the 4 groups. Late mortality was higher ($P < 0.05$; model 1) in the TL group than in the CNL and RNL groups, and was intermediate in the FL group (table IV). The difference was mainly due to the number of resorbed fetuses which was 3 times greater in the TL than in the CNL group ($P < 0.01$). The live-weight variation between d 14 and 28 (model 2) had no influence on

the number of resorbed fetuses and on late mortality.

The foetuses were lighter in the TL group than in the CNL and RNL groups, and intermediate in the FL group (table IV). The difference between groups was no more significant when $\delta p1428$ was added as a covariate, whereas this covariate had a highly significant effect on foetal weight ($P < 0.01$). Generally, the mean foetal weight per litter increased linearly with $\delta p1428$ ($r = 0.47$; $P < 0.001$) and decreased with litter size ($r = -0.35$; $P < 0.001$). The weight of the uterine horns was not influenced by the feed level in pregnant does or by the number of suckling young in pregnant-lactating does, but was lower in lactating compared with non-lactating females. The weight of the placentas did not differ between groups.

There was a significant interaction between treatment and stage of gestation for plasma progesterone. At d 7 and 17 of pregnancy, the plasma progesterone levels differed significantly between groups (fig 1, $P < 0.01$). At d 7, the progesterone concentration was significantly lower in the TL group than in the CNL and the RNL females, and

Table III. Traits of body development of slaughtered does at the end of the second gestation.

	Treatment				SEM*	R ² **
	CNL	RNL	FL	TL		
No of does	28	27	27	25	—	—
Live weight (g)	4329 ^a	4257 ^a	3943 ^b	3817 ^b	39	0.36
Digest tract weight (g)	425 ^b	398 ^b	476 ^a	490 ^a	7.3	0.27
Pregnant uterus (g)	546 ^a	565 ^a	475 ^b	444 ^b	11.8	0.22
Carcass weight (g)	2346 ^a	2311 ^a	2117 ^b	2021 ^c	24.1	0.33
Skin weight (g)	631 ^a	609 ^a	547 ^b	526 ^c	7.8	0.33
Adipose tissue weight (g)	118 ^a	118 ^a	53 ^b	43 ^b	5.0	0.58
Uterine weight (g)	49.9 ^a	52.6 ^a	44.8 ^b	41.3 ^b	1.0	0.24

^{abc} Values with different superscripts within the same row differ by $P < 0.01$. Females were non-lactating and fed *ad libitum* (CNL) or restricted (RNL), or pregnant and lactating with 10 (TL) or 4 (FL) young; * standard error of the mean; ** variance explained with the statistical model.

Table IV. Reproductive performance of does observed at the end of the 2nd gestation.

	Treatment				SEM*	R ² **	
	CNL	RNL	FL	TL		Model 1	Model 2
No of does	28	27	27	25	—	—	—
No of corpora lutea	11.3	11.6	11.1	11.2	0.15	0.13	0.14
Ovary weight (g)	0.45	0.45	0.44	0.44	0.01	0.03	0.03
Foetuses							
Live	9.1	9.7	8.4	8.3	0.2	0.11	0.15
Resorbed	0.36 ^b	0.30 ^b	0.78 ^{ab}	1.08 ^a	0.1	0.11	0.12
Dead	0.21	0.07	0.15	0.32	0.1	0.10	0.11
TM (%)	19.5	15.9	23.5	26.0	1.8	0.04	0.07
EM (%)	14.8	12.9	15.6	13.1	1.5	0.03	0.07
LM (%)	5.4 ^b	3.6 ^b	10.4 ^{ab}	15.5 ^a	1.2	0.13	0.14
Foetal weight (g)	39.7 ^a	39.3 ^a	37.5 ^{ab}	34.9 ^b	0.5	0.22	0.29
Placental weight (g)	7.6	7.3	7.0	6.9	0.1	0.17	0.21

^{ab} Values with different superscripts within the same row differ by $P < 0.05$. Females were non-lactating and fed *ad libitum* (CNL) or restricted (RNL), or pregnant and lactating with 10 (TL) or 4 (FL) young; TM = total mortality; EM = early mortality; LM = late mortality, for calculations see text; * standard error of the mean; ** variance explained with the statistical models 1 and 2.

intermediate in the FL females. At d 17, it was significantly lower in the FL than in the RNL females, and intermediate in the 2 other groups. The progesterone concentrations were always lower in lactating than in non-lactating does on d 7 and 17 (TL + FL vs CNL + RNL; $P < 0.01$). Generally, the concentration of plasma progesterone at d 7 decreased linearly with late foetal mortality ($r = -0.39$; $P < 0.001$).

DISCUSSION

Feed restriction in the RNL group led to a 42% lower live-weight increase between d 14 and 28 of gestation than in the CNL group, which is due to differences in digestive-tract contents but also in carcass and skin development, even though these differences are not significant. By drastically reducing litter size in the FL group, we tried to limit the nutritional deficiency while main-

taining the specific hormonal environment of lactation. However, estimations for milk production show that the latter was probably reduced to a much lesser extent (-12.6% during the first 3 weeks of lactation) than what would be expected from the reduction of litter size (-40%; Lebas, 1987) allowing a higher growth rate of the young (+95%) in the FL than in the TL group. As a consequence, the females in the FL group seem to have mobilized their body reserves, as indicated by the carcass traits, even though it was less pronounced than in females with 10 suckling young. At the end of gestation, lean (carcass, skin) and fat (adipose tissues) tissues were slightly more developed in lactating does with 4 young rather than 10 and much less than in non-lactating females, even those submitted to feed restriction.

Foetal growth was reduced in lactating females compared with non-lactating females and the effect was less marked in

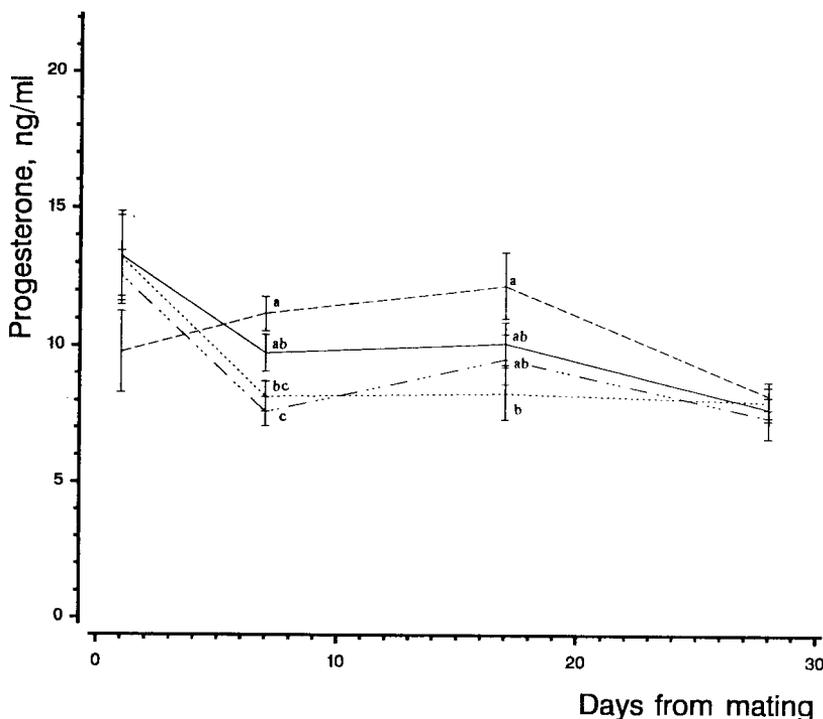


Fig 1. Influence of treatments on concentration of plasma progesterone throughout gestation (— CNL --- RNL ··· FL - · - · TL). ^{ab} Within a stage of gestation, means with different superscripts differ at $P < 0.01$.

females lactating a reduced rather than a full litter. Our data suggest that the detrimental effect of concurrent lactation upon foetal growth was due to the nutritional deficiency rather than to lactation *per se* because lactational status had no more effect upon foetal weight when the does' live weight variation between d 14 and 28 was included in the statistical model. The reduction of foetal weight in females with restricted feeding level has been previously reported for several species (Robinson, 1986). Late mortality was higher in does lactating 10 young than in non-lactating does without any influence of the live-weight variation at the end of gestation. Moreover, late mortality in females with a reduced litter size

was intermediate between females with a high litter size and non-lactating females. Thus, it seems that foetal survival is more dependent on the hormonal background associated with lactation than on the metabolic balance of the mother. In simultaneously pregnant and lactating does, prolactin concentrations are higher and progesterone concentrations are lower than in non-lactating pregnant does (Mac Neilly and Friesen, 1978; Fortun *et al*, 1993). Prolactin might be involved in the higher foetal mortality observed in lactating does since, in the rabbit, this hormone is known to affect luteal function (Holt, 1989) and uterine activity (Chilton and Daniel, 1987). Moreover, the negative relationship existing between

progesterone concentration and late mortality suggests that progesterone plays a role in foetal survival, in agreement with experiments of progesterone supplementation (Pratt and Lisk, 1991; Parr, 1992). This reduction in progesterone concentration can be explained by an excretion in the milk (Koldovsky, 1980), a higher metabolic turnover rate (Kirkwood and Aherne, 1985; Pharazyn *et al*, 1991) or a lower secretion by the corpora lutea due to prolactin (Lin *et al*, 1987).

In conclusion, the present study confirms that foetal survival and growth in primiparous rabbits are impaired in pregnant does which are simultaneously pregnant and lactating. In addition, it shows that the detrimental effect of lactation is decreased by reducing the number of suckling young and that foetal growth is mainly dependent on the nutritional balance of the mother. However, the influence of the hormonal background associated with lactation, and particularly the levels of prolactin and progesterone, on foetal survival remain to be elucidated.

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