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Effects of lactation, energetic deficit and remating interval on reproductive performance of primiparous rabbit does

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Abstract

Female rabbits ($n = 151$) were assigned at their first parturition (day 0) to one of three treatment groups (A: non-lactating does and ad libitum feeding, R: non-lactating does and restricted feeding, L: lactating does and ad libitum feeding). Additional females ($n = 18$) were slaughtered at parturition. Experimental females were presented to the male on days 3 (A3, L3 and R3 groups, $n = 25$, 26 and 26, respectively) or 10 (A10, L10 and R10 groups, $n = 25$, 25 and 24, respectively) and were slaughtered on day 28 after parturition. Compared to does slaughtered on day 0, adipose tissues were lighter in L (−66%) and R (−32%) females while they were heavier in A females (+40%; $P < 0.01$). These results suggest that both L and R females were in energy deficit. Receptivity (80% vs. 98%) and conception rate (51% vs. 83%) were lower in L compared to A females ($P < 0.01$) regardless the day of male presentation. Ovulation rate (−14%) and conception rate (−26%) were lower in R3 than in A3 does ($P < 0.05$). Ovulation rate was 24% lower in the L10 than in the A10 group ($P < 0.01$). The uterine contents were lighter (−25%) in L and R than in A does ($P < 0.001$) regardless the day of male presentation. These results suggest that the energy deficit associated with milk production can partly explain the negative influence of lactation on reproductive performance.

Keywords: Rabbit; Feeding and nutrition; Lactation; Fertility

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1. Introduction

Rabbit does can be mated shortly after parturition and throughout lactation. As a general rule, however, fertility and prolificacy are lower in lactating than in non-lactating females (reviewed by Theau-Clément and Roustan, 1992; Fortun-Lamothe and Bolet, 1995). The physiological mechanisms underlying these effects of lactation on reproductive performance have not been fully elucidated. Fortun-Lamothe and Bolet (1995) have formulated two hypotheses, which are not exclusive: the negative energetic balance of lactating does and(or) the hormonal milieu of lactation create an unfavorable environment for the establishment of a new pregnancy. Effects of the hormonal status on the reproductive performance of lactating does have been studied previously (Lamb et al., 1991; Fortun, 1994; Fortun et al., 1994a; Ubilla and Rebollar, 1995) and the results suggest that the high levels of prolactin which occur during lactation are involved. In order to investigate the influence of the nutritional status on the reproductive performance of lactating does, it is necessary to differentiate between the effects of the hormonal environment due to suckling and of the nutritional deficit due to the high metabolic demand for milk production. Thus, in the present experiment, we have compared three groups of does: lactating females fed ad libitum, non-lactating females weaned at birth and having either a positive (females fed ad libitum) or a negative energetic balance (feed-restricted females). Moreover, we have compared two remating intervals (3 or 10 days post partum) since the effects of lactation on the reproductive performance of does depend on the remating interval (Theau-Clément et al., 1990).

2. Materials and methods

2.1. Animals

A total of 169 22-week-old primiparous does were used (INRA line A2066 × A1077). Eighteen females were slaughtered on the day of their first parturition (day 0) to determine the initial body composition (group C, control). The 151 other females were assigned at parturition to one of three treatments according to their litter size and body weight. In A (ad libitum) and R (restricted) treatments, the young were removed immediately after kindling (non-lactating does). In the L treatment (lactating females), does were allowed to suckle 10 young (litter size was equalized at parturition by cross-fostering and/or culling) until the 28th day post partum. All females were caged individually with a controlled light/dark cycle (16:8 h) and were given a standard diet (17.5% crude protein and 9.7 MJ of digestible energy per kg of fresh feed). Females in A and L treatments had free access to the diet while females in the R treatment were given 95 g day^{-1} from days 0–3, 115 g day^{-1} from days 4–7, 80 g day^{-1} from days 8–21 and 120 g day^{-1} from days 22–28 in order to meet about 85% of the energetic maintenance requirements on average over the whole period (energetic maintenance requirement during pregnancy = 421 kJ day^{-1} $kg^{-0.75}$; Parigi-Bini et al., 1990). Does fed ad libitum were supplied with fresh food once a week and on the day of mating,

after collection of the residues. Feed restricted females were offered their ration each morning after collection of the residues. Does and their young were weighed weekly.

Fifteen males were used for mating. Each male was used to mate a similar number of females in each treatment. In each treatment, one half of the females was presented to the male 3 days after parturition (intensive reproductive rhythm) and, the second half was presented to the male 10 days after parturition (semi-intensive reproductive rhythm). Therefore, the 151 does were allocated to six experimental groups: A3 ($n = 25$), A10 ($n = 25$), L3 ($n = 26$), L10 ($n = 25$), R3 ($n = 26$) and R10 ($n = 24$). Females which were not mated when presented to the male were discarded from the experiment. Does were put on experiment in two batches, each batch starting over a period of 3 weeks. Some females were slaughtered at the first parturition (batch 1, $n = 8$; batch 2, $n = 10$: group C).

2.2. Reproductive performance

Receptivity was defined as follows: number of mated females $\times$ 100/number of females presented to the male. Does mated 3 or 10 days after kindling were slaughtered (electronarcosis followed by exsanguination) on day 28 post partum. The conception rate (number of pregnant females $\times$ 100/number of mated females) and the ovulation frequency (number of females which had ovulated $\times$ 100/number of mated females) were determined at that time. Ovulation rate was determined by counting the number of corpora lutea (CL). The genital tract was removed and dissected. Foetuses were counted and classified as live (L) or dead (D). Embryonic mortality was defined as $(CL - (L + D)) \times 100/CL$ and foetal mortality was defined as $D \times 100/(L + D)$. It should be noted that embryonic mortality included fertilization and implantation failures.

2.3. Body composition

After slaughter, the does were dissected and, carcass (muscles and bones), skin, digestive tract (full and empty), adipose tissues (perirenal + interscapular), liver, kidneys, heart + lungs, uterus (pregnant and empty) were weighed. Empty body weight was defined as the sum of carcass, skin, adipose tissues, empty digestive tract, liver, kidneys, heart, lungs, and empty uterus weights.

2.4. Statistical analyses

All data were analysed using the Statistical Analysis Systems Institute (1987) package. The acceptance and conception rates, as well as the ovulation frequency were analysed using generalised linear model with binomial errors and logit link function (Genmod procedure). Live weight, body composition, feed intake, ovulation rate and number of foetuses were analysed by analysis of variance (GLM procedure) using a 3×2 factorial model including the effects of treatment, remating interval and the interaction between treatment and remating interval. Analyses of mortality were not based on percentage but on actual numbers (e.g. $CL - (L + D)$ for embryonic mortality and D for foetal mortality) with ovulation rate added as a covariate. The interaction

between treatment and remating interval was significant for several parameters of reproductive performance. Therefore, reproductive performance was subsequently analysed separately for each remating interval. When treatments differed significantly ($P < 0.05$), differences between means were tested using the Ryan-Einot-Gabriel-Welsch multiple F test (regwf procedure).

3. Results

3.1. Feed intake

As expected, feed intake was very different between treatments. Total feed intake (days 0–28) was 89% higher in L than in A females (378 vs. 200 g day^{-1}; $P < 0.001$) and was 53% lower in R than in A females (94 vs. 200 g day^{-1}; $P < 0.001$). Remating interval had no effect on feed intake. In lactating does, feed intake during the parturition-to-remating interval did not differ between females accepting or refusing to mate on day 3 whereas it was higher in females which accepted the male ($n = 21$) than in others ($n = 4$) on day 10 (308 vs. 215 g day^{-1}; $P < 0.05$). Finally, regardless the

Table 1
Body composition (g, arithmetic means) of does slaughtered on day 0 (group C) and of pregnant does slaughtered on day 28 post partum (groups A, R and L)

	Treatment (T)				Remating interval (RI)			*P*	
	C	A	R	L	3	10	SEM	T	RI
Number of does	18	44	37	21	50	52			
Live weight on day 0	3569.6	3659.5	3649.0	3628.6	3630.2	3661.6	25.5		
Live weight on day 28	–	4339.0^{a}	3700.9^{b}	3773.4^{c}	3946.8	3935.9	35.5	***	
Empty body weight	3077.1^{b}	3589.3^{a}	3015.2^{b}	2875.1^{c}	3177.1	3283.9	50.4	***	+
Carcass weight	1928.3^{b,c}	2322.5^{a}	2037.6^{b}	1831.9^{c}	2071.6	2162.9	26.9	***	*
Skin weight	606.9^{a}	633.7^{a}	518.1^{c}	566.4^{b}	579.5	576.4	8.2	***	
Adipose tissue weight	108.4^{b}	151.9^{a}	74.2^{c}	37.1^{d}	97.1	101.6	5.7	***	
Digestive tract weight									
Full	467.3^{b}	520.7^{b}	486.1^{b}	642.4^{a}	478.1	586.1	9.9	***	***
Empty	207.9^{b}	255.9^{a}	206.0^{b}	214.4^{b}	225.7	228.8	4.1	***	
Liver weight	115.0^{b,c}	126.7^{a,b}	96.3^{c}	138.2^{a}	111.7	124.1	2.9	***	*
Kidneys weight	18.2^{b}	21.1^{a}	17.5^{b}	19.8^{b}	19.6	19.5	0.3	***	
Heart + lungs weight	35.9^{a,b}	38.6^{a}	32.1^{b}	33.9^{a}	33.5	37.1	0.8	***	**
Uterine weight									
Pregnant		353.6^{a}	265.8^{b}	275.1^{b}	427.5	188.3	14.6	***	***
Empty	56.5^{a}	38.9^{b}	33.4^{b}	33.4^{b}	38.4	33.5	0.9	***	**

Treatments: C, control females slaughtered on day 0; A, non-lactating females fed ad libitum; R, feed-restricted non-lactating females; L, lactating females fed to appetite.
Remating interval: 3, females which were mated 3 days after parturition; 10, females which were mated 10 days after parturition.
Groups (T: treatment, RI: remating interval) differ at ***$P < 0.001$, **$P < 0.01$, *$P < 0.05$, +$P < 0.1$.
Empty body = carcass + skin + adipose tissues + empty digestive tract + liver + kidneys + heart + lungs + empty uterus.

treatment, feed intake was similar for mated does which were thereafter pregnant or empty.

3.2. Live weight and body composition

On day 0, the live weight of the females was similar for all treatments (3645 ± 25 g). Does from the A treatment gained weight throughout the post partum period (175 g week^{-1}) while feed-restricted females lost weight during the first week post partum (−87 g) and gained weight thereafter (50 g week^{-1}). Lactating females gained weight during the first 2 weeks post partum (160 g week^{-1}) and lost weight thereafter (−97 g week^{-1}).

Weights of empty body, carcass, adipose tissues, kidneys and empty digestive tract were significantly higher in A females slaughtered on day 28 than in C females slaughtered on day 0 (Table 1). Weights of skin and adipose tissues were lower in R and L females on day 28 than in C females slaughtered on day 0 ($P < 0.05$; Table 1).

On day 28 post partum, live weight of the does was similar in R and L treatments, and was 14% lower than in the A treatment (Table 1; $P < 0.001$). This difference was essentially due to changes in carcass weight. However, several other components of the empty body were significantly heavier in A than in other females (skin, adipose tissues, empty digestive tract, kidneys, heart + lungs). Uterine contents (pregnant uterine weight − empty uterine weight) were 25% lower in L and R treatments than in the A treatment ($P < 0.001$, Table 1). Uterine weight of pregnant does on day 28 post partum was

Table 2
Reproductive performance of intensively reared does (mating on day 3 post partum) slaughtered on day 28 post partum

	Group			SEM	*P*
	A3	R3	L3		
Initial number of does	25	26	26		
Acceptance rate (%)	100.0[a]	92.2[a]	76.9[b]		**
Number of mated does	25	25	20		
Ovulation frequency (%)	96.0	92.0	85.0		
Conception rate	92.0[a]	68.0[b]	50.0[b]		**
Number of corpora lutea					
All mated females	12.5[a]	10.7	12.5[a]	0.3	*
Pregnant females	12.5	11.6	12.6	0.3	
Number of foetuses/pregnant does					
Alive	9.6	9.8	9.9	0.4	
Dead	0.4	0.5	1.2	0.1	+
Embryonic mortality (%)	20.0	11.2	11.9	2.8	
Foetal mortality (%)	4.0	4.9	10.8	1.5	+

A3, non-lactating females fed ad libitum; R3, non-lactating females subjected to feed restriction; L3, lactating females fed to appetite.
SEM, standard error of the mean.
For calculations of embryonic mortality and foetal mortality, see text.
Groups differ at ***$P < 0.001$, **$P < 0.01$, *$P < 0.05$, or +$P < 0.1$.

highly influenced by the remating interval ($P < 0.01$) being 56% lower for does mated on day 10 (day 28 = 18th day of pregnancy) than on day 3 (day 28 = 25th day of pregnancy).

3.3. Milk production and growth of suckling rabbits

At birth, prior to the start of experiment, litter size (9.8 ± 0.2 born alive) and litter weight (490 ± 11 g) were similar for the six treatments. Thereafter, survival (95%) and growth of suckling rabbits (16 ± 0.3 g day^{-1}) were similar in the L3 and L10 groups. Therefore, estimated milk production between kindling and day 21 of lactation (litter weight gain × 1.82; Lebas, 1969) was not significantly different between these two groups (3991 ± 176 g and 4160 ± 151 g, respectively).

3.4. Reproductive performance

The interaction between treatment and remating interval was significant for ovulation rate as well as for other parameters of prolificacy (number of foetuses, embryonic and foetal mortality). For this reason, reproductive performance of intensively- (groups A3, R3 and L3) and semi-intensively reared (groups A10, R10 and L10) does were analysed separately.

Table 3
Reproductive performance of semi-intensively reared does (mating on day 10 post partum) slaughtered on day 28 post partum

	Group			SEM	*P*
	A10	R10	L10		
Initial number of does	25	24	25		
Acceptance rate (%)	96.0	100.0	84.0		+
Number of mated does	24	24	21		
Ovulation frequency (%)	100.0	95.8	100.0		
Conception rate (%)	87.5[a]	87.0[a]	52.4[b]		*
Number of corpora lutea					
All mated females	14.2[a]	12.3[a,b]	10.8[b]	0.5	**
Pregnant females	14.9[a]	13.2[b]	14.4[a]	0.3	*
Number of foetuses/pregnant does					
Alive	13.1[a]	9.8[b]	11.9[a,b]	0.5	**
Dead	0.6	0.6	0.3	0.5	
Embryonic mortality (%)	8.0	21.2	15.3	2.9	+
Foetal mortality (%)	4.4	5.8	2.4	2.1	

A10, non-lactating females fed ad libitum; R10, non-lactating females subjected to feed restriction; L10, lactating females fed to appetite.
SEM, standard error of the mean.
For calculations of embryonic mortality and foetal mortality, see text.
Groups differ at ***$P < 0.001$, **$P < 0.01$, *$P < 0.05$, or +$P < 0.1$.

3.4.1. Intensive reproductive rhythm

The acceptance rate of the male was lower in the L3 compared to the other treatments and the conception rate was higher in the A3 than in other groups (Table 2; $P < 0.01$). The ovulation frequency was not influenced by treatment. The ovulation rate was 14% lower in the R3 than in the two other groups ($P < 0.05$). The number of viable foetuses was similar in the three groups. However, foetal mortality was 143% higher in the L3 group compared to the other groups because of a higher number of dead foetuses in this group ($P < 0.1$). A very high embryonic mortality was observed in two females of the A3 group, each of which had only one live foetus.

3.4.2. Semi-intensive reproductive rhythm

The acceptance rate of the male ($P < 0.1$) and the conception rate ($P < 0.05$) were lower in the L10 group than in the other groups (Table 3). The ovulation frequency was high (99%) and was not influenced by the treatment. The mean ovulation rate was 24% lower in L10 compared to A10 does ($P < 0.01$). This difference was essentially due to a very low ovulation rate in L10 females which did not become pregnant thereafter (6.8 corpora lutea), while the ovulation rate of pregnant females was similar in L10 and A10 groups. The number of corpora lutea in pregnant females was lower in the R10 group than in the two other groups ($P < 0.05$). The number of live foetuses was lower ($P < 0.01$) whereas embryonic mortality was higher ($P < 0.1$) in R10 than in A10 does. Lactating females were intermediate for these two parameters. The number of dead foetuses and foetal mortality were similar in the three treatments.

4. Discussion

4.1. Influence of physiological status on mobilization of body reserves

Females increase their feed intake during lactation compared to pregnancy, but this increase is generally not sufficient to meet the nutritional requirements for maintenance and milk production. Therefore, the energetic balance of lactating rabbit does is usually negative, especially at the time of the lactational peak and body reserves must be mobilized (-25 to -30% of initial energy body content; Xiccato, 1996). The lower weights of carcass, skin and adipose tissues at day 28 of lactation than at parturition observed in the present experiment support these assertions. By contrast, during the 28 days following parturition, non-lactating females fed to appetite gained weight. This gain was due to an increase in weight of fat and lean tissues in accordance with the results of Partridge et al. (1986) and Parigi-Bini et al. (1990, 1992). Compared to day 0, the weight of adipose tissues was lower at day 28 in lactating ad libitum and non-lactating restricted fed does whereas it was higher in non-lactating ad libitum fed does. Therefore, both lactating and non-lactating restricted fed does were in negative energetic balance.

4.2. Influence of lactation and nutritional status on reproductive performance

The receptivity of non-lactating fully-fed females was high regardless of the remating interval showing that recovery from the previous gestation is very rapid for this

reproductive activity. The acceptance rate is generally lower in lactating than in non-lactating does (previously reviewed by Fortun-Lamothe and Bolet, 1995). Such poor receptivity was observed for mating on days 3 and 10 even though receptivity it was slightly better with the longer parturition-to-remating interval. Feed-restricted non-lactating does did not mimic the low receptivity of lactating does. Therefore, the low receptivity of lactating does appears to be poorly related to the energetic balance.

Our results did not show any significant effect of lactation on ovulation frequency in contrast to previous observations (Foxcroft and Hasnain, 1973; Garcia and Perez, 1989). Studies of the effects of lactation on ovulation rate in the rabbit have produced conflicting results (reviewed by Fortun-Lamothe and Bolet, 1995). In the present study, the ovulation rate was similar in lactating and non-lactating full-fed females mated 3 days after parturition. However, on day 10 post partum, the ovulation rate was lower in lactating than in non-lactating females. Hyperprolactinemia in the lactating rabbits could explain this phenomenon because an inhibitory effect of high prolactin levels on ovulation rate has been demonstrated in the rabbit (Hamada et al., 1980; Lin et al., 1987; Yoshimura et al., 1992). Additionally, the present results show that ovulation rate was lower in restricted than in full-fed non-lactating does, suggesting that the energy deficit due to milk production could also be responsible for the lower ovulation rate in lactating does. Such influence of the nutritional status on ovulation rate has often been observed in gilts even though the endocrine mechanisms remain poorly understood (Aherne and Kirkwood, 1985; Booth, 1990).

Regardless of the remating interval, conception rate was lower in lactating than in non-lactating does. Since conception rate depends on ovulation frequency, fertilization rate, success of implantation and early litter survival, its variation may be related to various causes. As already discussed, ovulation frequency was similar among treatments. Therefore, differences between treatments must involve the others factors. Several authors have shown that fertilization rate is 10 to 20% lower in lactating than in non-lactating does (Foxcroft and Hasnain, 1973; Torrès et al., 1977; Theau-Clément et al., 1990). High levels of prolactin in lactating females could create an uterine environment unfavorable to game migration and fertilization (Chilton and Daniel, 1987; Daniel and Juneja, 1989). The present results suggest, in addition, that the energetic balance of the mother can influence conception rate, at least when mating occurs 3 days after parturition. This is in accordance with a positive effect of increased energy intake before mating on the conception rate of multiparous rabbit does (Fortun-Lamothe, 1998).

When mating occurred at day 10 after parturition, embryonic mortality was slightly higher in lactating than in non-lactating full-fed females. The energy deficit induced by milk production could be partly responsible for this phenomenon since embryonic mortality was also relatively high in restricted non-lactating does mated at the same stage. When mating occurred 3 days after parturition, foetal mortality was increased in lactating females as previously described by Fortun et al. (1993). When mating was delayed to day 10, foetal mortality was not altered in lactating does. However, it was probably underestimated since slaughter was at day 28 post partum in all treatments which corresponded to days 18 and 25 of gestation for mating on days 10 and 3 post partum, respectively. Hyperprolactinemia of lactation might be responsible for the high

foetal mortality in lactating does mated at day 3 (Fortun et al., 1994a). The negative energetic balance per se has probably no influence as shown by present data and previous results from the same laboratory (Fortun et al., 1994b).

The weight of the uterine contents was lower in lactating and non-lactating feed-restricted does than in non-lactating ad libitum fed does. This result confirms the negative influence of lactation on foetal growth (Fortun et al., 1993) and the negative role of the maternal energy deficit (Fortun et al., 1994b). Therefore, it seems that the energetic deficit which occurs in simultaneously pregnant and lactating does leads to a competition for nutrient utilization between the mammary gland and the uterus which is detrimental to foetal growth.

4.3. Influence of the parturition-to-remating interval on reproductive performance

Induction of ovulation was influenced by the remating interval: females mated 3 days after parturition ovulated less frequently than females mated 10 days after parturition, in accordance with the results of Theau-Clément et al. (1990). In several species, pituitary sensitivity to GnRH is decreased during pregnancy, due to high levels of progesterone, and both synthesis and release of LH are inhibited after parturition (McNeilly, 1988). Lamb et al. (1991) have shown that failure of the preovulatory LH surge is associated with anovulation in the rabbit. Therefore, a progressive restoration of pituitary sensitivity to GnRH and of LH secretion during the post partum period could explain the positive effect of increased duration of the remating interval on the ovulation frequency observed here. Other reproductive criteria were not affected by the length of the remating interval.

5. Conclusion

The results of the present experiment show that lactation may lower receptivity, conception and ovulation rates, embryonic and foetal survival as well as foetal growth in primiparous rabbit does. Some of these effects, however, especially those on ovulation rate and embryonic survival, are exhibited only if mating occurs when lactation is fully established (day 10). The energetic deficit associated with milk production only partly explains the harmful influence of lactation on reproductive performance.

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