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ENERGY BALANCE AND BODY RESERVES IN RABBIT FEMALES SELECTED FOR LONGEVITY

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Abstract: The aim of this study was to compare the energy balance and dynamic of body reserves in rabbit females divergently selected for longevity. One hundred and twenty-nine females from a high longevity line (HL) and 131 females of a low longevity line (LL) were studied from the 1st to the 3rd kindling. Litter size and weight and female body weight were measured at kindling (1st, 2nd and 3rd), insemination (2nd and 3rd) and at weaning (1st and 2nd). The total body electric conductivity (TOBEC) method was used to estimate the body reserves in all females at artificial insemination and at weaning, and at kindling in females that achieved parturition. Energy balance between the 11th and the 21th d of lactation was also calculated for these females. No significant difference was found for fertility or for the number of offspring born alive and weaned. However, the total number of offspring born was higher in the LL line than in the HL line at the 2nd parturition (+1.12±0.46 g; $P<0.05$). Consequently, the number of stillborn offspring was higher in the LL line. LL females were 4% heavier than HL females at the first parturition ($P<0.05$), but then HL females had a higher live weight gain than LL females from the 1st parturition to the 2nd artificial insemination (+107.0±29 g; $P=0.049$), leading to a similar weight between the lines at the 2nd artificial insemination. There was no significant difference between lines for estimated energy used for growth between the 11th and the 21th d of lactation, or for estimated milk production (2365±30 g in HL line vs. 2398±30 g in LL line), estimated using the weight gain of the kits between the 11th and 21st d of lactation, for feed intake measured during this period (351±5 g/d in HL line vs. 359±5 g/d in LL line) or for energy balance (-6.11±0.3 MJ in HL line vs. -6.30±0.3 MJ in LL line). However, body energy content was higher in HL females than in LL (+2.72±0.64 MJ; $P=0.001$). In conclusion, selection for higher functional longevity results in a better ability of females to use body reserves in their early reproductive life.

Key Words: rabbit, selection, longevity, energy balance, body reserves.

INTRODUCTION

In standard French rabbit breeding, females are normally inseminated every 42 d and spend their productive life either gestating, lactating, or both lactating and gestating. Thus, females have to simultaneously allocate the acquired resources to maintain their body and produce milk for the current litter, while the future litter is developing in utero. This situation not only increases their nutritional requirements (Fortun-Lamothe, 2006), but is also more demanding due to the genetic progress for prolificacy (Bolet and Fortun-Lamothe, 2002; Castellini *et al.*, 2010). Coutelet (2011) showed that in French commercial farms the replacement rate is high (114%). This is due to mortality (30 percentage points) and culling (84 percentage points) (Lopez *et al.*, 2013a). The main causes for culling are health problems (39.7%), reproduction issues (poor prolificacy or fertility: 21.7%), poor body condition (9.6%) and age (12.4%) (Lopez *et al.*, 2013b). In Spain, Rosell and de la Fuente (2009) determined culling and mortality in adult breeding rabbits on 130 commercial farms from 2000 to 2005. The median monthly removal risk in females was 9.3%, with 3.4% dead and 5.7% culled. The highest causes of culling were low productivity, mastitis, poor body condition and sore hocks.

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As stated by Castellini *et al.* (2010), the energy deficit caused by milk production, especially in primiparous rabbit females, is responsible for intense body mobilisation. It is therefore indirectly linked to reduced lifespan of reproductive females. Energy deficit frequently leads to poor fertility (Fortun-Lamothe, 2006), a decrease in immunity defence and, in extreme cases, death of females (see review of Castellini *et al.*, 2010). Theilgaard *et al.* (2007) observed that females selected for reproductive longevity and average reproductive performance increased their body energy reserves and delayed their reproductive senescence. They seemed to be more robust and present a greater plasticity, as they were able to exploit a greater soma to cope with production challenges (Theilgaard *et al.*, 2009).

A divergent genetic selection for longevity was carried out by Larzul *et al.* (2014). The aim of that experiment was to demonstrate the possibility of improving functional longevity in rabbits using survival analysis. The selection criterion was the length of productive life of the females, estimated as the total number of artificial insemination after the first parturition. As all females were inseminated at the same time every 42 d, this measure is proportional to the length of presence of does in the herd, and is not influenced by minor variations in the length of gestation or lactation periods. After one generation of selection, the females showed a difference of 0.75 in the total number of artificial inseminations and parturitions during their reproductive career between the 2 divergent lines. In the present study, we focused on estimating the consequences of this selection on reproductive performance, the body reserves dynamic and the energy balance. These lines are a very useful material to provide a better understanding of the relationship between longevity and the ability of females to cope with energy requirements.

MATERIAL AND METHODS

Animals

Females came from the second generation (G2) of a divergent selection experiment detailed by Larzul *et al.* (2014). In the first generation (G1), breeding values of longevity of 48 bucks of the INRA 1077 line were estimated from the length of productive life (number of artificial inseminations) of ten of their daughters. In G1, the mean fertility, litter sizes at birth and at weaning were 69%, 9.6 and 7.6, respectively. The 5 bucks with the lowest and the 5 bucks with the highest longevity breeding values, respectively, were selected to give birth to 24 bucks for the low longevity line (LL) and 24 bucks for the high longevity line (HL), respectively (Larzul *et al.*, 2014). In the second generation (G2), the 24 LL bucks and the 24 HL bucks produced 120 LL females and 120 HL females, respectively. Females were reared at the INRA EASM (Elevage Alternatif et Santé des Monogastriques) experimental farm (Surgères, France). They were first artificially inseminated (AI) at 19 wk of age and then at 11 d postpartum for 3 consecutive parturitions. Artificial inseminations were performed using 0.5 mL of heterospermic pools (Grimaud Frères S.A) and 0.2 mL intramuscular of GnRH (Receptal®) to induce ovulation. No hormonal synchronisation was performed. No voluntary culling for infertility was done, but 4 females (2 in each line) were culled due to health problems and poor live weight (3 standard deviations from the average). Litter size was not standardised after birth and offspring were weaned at 30 d of age.

Females were kept in individual cages throughout the experiment with a controlled light/dark cycle (16/8 h). They had free access to fresh water and a commercial diet (estimated digestible energy: 10.57 MJ/kg, crude proteins: 166 g/kg, acid detergent fibre: 17.25 g/kg, neutral detergent fibre: 31.34 g/kg, and lignin: 4.64 g/kg, SA Arrivé-Bellanné, France) formulated to meet the nutritional requirements of reproductive rabbit females (De Blas and Mateos, 2010). All procedures and manipulations involving animals followed the animal research guidelines of the French Ministry of Agriculture (Decree n° 2013–118, dated 1st February 2013, issued by the French Ministry of Agriculture).

Reproductive traits

Fertility, measured as the success at insemination, and prolificacy (number of offspring born alive, stillborn, and offspring weaned) were recorded at birth (parities 1, 2, and 3), at 21 d postpartum (parities 1 and 2), and at weaning (parities 1 and 2) in the 260 females. Weight of each litter (live offspring) was measured at birth (parities 1 and 2) at day 21 postpartum and at weaning (30 d postpartum).

Table 1: Number of live females (No. alive) and data analysed (i.e. lactating females that were weighed) at each time and fertility at each artificial insemination (AI) (HL: high longevity line; LL: low longevity line).

Time	HL			LL		
	No. alive	No. analysed	Fertility	No. alive	No. analysed	Fertility
First AI	129	129	0.78	131	131	0.89
First parturition	128	93		128	106	
Second AI	127	127	0.69	125	125	0.70
First weaning	125	90		120	98	
Second parturition	121	87		115	78	
Third AI	118	118	0.73	114	114	0.72
Second weaning	117	83		113	76	
Third parturition	117	84		101	78	

Body reserve and energy balance

Live weight of females was measured at first and second kindling after parturition, at the second and the third artificial insemination and at first and second weaning for females that were lactating only. At each of these times, the body reserve was estimated through the total body energy content. This was later measured *in vivo* using the TOBEC method (total body electrical conductivity), as described by Fortun-Lamothe *et al.* (2002). As the study focused on evaluating the consequences of selection on reproductive performance, the body reserves dynamic and the energy balance, non-lactating females, i.e. females that had no parturition, were not weighed or evaluated for body reserves at the time of parturition and weaning. Numbers of females alive and taken into account for the calculations are given in Table 1. This is why among the 260 females inseminated at the beginning of the experiment, only 221, 202 and 185 kindling females were weighed and analysed at the first, second and third parturition, respectively.

The energy balance of females from days 11 to 21 was estimated in the first 2 reproductive cycles as the difference between energy requirement and energy intake according to Fortun-Lamothe (2006). This period was chosen because the high energy deficit resulting from the milk production could be responsible for lower longevity. Energy requirement was estimated according to the equations reported in Xiccato and Trocino (2010) and included maintenance and milk production. Indeed, energy requirement for foetal growth is only significant during the last week of pregnancy (Parigi-Bini *et al.*, 1990), so it was deemed negligible during the period considered in the present study, which corresponded to the first week after conception. Milk production during this period was estimated using the weight gain of the kits (Fortun-Lamothe and Sabater, 2003), as solid feed intake of offspring is negligible until 21 d of age (Gidenne and Fortun-Lamothe, 2002). The individual feed consumptions of females were measured from days 11 to 21 by weighing distributed feed during the whole period and weighing refusals at day 21 d. Energy intake was calculated combining dietary digestible energy content and individual feed intake of females from days 11 to 21.

Statistical analysis

Variables were analysed with a repeatability model including fixed effects of line (2 levels), parity (3 levels) and the line \times parity interaction. This model was used in the GENMOD procedure of the SAS software for fertility and in the MIXED procedure for all other traits but body weight and body energy content. These last traits were analysed adding stage in reproduction (3 levels: parturition, AI, weaning) to the previous model. The three-way interaction was found not to be significant for each of the studied traits, so it was excluded from the final model.

RESULTS

Reproductive traits

Fertility was higher at the first AI than at the second and third (85 vs. 72% and 74% respectively; $P < 0.05$). It was similar in the HL (75.5%) and the LL (78.8%) line. Prolificacy results are given in Figure 1 for the first 3 parturitions. No significant difference was found for these traits between the 2 lines, except for stillborn and total number of

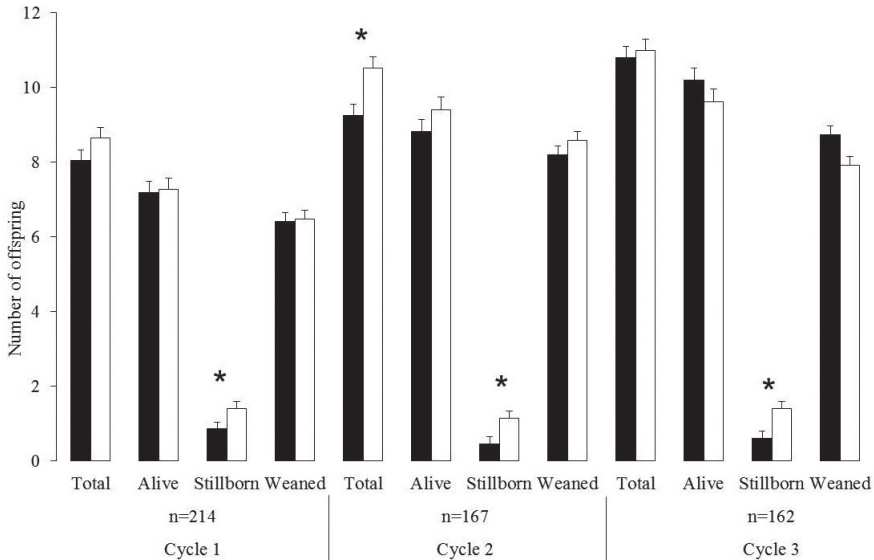


Figure 1: Litter size (total, alive and weaned) in the first 3 reproductive cycles for high-longevity (HL, n=129) and low-longevity (LL, n=131) populations. ■ HL; □ LL. Star represents a significant difference ($P<0.05$).

offspring born. Stillborn was higher in LL than in HL ($+0.67\pm 0.19$; $P=0.001$) and the total number of offspring born was also higher in the LL line than in the HL line at the second parturition ($+1.26\pm 0.41$; $P<0.05$). The line by parity interaction was significant only for the number of weaned offspring ($P<0.05$), which was higher in LL line in cycle 2 ($+0.37\pm 0.33$) but lower in LL line in cycle 3 (-0.83 ± 0.34).

At birth, weight of offspring born alive was higher in litters born from LL females than in litters born from the HL females. The difference was 7.4% in the first reproductive cycle and 9.5% in the second one (Figure 2; $P<0.01$).

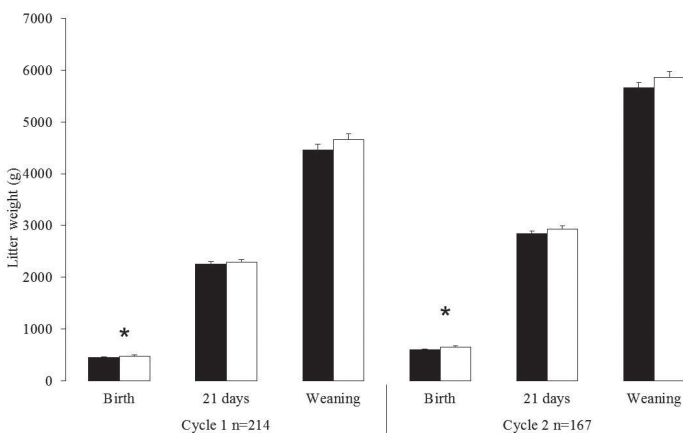


Figure 2: Litter weight (at birth, at 21 d of age and at weaning) in the first 2 reproductive cycles for high-longevity (HL, n=93) and low-longevity (LL, n=106) populations. ■ HL; □ LL. Star represents a significant difference ($P<0.05$).

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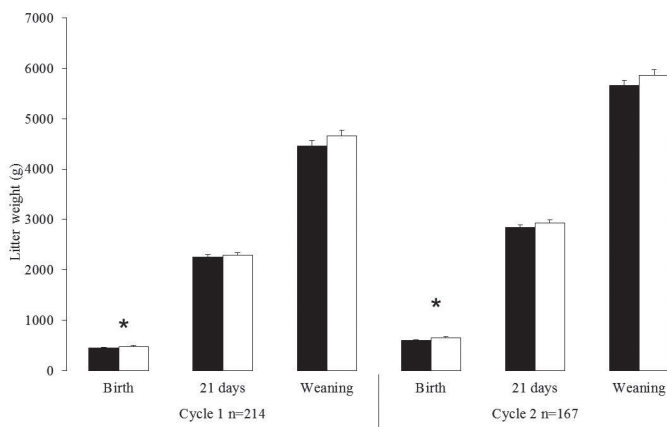


Figure 3: Female's live weight (at parturition, at artificial insemination and at weaning) in the first 2 reproductive cycles for high-longevity (HL) and low-longevity (LL) populations. ■ HL; □ LL. Star represents a significant difference ($P < 0.05$).

No significant difference was found for litter weight at 21 d and at weaning between both lines for first and second parturition.

Dynamic of body weight and reserves

No significant difference was found for body weight of females between both lines except for weight at parturition in the first cycle ($+109 \pm 47$ g in the LL line; $P = 0.02$; Figure 3) with a significant line by parity interaction. HL females had a higher growth than LL females from the second insemination to the first weaning ($+59 \pm 29$ g; $P = 0.049$) leading to a similar weight between the lines at the first weaning. Body energy content was higher in HL females than in LL ($+2.72 \pm 0.64$ MJ; $P = 0.001$). This difference was significant at each time point except at the first parturition ($+1.18 \pm 1.12$; $P = 0.2943$) (Figure 4). The increase in body energy content between parturition and AI was higher in HL females than in LL females in the first reproductive cycles ($+1.68 \pm 0.78$ MJ; $P = 0.03$), illustrating a higher

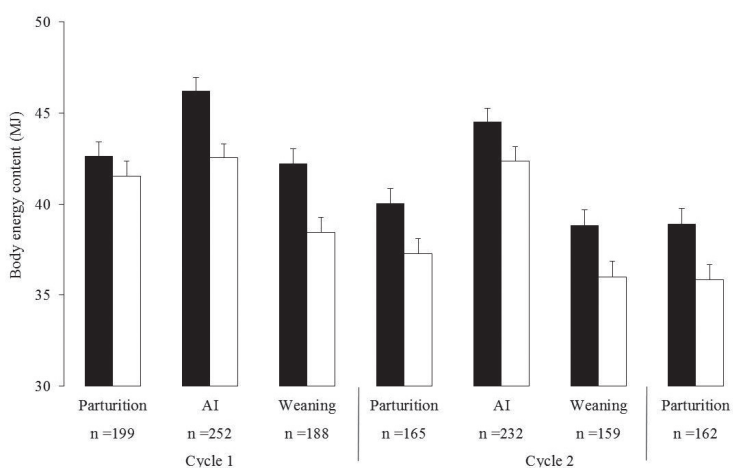


Figure 4: Dynamic of body energy content between the first parturition and the second weaning for high-longevity (HL) and low-longevity (LL) populations. Body energy content was predicted using the TOBEC (Total Body Electrical Conductivity) method (Lamothe *et al.*, 2002). ■ HL; □ LL.

Table 2: Energy supply, needs (maintenance and lactation) and balance between days 11 and 21 for the first 2 reproductive cycles for females of both lines (HL: high longevity line; LL: low longevity line). Standard error and *P*-value of the difference between lines.

	Variable	HL	LL	Standard error of difference	<i>P</i> value of difference
Cycle 1 (n=199)	Maintenance requirement (MJ)	13.90	13.98	0.11	0.463
	Milk production (g)	2165	2211	52	0.820
	Lactation requirement (MJ)	28.87	29.48	0.70	0.817
	Growth requirement	0.42	-0.13	0.50	0.723
	Feed intake (g/day)	312	318	7	0.889
	Energy intake (MJ)	34.39	35.02	0.88	0.889
	Energy Balance (MJ)	-7.17	-7.81	0.70	0.797
Cycle 2 (n=165)	Maintenance requirement (MJ)	14.16	14.21	0.11	0.965
	Milk production (g)	2565	2586	56	0.981
	Lactation requirement (MJ)	34.20	34.48	0.75	0.982
	Growth requirement	0.55	1.01	0.56	0.842
	Feed intake (g)	391	402	8	0.494
	Energy intake (MJ)	43.05	44.36	0.92	0.494
	Energy Balance (MJ)	-5.91	-5.61	0.75	0.979

deposition of fat body reserves, but equivalent in both lines in the second cycle. The decrease in body energy content between AI and weaning was then similar in both lines in first and second reproductive cycle (-1.48 ± 0.57 in HL line vs. -2.59 ± 0.60 in LL line and -2.68 ± 0.57 MJ in HL line vs. -2.87 ± 0.57 MJ in LL line, respectively).

Energy balance

Estimations of energy supply, requirements and balance between days 11 and 21 for the first 2 reproductive cycles for females of both lines which succeeded in the first 3 parturitions are given in Table 2. The estimated milk production between days 0 and 21 (2365 ± 30 g in HL line vs. 2398 ± 30 in LL line), and consequently the estimated energy requirement for lactation, was similar for females in the 2 lines. Due to similar body weights (Figure 3), the energy requirement for maintenance and for live weight gain was similar in the 2 lines. Overall energy requirement between days 11 and 21 was similar for the females of both lines (data not shown). Feed intake (351 ± 5 g/d in HL line vs. 359 ± 5 g/d in LL line), and thus energy supply (38.72 ± 0.5 MJ in HL line vs. 39.69 ± 0.5 MJ in LL line) was similar in both lines. Finally, there was no significant difference in energy deficit from days 11 to days 21 between the 2 lines (-6.11 ± 0.3 MJ in HL line vs. -6.30 ± 0.3 MJ in LL line), despite a different dynamic of estimated body energy between AI and weaning.

DISCUSSION

In the present work, we compared energy balance and dynamic of body reserve during the first 2 reproductive cycles in females divergently selected for functional longevity which succeeded in their first 3 parturitions.

Reproductive traits

Similar reproductive performances in both lines were expected. Larzul *et al.* (2014) showed that females of the high or the low longevity line had similar reproductive performances, up to the 7th reproductive cycle. Additionally, genetic correlations between longevity and litter size at birth or at weaning are low (Sánchez *et al.*, 2006). Theilgaard *et al.* (2006) reported that selection for litter size at weaning over 12 generations did not impair length of productive life. Studies detailing the whole career of females showed that the relation between longevity and litter size might depend on the parity. Females from a high longevity line had a lower litter size at weaning for the first cycles, but performed better from the fourth cycle than females selected for litter size (Theilgaard *et al.*, 2007; Sánchez *et al.*, 2008), or

equally well. The relation might also depend on the environment. In a less favourable environment characterised by severe feed restriction, Sánchez *et al.* (2008) observed larger litter sizes in females selected for longevity than those selected for litter size.

Body weight and reserves

As all females were treated equally during their whole career and no problems were observed that might have negatively affected the females' growth, the higher body weight of females from the low longevity line might demonstrate an earlier maturity, considering that thereafter the body weight of females was similar in both lines. This result disagrees with those of Nagai *et al.* (1995) and Theilgaard *et al.* (2007), which had shown, in mouse and rabbit respectively, that a selection for longevity leads to an increase in the weight of the females in the overall career. In rabbit, Theilgaard *et al.* (2007) also observed that, in response to an environmental challenge, females selected for litter size decreased reproductive performance dramatically but maintained body weight, whereas females selected for longevity decreased body weight and maintained reproductive performances. However, these results were recently contradicted by Savietto *et al.* (2013), who did not observe any difference in live weight between these lines under normal and constrained environmental conditions.

The dynamic of body reserves during the reproductive cycle or between successive reproductive cycles was largely described in rabbits using comparative slaughter (Parigi-Bini and Xiccato, 1990, 1992; Parigi-Bini *et al.*, 1990; Fortun-Lamothe *et al.*, 1999; Xiccato *et al.*, 2004; Feugier and Fortun-Lamothe, 2006), TOBEC (Fortun-Lamothe, 2006), bioelectrical impedance analysis (Nicodemus *et al.*, 2009), body reserve scoring (Bonanno *et al.*, 2005; Rosell and de la Fuente, 2008) or ultrasound measurements of perirenal fat thickness (Pascual *et al.*, 2002; Castellini *et al.*, 2006; Theilgaard *et al.*, 2007, 2009). In agreement with the previous results, we observed an accretion of body reserves at the onset of lactation and a mobilisation at the end of the lactation. Indeed, just after parturition, the milk production is low and feed intake is generally sufficient to cover the nutritional needs for both maintenance and lactation (Feugier and Fortun-Lamothe, 2006). Repletion of body reserves could then occur as the present results showed during the first 2 lactations for females of both lines. In contrast, from the lactation peak (17 d) until weaning, feed intake is generally insufficient to face the nutritional needs for maintenance, milk production and foetal growth, which are exponential. A depletion of body reserves is then necessary to meet the nutritional needs, as observed here during the 2 cycles in females of the 2 lines and in previous studies (Xiccato *et al.*, 2004; Castellini *et al.*, 2006). However, the repletion of body reserves that occurred at the beginning of the reproductive cycle was lower than the depletion that occurred at the end. Additionally, under an intensive (fertilisation just after partum) or semi intensive (as in the present study) reproductive rhythm, females which succeed at each AI had no unproductive period during which they could reconstitute their fat stores. Thus, body reserves seemed to be progressively reduced in the course of the first 2 reproductive cycles—compared to the initial values—in females having strictly followed the pre-programmed reproductive rhythm. Similar results were obtained by Fortun-Lamothe (2006).

The relationship between body fat, fat mobilisation and reproductive life was explored by Theilgaard *et al.* (2006) as well as Savietto *et al.* (2013, 2015). They showed that not only the level of body reserves, but also the body reserves dynamic, is related to lifespan. More especially, they observed that mobilisation has negative consequences only when its amplitude is extremely high, which almost never happened in thin animals. Additionally, Fortun-Lamothe *et al.* (2000) showed that an increase in the number of suckling offspring (4, 7 or 10) during four successive reproductive cycles lead to a decrease in fat reserves, but had no influence on career length. Females from the high longevity line accreted higher body reserves from the first parturition to the second artificial insemination, and thereafter maintained higher body reserves until the third parturition. This ability to store reserves at the beginning of the reproductive career, which can be the consequence of the selection, may explain their higher longevity.

Energy balance

One of our objectives was to evaluate if selection for longevity altered the energy balance of reproductive rabbit females. Energy balance was estimated from equations available in the literature. Although no digestibility trial was performed in this experiment to estimate the nutrition needs of females accurately, estimated energy balance is an interesting tool to understand the changes in the body energy observed between AI and weaning. To this end, the

period between the 11th and 21st d of lactation was very even more pertinent, as it corresponds to the lactation peak when the need for milk production was the highest. Our results showed that, as expected, energy balance of females during that period was negative for the females of the 2 lines and for the 2 reproductive cycles. Energy deficit of similar extent was previously observed by Feugier and Fortun-Lamothe (2006).

The energy deficit between the 11th and 21st d of lactation was not significantly different between the 2 lines. Neither energy supply nor needs for maintenance, live weight gain or milk production differed between the 2 lines. These results justify the interest in combining the evaluation of needs, supply, energy balance and dynamic of body reserves. As previously demonstrated (Fortun-Lamothe, 2006), measuring the live weight of females is really insufficient to describe and understand the reproductive challenge that the rabbit female has to overcome.

In females from both lines, the energy deficit was higher during the first reproductive cycle than the second, as previously observed by Xiccato *et al.* (2004). The rise in feed intake during the second cycle was more important than the increase in milk production.

Taken together, our results suggested that, in rabbit, divergent selection for longevity mainly affects the body weight and the body reserves dynamic of females. Nevertheless, these traits had long term consequences, as demonstrated by the slightly higher body reserves for females of the high longevity line at the third parturition ($P=0.13$), even though the energy balance between days 11 and 21 was similar in the 2 lines.

CONCLUSION

This study provides useful information for a better understanding of the influence of selection for longevity on the ability of rabbit females to face energy requirements for reproduction. The results presented showed that selection for longevity led to a higher live weight of females at the beginning of their reproductive life and a higher body energy content due to a higher deposition of fat reserves between parturition and insemination in the first reproductive cycle. These traits seemed to favour the females in terms of durability and could explain their better longevity. A study of performance and energy balance over a longer period than here seems interesting to confirm these first results and our hypothesis.

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