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The length of productive life can be modified through selection: An experimental demonstration in the rabbit[1]

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ABSTRACT: The objective of this study was to assess the feasibility of selecting for functional longevity in rabbits, defined as an ability to delay involuntary culling. Functional longevity was measured as the total number of AI performed after the first kindling. Breeding values were estimated using a discrete survival model. Male parents were selected on the basis of their progeny test results, and the efficiency of selection was estimated in the second generation, as was the correlated response on reproduction traits. A total of 48 males were progeny tested, based on the longevity of 10 daughters bred in 2 different farms. Based on their estimated genetic merit, 5 "high longevity" (HL) and 5 "low longevity" (LL) males were selected divergently and produced a new generation (5 bucks/sires and 10 daughters/bucks). A difference in longevity (+0.75 AI, i.e., 32 d) was observed between the 2 lines. In farm 1, the differences were mainly due to culling (26% in the LL line vs. 14% in the HL line) whereas mortality was similar in the 2 lines. In farm 2, mortality and culling were both higher in the LL line than in the HL line (33 vs. 15% and 19 vs. 7%, respectively). There was no difference between the 2 lines in terms of the reproduction traits recorded for each kindling. Nevertheless, because of the difference in the litter number between the 2 lines, the sum of young rabbits born alive per doe over her lifetime and the sum of young rabbits weaned per doe were higher in the HL line (+5 kits; $P < 0.01$). Selection for functional longevity using survival analysis is feasible for modifying lifetime reproduction traits.

Key words: longevity, rabbit, selection experiment, survival analysis

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INTRODUCTION

Involuntary culling and replacement are sources of management and welfare issues. High replacement rates increases the replacement cost of females, induces a higher proportion of immature females (young females are still growing and are less immunologically mature at parturition, litter sizes are smaller, and health problems are increased), and in some cases, the introduction of young animals from other farms favors pathological complications. Due partially to negative correlated response to the very high selection for production, functional traits have continuously been declining, to such a point that voluntary culling of low production animals is barely an option in some specialized cattle breeds (Ducrocq, 2010). The economic importance attached to involuntary culling is such that longevity and correlated traits are included in selection objectives. All these considerations have led to a strong demand for improved functional longevity, defined as the ability of the female to delay involuntary culling.

The difficulty in improving longevity through conventional breeding methods is mainly due to the time required obtaining pertinent information. In mice, it has been shown experimentally that reproductive life and the number of parities can be improved by selection on phenotypic performance (Farid et al., 2002). In rabbits, various studies have reported a moderate heritability of functional longevity (Sánchez et al., 2006; Piles et al., 2006). Recently, a synthetic rabbit line was created by selecting does with an outstanding number of parturitions and prolificacy above the population mean; this line displayed increased functional longevity (Sánchez et al., 2008).

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The aim of this study was to perform a divergent selection experiment to demonstrate the possibility of improving functional longevity genetically evaluated in rabbits using survival analysis, to validate the prediction of expected genetic gain, and to estimate the consequences on reproductive performance.

MATERIALS AND METHODS

Experimental Design

The experimental rabbit population was bred at experimental INRA farms, in accordance with the French regulations for human care and use of animal in research.

Under batch management, female rabbits were inseminated every 42 d. The length of productive life is measured as the number of inseminations completed before culling (Piles et al., 2006). The length of presence of does in the herd is proportional to the number of inseminations and is not influenced by minor variations in the length of gestation or lactation periods. To estimate the response to selection, divergent selection was performed over 2 generations, 1 for the selection process and 1 to estimate the response to selection. Selection was performed on males only, based on their EBV derived from their daughters' performance. The experiment was designed for a given number of recorded females per year. The appropriate numbers of males and females per sire were chosen as a compromise between breeding value accuracy, selection intensity, genetic variability of the trait, the censoring rate, and the expected survivor curve assuming a theoretical Weibull distribution for the length of productive life. As an illustration, the theoretical expected genetic gains (Yazdi et al., 2002) in male offspring, compared to a nonselected population, are shown in Table 1. They are estimated as a function of the number of tested males and the length of the test period, considering 500 recorded females, 10 selected males, a sire genetic variance of 0.05 (Piles et al., 2006), and realistic parameters from the Weibull distribution ($\rho = 1.8$, $\lambda = 0.114$).

Finally, we were able to test 480 does per generation and considered that 10 daughters recorded per male is an optimum. As a compromise, the design chosen assumed 48 tested males, 10 recorded daughters per tested male, and an objective number of inseminations limited to 7 to limit the duration of the experiment.

First Generation

A total of 48 bucks of the INRA 1077 line were mated twice with 200 does from the same line to produce, within a 4-mo period, 2 batches. Within each batch, 5 daughters per buck were kept, their progeny totaling 240 does. Mating and kindling were performed at the Station Expérimentale Lapin (**SELAP**) INRA (Pompertuzat, France) experimental farm. Young does from the first batch were transferred after weaning to the Station d'Amélioration Génétique des animaux SAGA INRA (Castanet-Tolosan, France) experimental farm (farm 1). Does from the second batch were transferred the day after birth to the Elevage Alternatif et Santé des mongastriques EASM INRA (Surgères, France) experimental farm (farm 2) and fostered to specific pathogen-free lactating does to limit further contaminations. The does were inseminated every 6 wk and at most 7 times from the age of 19 wk at the 2 farms. Does that were still alive were then culled after weaning of the seventh cycle. To ensure constant production conditions, replacement does were introduced regularly into the farm without being involved in the experiment. On both farms, does were only culled before the end of the experiment because of poor physiological or health conditions. There was no standardization of litter size.

Table 1. Theoretical expected genetic gain, estimated as the difference between selected and unselected males, as a function of the length of the test period (expressed in total number of artificial inseminations) and the number of tested males. The number of recorded females is fixed at 500.

Number of males on test	Number of artificial inseminations						
	9	8	7	6	5	4	3
30	0.58	0.57	0.55	0.53	0.48	0.42	0.34
50	0.63	0.61	0.58	0.56	0.50	0.44	0.35
70	0.62	0.60	0.57	0.55	0.49	0.42	0.34
90	0.60	0.58	0.55	0.53	0.47	0.40	0.32

Selection of Bucks

At the end of the seventh cycle, survival analysis was performed. The number of AI from the first fertile cycle was considered as the longevity measurement, causing many animals to have the same length of productive life (ties). A frailty model was applied. The effects included in the model used are described below. As a first step, the sire genetic variance σ_s^2 was estimated using a sire–maternal grandsire model. We retained the value of 0.057, corresponding to a heritability value of 0.158. Second, by fixing genetic variance to 4 times the sire genetic variance, an animal model was used to estimate genetic effects (EBV) accounting for all relationships. Estimated breeding values were then used to rank the sires. The 5 bucks with the lowest longevity EBV and the 5 bucks with the highest longevity EBV, respectively, were selected to give birth to bucks from the low longevity (**LL**) line and the high longevity (**HL**) line, respectively.

Each of the 10 bucks was mated to 4 INRA 1077 does at the SELAP experimental farm. A total of 48 males resulting from this mating were then chosen at random, 4 to 5 in each buck family.

Selection Response

As in the first generation, the 48 bucks of the second generation were mated twice with 200 does to produce 2 batches of 240 does. For the HL (and, respectively, LL) males, does to be mated to the 48 selected males were not completely chosen at random in the original INRA 1077 line but with a HL (and, respectively, LL) EBV, estimated by the same model as bucks, using all the information available in that line. The does were then transferred to the 2 experimental farms under the same conditions as for the first generation does. The does were then kept for a little longer, until weaning of the eighth litter.

Measurements

Does were inseminated every 6 wk with semen from a paternal heavy line. Young rabbits were weaned at 30 d. After each AI, the weight of all does was recorded. Fertility was defined as the success or failure of each AI. For each litter, the total numbers of rabbits born, born alive, and weaned were also recorded. The sum of total born and born alive over the whole herd life was calculated for each doe. Once again, the longevity measure was the total number of AI. Records on does still alive after their eighth AI were considered as censored. A further survival analysis was performed on records regarding second generation does. The statistical model was the same animal model as the 1 used to select bucks of the first generation.

Survival Analysis Model

A frailty discrete model was used. Frailty models are mixed model extensions of proportional hazard models (Cox, 1972; Kalbfleisch and Prentice, 1980), the most popular class of survival analysis models. Under such models, the hazard of an animal (h(t; **x**)), that is, its probability of being culled at time t, given it is alive before t, is described as a function of a baseline hazard model and the exponential of a linear function of fixed (possibly time-dependent) effects. When the baseline hazard function is left unspecified, a so-called Cox model is used (Cox, 1972). However, the Cox model is not suitable for discrete measures of length of life, with many ties between animals (Kalbfleisch and Prentice, 1980), as in our experiment. In this case, the grouped data model developed by Prentice and Gloeckler (1978) is preferred. This model is also a proportional hazard model but the baseline hazard is a step function of time, which is estimated together with the fixed effects. The extension of this model to a frailty model by adding the random additive genetic effect of the doe is straightforward (Ducrocq, 1999). The hazard function of a doe i (i = 1, …, n) at time t is modeled as

$$h_i(t) = h_0(t)\exp\left[\mathbf{x}_i'(t)\boldsymbol{\beta} + \mathbf{z}_i'\mathbf{a}\right],$$

in which $h_0(t)$ is the baseline hazard at time t, t being the number of AI, $\mathbf{x}_i$ and $\mathbf{z}_i$ vectors of indicator variables, and $\boldsymbol{\beta}$ a vector of fixed effects.

Two models were used for estimating genetic variance and EBV. To estimate genetic variance σ_s^2, **a** is the vector of random additive genetic effects of the sire and maternal grand sire (0.5 × sire effect) of the does, and to estimate breeding values (EBV), **a** is the vector of random additive genetic effects of the animals.

The additive genetic effects are supposed to be distributed normally with a variance covariance matrix proportional to the relationship matrix between all animals in **a.** The effective heritability is calculated as $h^2 = 4\sigma_s^2 / \left(4\sigma_s^2 + 1\right)$ (Yazdi et al., 2002). This expression of h^2 was used to be consistent with other estimates presented in the literature. It is the heritability of the trait in absence of censoring. Yazdi et al. (2002) also presented a formula $h^2 = 4\sigma_s^2 / \left(4\sigma_s^2 + 1/p\right)$, with p the percentage of uncensored records, which properly accounts for the (planned or observed) amount of censoring and which is consistent with the usual parameter for estimating response to selection.

Survival Analysis Effects

The fixed effects included in the model were chosen according to Piles et al. (2006):

1. a time dependent effect of the reproduction cycle with 3 classes (first parity, second parity, and third parity or more),
2. a time dependent effect of litter size, with 8 classes as before (0, 1 to 2, 3 to 4, 5 to 6, 7 to 8, 9 to 10, 11 to 12, and 13 or more). Changes of level occur at the time of parturition. Because only females with at least 1 litter were considered in the analysis, there were no nulliparous does.
3. a time dependent combination of the season of insemination by farm (8 levels), and
4. a time independent continuous covariate of age at the first fertile mating, expressed in days.

Random genetic effects were added to the above model. All analyses were performed using the Survival Kit version 3.12, a FORTRAN package devoted to the analysis of survival data (Ducrocq and Sölkner, 1998). To estimate the EBV of bucks using an animal model, the genetic variance was fixed at $4\sigma_s^2$ (Jenko et al., 2013).

Model for Reproduction Traits and Body Weight

For all traits, fixed effects for line and farm were compared. The total number of litters, kits born, kits born alive, and weaned kits per doe were analyzed using the GLM procedure under the SAS software (SAS Inst. Inc., Cary, NC). Body weight, total number of kits

Table 2. Estimated breeding values for male longevity[1]

n	Mean	Minimum	Maximum
39	–0.0051	–0.638	0.725
Males selected for the high longevity line			
5	0.406	0.25	0.725
Males selected for the low longevity line			
5	–0.499	–0.638	–0.396

[1]Estimated breeding value SD equals 0.329.

born, number of kits born alive, and number of weaned kits per litter were analyzed with a repeatability model including fixed effects for line, parity (8 levels), farm combined with the season of kindling (8 levels), and the line × parity interaction. The MIXED procedure of SAS software was used for this analysis. Fertility was analyzed under the GENMOD procedure.

RESULTS

Selection Process

The actual selection intensity on bucks was lower than planned. Of the 48 initial bucks, only 39 were available when offspring performance was recorded to estimate breeding value: 9 males had to be culled because of health or semen production problems. The summary statistics (mean and SD) of the EBV for male longevity in SD are reported in Table 2. The accuracy for the EBVs was around 0.8. The average difference between the 2 groups of sires was approximately equal to 3 EBV SD or 2 genetic SD.

The raw survival curves for the 2 batches in the first generation are shown in Fig. 1. Mortality was higher in the batch housed at farm 1 (Fig. 1a) than at farm 2 (Fig. 1b).

Direct Response to Selection

The raw survival curves for the 2 divergent lines (LL and HL) for the second generation at the 2 farms are shown in Fig. 2. As in the first generation, survival was higher at farm 2 than at farm 1. A survival analysis of this generation revealed a significant effect of the line ($P = 0.001$) on the number of AI. Combining the results from the 2 farms, the difference in the average length of productive life between the 2 lines was 0.75 insemination over an observation period of 8 AI. This difference was higher at farm 2 than at farm 1 (1.06 AI vs. 0.49). At the fifth AI, 6 mo after the first AI, the proportion of does still alive at farm 1 was 51.6% in the high line and 41.0% in the low line. At farm 2, these proportions were 83.7 and 67.2%, respectively. At the end of the experiment, the proportions were 32.2 and 19.7% at farm 1 and 72.9 and 47.3% at farm 2, respectively.

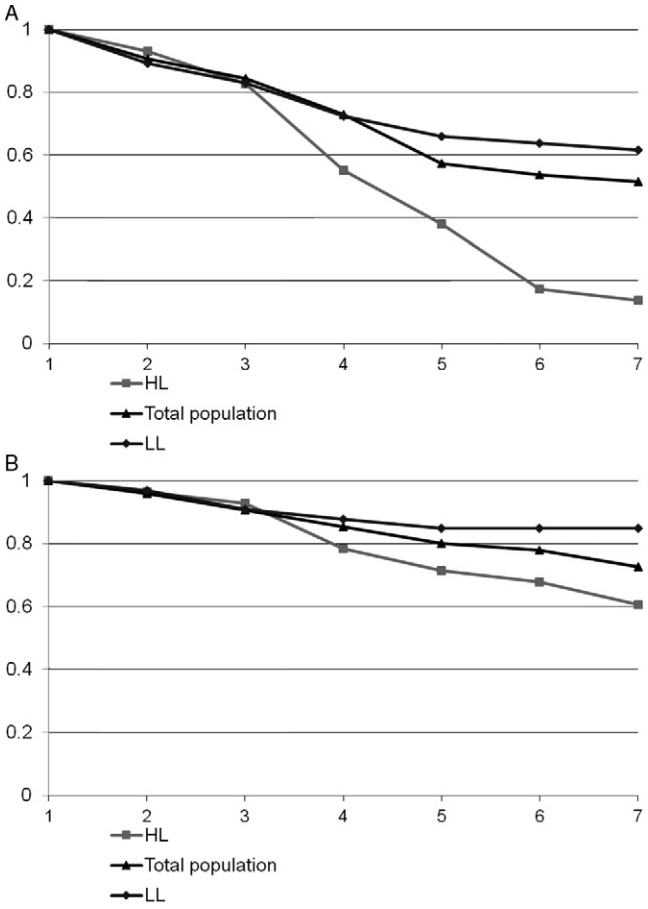

Figure 1. Raw survival curves of does at farm 1 (a) and farm 2 (b) from the first generation for whole batch (grey) and offspring of the top 5 sires (high longevity [HL]; square) and bottom 5 sires (low longevity (LL); diamond).

Table 3 reports the proportions of mortality and culling in the 2 lines. Mortality was higher at farm 1 than at farm 2. At farm 1, mortality was similar in both lines; the differences observed in the length of productive life between the 2 lines were mainly due to differences in culling. At farm 2, both the mortality and culling rates were lower among HL females.

Indirect Responses to Selection

As far as reproductive traits are concerned (Table 4), the number of litters per doe was significantly higher in the HL line than in the LL line (5.14 vs. 4.60). Because of this difference between the 2 lines, the total numbers of young rabbits born alive and weaned per doe were higher in the HL line (around +5 kits).

Significance of the different factors in the repeatability model for reproduction traits and body weight were tested using *P*-values from the *F* test (Table 5). The line effect and the interaction between parity and line were not significant for any trait.

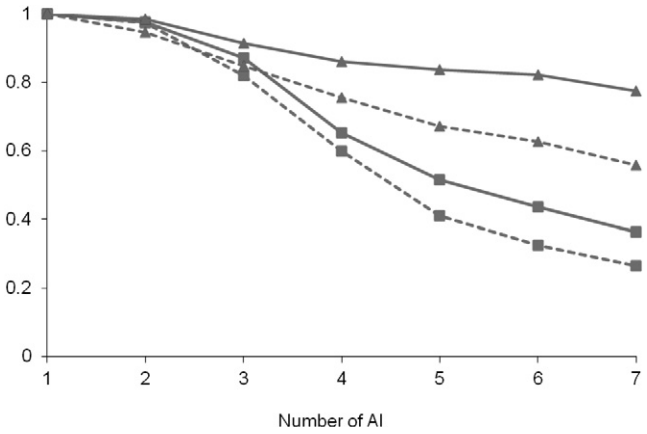

Figure 2. Raw survival curves for the 2 farms (square red line: farm 1; triangle blue line: farm 2) and the 2 divergent lines (plain line: high longevity; dotted line: low longevity) in the second generation.

DISCUSSION

To avoid confusion with fertility problems, the starting point for productive life in the current study was chosen to be the first fertile event. Culling and deaths were mainly observed just after parturition, every 42 d (Piles et al., 2006). Within the same study, it was indicated that a Weibull baseline hazard function underestimated survival rate in rabbits, and sire variance estimation was affected by the choice of model (continuous vs. discrete). For this reason, a continuous model was not considered to be appropriate, and a discrete model was applied to the number of AI starting from the first fertile AI.

The estimation of heritability was within the range of estimates obtained in rabbit using survival analysis (Sánchez et al., 2004, 2006; Piles et al., 2006). Mészáros et al. (2010) showed that heritability values decrease with increasing recording period, undoubtedly because culling causes evolve with age. In our study, heritability tended to be lower than the one reported by Piles et al. (2006), although data were only recorded up to the seventh parity rather than the 15th or 16th. This might be a consequence of performance being recorded in 2 different environments. The difference in longevity between the 2 farms could mainly be explained by disparities in health status. At farm 1, does suffered from health problems due to pasteurellosis after the third AI in generation 1 and to colibacillosis after the second AI in generation 2. By contrast, the health status at farm 2 was very good and no antibiotic treatment was used on the animals.

The selection experiment demonstrated that selection based on EBV for longevity was efficient. Using parameters from generation 1 (i.e., genetic variance, censoring rate, and selection rate), the theoretical expected difference between the 2 lines at generation 2 was 1.2 AI. The global realized difference (0.75 AI) was lower than expected, as computed from Table 1. Indeed, at farm 1, in a context of poorer health conditions, the genetic gain observed was far lower than expected. At farm 2, it was as expected from theoretical computation. Based on this latter observation, we can infer that the formula used to estimate genetic progress was relatively accurate and the estimates of genetic variance were appropriate. An apparent contradiction was found in the results. In generation 1, the differences between the survival of offspring from the top 5 and bottom 5 selected males appeared to be higher at farm 1 than at farm 2. This observation was consistent with the higher censoring rate at farm 2. Hence, in the second generation, a higher difference between does of the HL and LL lines would have been expected at farm 1 than at farm 2. However, the opposite happened, that is, higher differences between HL and LL lines were observed in farm 2 than in farm 1. Our results could be explained by the fact that health issues combined with the use of antibiotic therapy in farm 1 reduced the difference in survival between the 2 lines. Unexpectedly, this observation leads us to propose the hypothesis that the difference between the 2 lines was proportionally higher in a favorable environment (good sanitary status and no antibiotic treatment) than in an unfavorable one. A more in-depth analysis of the survival

Table 3. Mortality and culling in the second generation at farms 1 and 2 for the low longevity (LL) and high longevity (HL) lines

	Farm 1		Farm 2	
Item	LL	HL	LL	HL
Mortality, %	56	54	33	15
Culling, %	26	14	19	7

Table 4. Number of litters and total number of kits born, born alive and weaned kits during the entire doe career in the low longevity (LL) and high longevity (HL) lines

Item	LL	HL	Line effect
Number of litters	4.60	5.14	**
Total number born/doe	36.86	40.39	NS[1]
Born alive/doe	32.98	37.59	*
Weaned/doe	26.28	31.17	**

[1]NS = NS = not significant.
* $P < 0.01$; ** $P < 0.05$.

Table 5. Estimated *P*-values to test the effects of line, parity, the lactating status (only for body weight), the line × parity interaction, and the farm × season interaction on reproduction traits and body weight

Trait	Line	Lactating	Parity	Parity × line	Farm × season
Fertility	0.655	_	<0.0001	0.719	<0.0001
Total number born	0.281	_	<0.0001	0.721	<0.0001
Number born alive	0.855	_	<0.0001	0.796	<0.0001
Number weaned	0.915	_	<0.0001	0.235	<0.0001
Body weight	0.386	0.144	<0.0001	0.052	<0.0001

curves for generation 1 revealed differences between the offspring of the top 5 and bottom 5 selected males, starting at the fourth parity. One of the points to be clarified is the very beginning of the survival curve. This result would also be of interest because one of the general objectives in breeding is also to avoid very short careers, that is, to improve survival during early cycles. Because no control line was used in this experiment, it is not possible to conclude on the symmetry or asymmetry of the response to selection; consequently, there is no clear evidence that the difference did not mainly result from a decrease in the low line rather than a symmetric response in both lines.

Until now, no study has presented the realized genetic response for selection in an experimental context, achieved with respect to the length of productive life using survival analysis. A few previous studies estimated the response to selection based on "a posteriori" selection. In chickens, Ducrocq et al. (2000) estimated the EBV for both males and females. They grouped animals of the last generation based on a high or low EBV and drew the raw survival curves for the offspring of each group. A similar approach was also used in cattle (Ducrocq, 2005).

To our knowledge, only one other experiment aimed at increasing longevity in rabbits has been performed (Sánchez et al., 2008). However, their approach was completely different: a line was founded by selecting females from commercial farms that displayed an extremely high number of parturitions with a constraint on prolificacy. When compared with a conventional maternal line, at the end of the sixth pregnancy test, there was a 10% difference (48% alive in the HL line and 38% alive in the prolific line). In 1 generation of selection, the results obtained were quite similar under comparable breeding environments: 43% does alive at the sixth AI at farm 1 for HL vs. 33% for LL (82% for HL at farm 2 and 62% for LL). Sánchez et al. (2008) also reported that the differences between the 2 lines were not significant in a favorable environment. They stated that the survival ability of their long-lived line was favored under poor environmental conditions because of the better robustness of the does. In contrast, the present study showed that selection for the length of productive life was efficient in changing longevity whatever the health status of the farm.

Perhaps the main difference between the 2 experiments is the fact that the present one concentrated on the ability to delay the culling or death of a doe during the early part of her productive life, while the Spanish experiment relied on outstanding animals that appeared to be inexhaustible for months. Both selection experiments were successful in achieving their objective, with a favorable response on the early culling rate in our case and only later in life in the Spanish study. The absence of an early response in the latter case could be attributed to genetic differences in the reasons for culling in early and later life.

The absence of a significant difference between the 2 lines with respect to prolificacy traits was expected. Genetic correlation between longevity and prolificacy appears to be low. Sánchez et al. (2006) estimated genetic correlations between longevity and litter size at birth and at weaning. Their correlation estimates were weak (0.16 and –0.17, respectively) and did not differ significantly from 0. When studying the evolution of litter size during successive parities in the Spanish HL line, Theilgaard et al. (2007) demonstrated its superiority after the third parity. Sánchez et al. (2008) showed a superiority of the conventional maternal line but only for the first 3 parities. In both studies, over the whole herd life, HL does performed better. The present results showed that through the use of a suitable selection criterion and accurate modeling, it was possible to modify longevity with very limited impact on reproductive functions at each parity, at least in early reproductive life. When each parity was considered separately, no significant differences could be seen between the HL and LL lines in terms of reproductive performance. When considering the herd life up to seventh AI, HL does achieved a higher number of parities. Although the number of total born was similar in both lines, the number of born alive and weaned kits was higher in HL does than in LL does. Overall, HL does displayed better peri- and postnatal survival of the litter.

One of the keys to understanding longevity in does may lie in body reserves and their mobilization, particularly at the beginning of productive life. Theilgaard et al. (2007) suggested that HL and conventional maternal lines had different physiological priorities. Their hypothesis was that the conventional maternal line might not have sufficient body reserves to meet an environmental challenge without there being negative consequences on reproduction, whereas the HL line had more abundant resources to sustain a decline in body weight, which could be recovered subsequently. This theory might not completely fit the findings of the present study. High longevity and LL rabbits displayed similar reproductive results. Garreau et al. (2010) showed that does from the HL line only had a lower energy deficit during the first reproductive cycle, which means they had a lower level of body mobilization, combining a lower energy requirement and a higher energy intake.

The present study experimentally confirmed in rabbit that introducing the length of productive life, genetically estimated using survival analysis, in breeding schemes will not impair reproductive performances. Second, the formulas produced by Yazdi et al. (2002) appeared to be sufficiently accurate to estimate genetic response and construct an optimal experimental design. For each breeding scheme, it is now necessary to determine the correct balance between reliability, partly determined by heritability of the trait and thus by both the censoring rate and family structure, the generation interval, and other selection criteria.

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