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Marie Ithurbide, C Huau, I Palhière, T Fassier, N C Friggens, et al.. Selection on functional longevity in a commercial population of dairy goats translates into significant differences in longevity in a common farm environment. Journal of Dairy Science, 2022, 105 (5), pp.4289 - 4300. 10.3168/jds.2021-21222 . hal-04409051

HAL Id: hal-04409051
https://hal.science/hal-04409051

Submitted on 22 Jan 2024

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J. Dairy Sci. 105
https://doi.org/10.3168/jds.2021-21222
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Selection on functional longevity in a commercial population of dairy goats translates into significant differences in longevity in a common farm environment

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ABSTRACT

Resilience is the ability of an animal to cope with environmental disturbances, such as pathogens or negative energy balance. To improve resilience through breeding, we need resilience indicators. Functional longevity might be a good indicator of a dairy goat's lifetime resilience as it results from the ability to cope with and recover from all the challenges faced throughout its lifetime. The aim of this study was to validate the use of functional longevity as an indicator of resilience for selection. To address this question, we created 2 genetic lines of Alpine goats using hyperselected artificial insemination bucks with the most extreme estimated breeding values for functional longevity and the same milk yield performance. A total of 440 goats, 228 in the high longevity (high_LGV) and 221 in the low longevity (low_LGV) lines, were bred and monitored for 4 yr. Health treatments, serum IgG concentration as a proxy of passive immune transfer in early life, kidding, age, and reason of culling were systematically noted. Weight and body morphology were monitored. Weight and growth during the first year of life were similar in both goat lines. In contrast, the low_LGV goats had a lower weight during the beginning of first lactation than high_LGV goats. The milk fat-to-protein ratio was also significantly higher in low_LGV goats during first lactation. A multivariable Cox regression was fitted to the data to decipher survival at different stages of life in the 2 lines. The overall survival of high_LGV goats was significantly better than low_LGV goats (hazard ratio = 0.63, confidence interval = 0.47; 0.86) even after we included treatment, growth, serum IgG concentration at birth, and year effects in the model. The line effect was not constant over time; no significant effect was found during the first year, and the difference was observed after first kidding. This result suggested that survival at an early stage of life and during later productive life are under different genetic regulation. Altogether, this monitoring of the goat lines indicated that functional longevity-based selection helps to improve resilience by improving survival and mitigating some indicators of fat mobilization during early lactation.

Key words: functional longevity, hyperselection, survival analysis, dairy goat

INTRODUCTION

There is increasing interest in animal robustness as a trait of importance in the future design of livestock systems, and genetic selection strategies to select for it are increasingly being sought. Food security in a world affected by climate change means that animals will be exposed to, and have to cope with, harsher and more variable environments. More specifically, small ruminants have shown great ability to thrive in very harsh environments (i.e., they can display a high level of robustness). In the context of robustness, it is useful to consider the environment as having 2 components (Friggens et al., 2017). The first is general "harshness" of the environment, requiring long-term adaptation mechanisms as a first aspect of robustness. The second component of the environment relates to the frequency and intensity of environmental perturbations. Animals respond to these shorter-term perturbations by a dynamic pattern of response and recovery that is usually referred to as an animal resilience mechanism (Colditz and Hine 2016). The animal's resilience can be seen as the most determinant part of robustness in a well-controlled farming environment (i.e., when harshness of the environment is low).

It is relevant to see functional longevity as strongly correlated with resilience because it results from the accumulated consequences of ability to cope with and recover from all the challenges faced throughout an animal's lifetime. Thus, it can be assumed that animals

Received August 30, 2021.
Accepted December 28, 2021.
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with poor resilience have shorter longevity. Longevity corresponds to (1) true longevity that includes all culling reasons and (2) functional longevity (all culling reasons, except productivity; Sasaki, 2013). It has recently been proposed that functional longevity may be a good proxy for resilience (Rostellato at al., 2021). There is evidence that functional longevity has a genetic control and can be transmitted to progeny, as heritability estimates were around 0.10 (ranging from 0.1–0.29) in cattle (Sasaki, 2013) and in the range of 0.10 to 0.14 in goats (Castañeda-Bustos et al., 2017; Palhière et al., 2018). Accordingly, functional longevity has already been included in breeding programs of cattle (Miglior et al., 2005, 2017; Tsuruta et al., 2005) as a proxy for improving animal resilience and overall lifetime efficiency together with improving productivity. However, functional longevity is a complex trait, and the underlying mechanisms that are selected remain largely unknown. Furthermore, as genetic evaluation is made from commercial population data (i.e., numerous farms with different environments), there is a need to check the validity of the genetic response in the same farm environment.

Accordingly, the aims of this study were to (1) validate the creation of hyperselected lines of goats for functional longevity, (2) compare the longevity of the 2 lines raised in the same environment, and (3) explore factors that contribute to the difference of longevity to better understand the resilience mechanisms involved.

MATERIALS AND METHODS

The experiment was carried out in agreement with French National Regulations for the humane care and use of animals for research purposes. Animals were bred at the experimental INRAE farm (La Sapinière, Osmoy, France, experiental approval: C18–174–01). The experimental approval was APAFIS#8613–2017012013585646 V4.

Animals

Following the method developed by Palhière et al. (2018), a genetic evaluation for functional longevity of 8,787 Alpine AI bucks was carried out. Briefly, length of productive life was computed for 84,454 Alpine goats as the time interval (in days) between first kidding (first milk recording) and the last milk recording registered in the national performance-recording database. Estimated breeding values for length of functional life were then estimated for AI bucks using BLUP based on phenotypic information, pedigree information, and variance component estimates. Sires of the 2 lines were also required to show similar and favorable EBV for milk production traits to avoid confounding effects from an indirect response to selection for production traits. In 2020, the EBV of the bucks used were +85.1 d of functional life for the bucks of high longevity (**high_LGV**) lines and −108.7 d for the bucks of low longevity (**low_LGV**) lines (Table 1). From 2017 and until 2021, we selected 35 AI bucks in total as follows: the 16 bucks who had the highest EBV among the whole AI bucks population founded the high_LGV line and the 19 bucks who had the lowest EBV founded the low_LGV line (Table 1).

The selection was mainly made on the males; the very strong selection that was made on the buck (the most extreme EBV of the national database) was relevant to create a model to produce the most divergent animals possible using functional longevity-based selection (high selection pressure on males: 36 out of 8,787 bucks with breeding values). In the later years of the

Table 1. Estimated breeding values for length of functional life and production traits for 35 bucks that sired the high longevity (high_LGV; n = 16) and low longevity (low_LGV; n = 19) lines; the contemporary bucks (n = 228) were chosen with minimum of 100 progeny tested daughters (228 bucks)

Trait[1]	high_LGV line, mean (SD)	low_LGV line, mean (SD)	Contemporary, mean (SD)
EBV for functional longevity (d)	85.1 (89.3)a	−108.7 (121.0)[b]	−12.5 (122.3)[a,b]
Number of daughters involved in the genetic evaluation by sire	490 (450)	380 (336)	365 (283)
EBV for milk yield (kg)	2.4 (58.3)[a]	8.5 (66.5)[a]	−39.2 (73.8)[a]
EBV for milk fat content (g/kg)	0.86 (2.87)[a]	−0.37 (2.12)[a]	0.37 (2.22)[a]
EBV for milk protein content (g/kg)	0.13 (1.29)[a]	0.08 (1.09)[a]	0.14 (1.40)[a]
EBV for SCC	104.1 (7.1)[a]	92.2 (6.6)[b]	98.2 (9.0)[a,b]
Genetic merit for udder type traits	101.0 (8.7)[a]	96.7 (11.7)[a]	97.5 (9.1)[a]
Total number of daughters within group	7,890[a]	7,309[b]	84,198[c]
LPL (d)	1,071 (722)[a]	909 (651)[b]	1,006 (697)[c]
Total DIM (d)	865 (539)[a]	752 (496)[b]	824 (529)[c]
Number of lactations	3.39 (1.96)[a]	2.95 (1.76)[b]	3.22 (1.90)[c]

[a–c]Letters correspond to significant differences within a row ($P < 0.001$).

[1]LPL = length of productive life. Genetic evaluation for longevity was run on May 2021; genetic evaluation for milk yield, SCC, and body morphology was run on January 2021.

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Table 2. Distribution of the 440 goats within the 2 lines selected on high longevity (high_LGV) or low longevity (low_LGV) bred at INRAE facility of Bourges between 2017 and 2021

	Year of birth of each cohort					
Item	2017	2018	2019	2020	2021	Total
low_LGV	48	46	39	40	39	212
high_LGV	45	45	42	68	28	228
Total	93	91	81	108	67	440

study, some animals were daughters of high_LGV or low_LGV mothers (of the 440 females used, 262, 144, 41, and 3 were from generation 1, 2, 3, and 4, respectively). We produced goats belonging to the high_LGV and low_LGV lines at the experimental INRAE farm (La Sapinière, Osmoy, France). Numbers of goats bred per year are shown in Table 2.

All goats were managed identically in the same facility. The farm staff did not know which line the goats belonged to. They were reared indoors all year round, and inseminated at about 7 mo of age. Reproduction was seasonal, and kidding ranged from January until early February. Milking occurred twice a day with a DeLaval milking machine (DeLaval France) in a Rotolactor parlor (Eurl Gabard Systeme) from February to October. Goats were then dried off for 3 mo. The ration was based on Lucerne hay and complemented with concentrates dispensed in the milking parlor and in collective troughs. No culling for low production reasons took place during lactation or at drying off during this period (up to the end of third lactation). At the age of 2 mo, all goats were treated against coccidiosis (Toltrazuril, Baycox) and were vaccinated against Q fever at the age of 4 mo (Coxevac). The kids that died before 24 h of life were not included in the analysis (they corresponded to abortions).

Survival Length

Throughout the study, for a cleaner assessment of functional longevity, goats were not culled for performance reasons, which included not being culled for failure to conceive. This resulted in a small number of goats being kept for years without giving birth. However, this does not correspond to what is done in commercial farms. Therefore, it was decided to adjust the culling age for goats that were not pregnant during 2 successive years (1 yr of reproductive failure was tolerated). In this situation, the date of the last negative pregnancy determination (by ultrasound) was set as the culling date. This equated to culling ages of 680 or 1,080 d, depending on the year of the first nonbirth. Consequently, we modified 15 dates of culling for 2 yr of successive reproductive failure.

Data Used to Decipher Survival

Each reason for culling was indicated by the farm staff. For processing, these data were grouped into the following 6 classes of culling reason: birth-associated, infection, accident, metabolic, skinny, and other. The passive immune transfer from the goat to the kid can be evaluated measuring serum IgG concentration at birth (Weaver et al., 2000). It was done by a radial immunodiffusion technique between 1 and 14 d of age. Logarithmic transformation was applied to values before statistical analysis to normalize the distribution of the data. The date of each kidding was recorded, as well as any difficulties during kidding, the number of kids, and the weight of the litter. All health treatments were recorded in the same way and then grouped into the following 5 groups: infection, accident, metabolic, mechanical, and other.

Milk yield, milk fat content, milk protein content, and SCC were measured every 3 wk in first lactation, as part of the official milk records for the herd. The lactation somatic cell score (**LSCS**) was computed from the monthly test-day SCC in a 250-DIM period as described by Rupp et al. (2019). Briefly, the test-day SCC were transformed to SCS by logarithmic transformation to achieve a normal distribution. The LSCS was then computed as the weighted arithmetic mean of the test-day SCS, adjusted for DIM. Total milk was calculated with the Fleishmann method using test-day records of each in 90 (**MY90**) or 250 DIM (**MY250**) lactation periods (Ruiz, Oregui, and Herrero 2000). The milk fat-to-protein ratio was calculated for the first test day in lactation (between 1 and 45 DIM).

Chest size and height at the withers were measured every 2 mo during the first year and from then on 1 to 4 times per year. Goats were weighed every single month from birth to the age of 1 yr and from 2 to 5 times a year thereafter. The BW data were processed for inclusion in the survival analysis, as follows.

Integration of Weight Data During the First Year of Life

We used the functional data analysis smoothing method described by Ramsay and Silverman (2005). The application of this method to the BW data made it possible to estimate a corrected weight of individuals for every month from birth to 1 yr old as well as the first derivative. We used B-spline basis functions, which can construct piece-wise polynomial functions joined at the knots. The roughness penalty is adjusted by the scalar λ, (as λ increases, the penalty term becomes more decisive, and thus the second derivative converges to a straight line). The B-spline smoothing was run

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over 6,747 BW records for the 364 goats that were weighed at least 5 times (from 5–27 times). The age of the 75 goats for which less than 5 weight measures were recorded ranged from 1 to 30 d old.

To deal with the inevitable correlation between BW and age (thus BW and survival), a weight deviation (**WD**) was calculated, allowing the weight of an individual to be compared with that of other individuals of the same age as follows:

$$WDij = \frac{Wij - \text{mean}(Wj)}{\text{SD}(Wj)},$$

where $WDij$ is the WD value of animal i for month of age j; Wij is the estimate of the weight after smoothing of individual i for month j. Mean(Wj) and SD(Wj) are the mean value and the standard deviation of the estimated weights in month of age j.

To include the weight record of kids who died early in the survival analysis, as all goats were weighed at birth, we decided to use the raw weight value (not estimated by B-spline analysis) for the first month WD calculation. A single value per animal was also calculated to summarize the average WD during the first year of age as follows:

$$\text{mean_}WDi = \text{mean}(WDij),$$

where $WDij$ are all weight deviations of the ith animal for months ranging from $j = 1$ to 12. The same method was applied on the first derivative of the weight curves to calculate the growth rate deviation and the mean speed of growth deviation as follows: $dWDij$ and mean_$dWDi$. The effect of mean_WDi and mean_$dWDi$ were tested in the survival analysis after 1 yr of age to check if the growth during the first year of life had an effect on later survival.

Statistical Tests

All statistical analysis were done in the R statistical environment (https://www.r-project.org/). We ran linear regression using the lm and glm to compare between the 2 lines as follows: weight at birth, mean WD (meanWD), mean growth rate deviation (mean_dWD), log-transformed serum immunoglobulin concentration, and first lactation MY90, MY250, milk fat-to-protein ratio, and LSCS. Fixed effects were as follows: line and year in all models, as well as number of kids for weight at birth and age at first kidding for MY90, MY250, milk fat-to-protein ratio, and LSCS.

Mixed models with an animal random effect were run for repeated data as follows: weight, chest size, height, number of treatments per year, kidding per adult year (logistic regression), and number of kids per kidding. We used the lme4 package in R (Bates et al., 2015). Only months when at least 20 goats were recorded were included in the analysis for weight and body morphology. We used raw data (no Spline transformed) to compare weights after the first year of life. We included the fixed effect of gestation during the 3 last months before kidding (0 vs. 1) for weight analysis. Supplementary analyses were run where line effect was nested into month for weight and body morphology analysis.

Survival Analysis

The R package 'survival' was used for the survival analysis (Zhang et al., 2018). Survival analysis was performed using a Cox model (Cox, 1972) as follows:

$$\log\left(h\left(t|x\right)\right) = \log\left(h0\left(t\right)\right) + x'\beta,$$

where h(t) is the expected hazard at time t, h0(t) is the baseline hazard, and β is the coefficient associated with the covariate x′. The model included both fixed effects (i.e., those that were the same through all the animal's life including line, year of birth) and time-dependent covariates using the monthly records for data that changed with time (Zhang et al., 2018).

The physiological status of the goats (kidding or not), their weight, and any treatments received could change every month. Before 1 yr old, the weight variable affecting survival at month j was assumed to be the weight deviation value at month $j - 1$ ($WDj - 1$). After the first year, the weight variable used was meanWD fitted as a fixed effect. The effect of the occurrence of a treatment or a kidding (both coded as 0 or 1) was evaluated over 3 mo after the event recording (i.e., the dummy variables were set to 1 if the event had occurred during the last 3 mo).

The proportional hazards hypothesis of the Cox's model [which is that the risk ratio (β) is assumed to be constant regardless of the age considered] was tested by visual inspection of the standardized Schoenfel residuals (Zhang et al., 2018). When the proportional hazards hypothesis was not found to hold, the hazard ratio was calculated separately over different time intervals using a stratification method (β is then considered constant within the different time intervals but differs between time intervals).

We selected the co-variables that remained in the survival model with a downward stepwise method from the maximum model, using a P-value threshold of 0.05. Because of the number of goats included in the survival analysis, interactions were not included in the model.

RESULTS

Proportion of Culling, Health Treatments, and Reproductive Performances

No significant differences were found between lines in the causes of culling. Cullings related to infections and accidents represented the 2 largest groups (54 goats each) followed by the birth-related group (48 goats). The birth group consisted of all deaths registered before 5 d and is the largest group of culling reasons that occurred in the first year of life (Figure 1). This represented 27% of culling in the first year on average (31% and 23% in the high_LGV and low_LGV lines, respectively). After the first year of life, infections represented the main cause of culling (11.6% and 20.3% in the high_LGV and low_LGV lines, respectively). Despite the small number of cullings in each group, low_LGV goats were more numerous in the infection group as follows: 7% of high_LGV goats (16/228) and 12.7% of low_LGV goats (27/212).

There was no significant line effect on the number of treatments received per year (Table 3). Between 2017 and 2021, 344 treatments were given as follows: 171 (49% of goats) to high_LGV goats and 173 (51% of goats) to low_LGV. Age at treatment ranged from 8 to 1,576 d. Infections represented 269 (78.2%) of these treatments (Figure 2).

No line effect on number of kiddings was found ($P = 0.7$). On average, 67.8% of goats had a kidding per adult year (Table 3). There were 424 kiddings, of which 199 were low_LGV, and 225 were high_LGV. Similarly, the mean number of kids per kidding was 1.45 (min = 1, med = 1, max = 5) and was the same for the 2 lines (Table 3). The majority of kiddings were recorded as "normal" and 49 were "difficult" (12.8% of low_LGV kiddings and 12.7% of high_LGV kiddings). There were 247 goats with at least 1 kidding recorded.

The median number of body morphology records per goats was 6. Mixed models were applied to height and chest size data over the whole life of goats. A line effect was found for chest size ($P = 0.03$), with high_LGV goats having a greater chest size than low_LGV goats (83.7 cm vs 83.0 cm).

The weight at birth was similar for low_LGV and high_LGV (mean = 3.94 kg, min = 1.6, max = 5.9, n = 440), as well as mean weight deviation (mean_*WD*) and mean speed of growth deviation (mean_*dWD*; Table 3). No line effect was found. However, when the line effect was nested into the month effect, high_LGV goat were significantly heavier than low_LGV line between 12 and 16 mo (F test; $P < 0.05$), with a difference of 1.5 kg between lines at 13 mo of age (t-test; $P = 0.003$). Differences between lines were also significant at 24, 25, and 35 mo of age (Table 4). Smoothed weight curves of the 341 goats who had at least 5 weight measurements are shown in Figure 3.

Survival Analysis

There were 440 goats included in our study; 246 of them had been culled at the time of analysis. More low_LGV goats had been culled than high_LGV goats (62.4% and 49.5%, respectively; Table 3). Out of 440 goats, the 194 (44.1%) animals that did not exit the flock before the end of the study were considered as

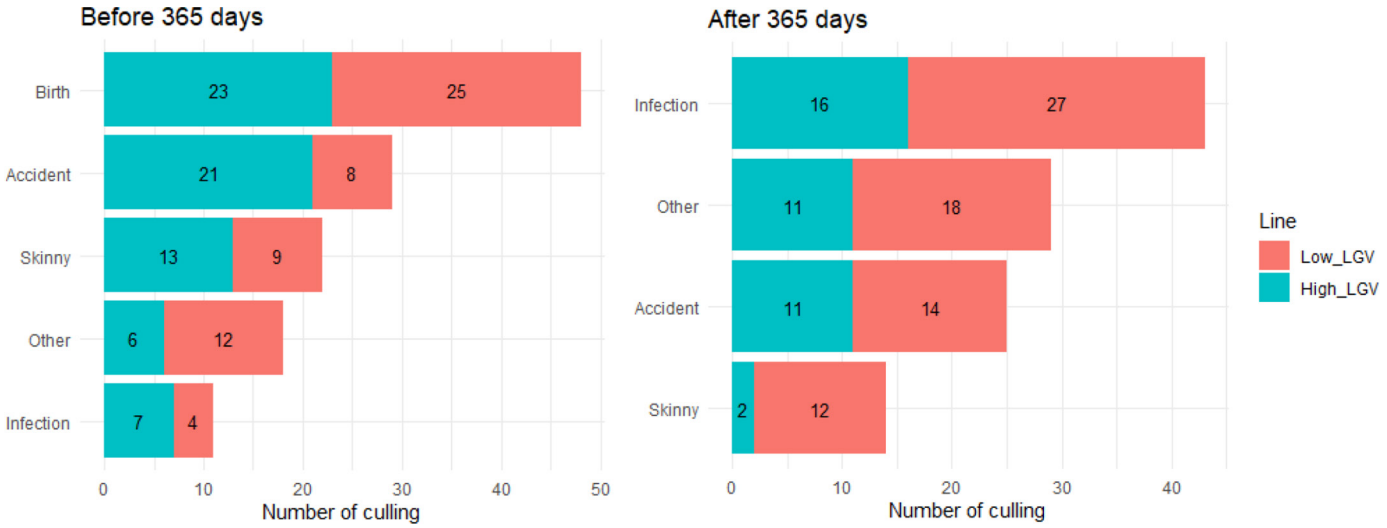


Figure 1. Distribution of culling reasons that occurred before and after 365 d of age in the high longevity (high_LGV; n = 111 goats) and low longevity (low_LGV; n = 135 goats) lines.

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Table 3. The ANOVA testing for the difference between lines (LSM or odds ratio) for the high longevity (high_LGV) and low longevity (low_LGV) divergent goat lines

	high_LGV line		low_LGV line		Analysis of variance
Item	No. of records	Mean (SD)	No. of records	Mean (SD)	*P*-value
Percentage of culling at the end of the study	228	49.5 (3.1)	212	62.4 (3.1)	0.004**
Number of treatments per year	228	0.23 (0.04)	212	0.3 (0.05)	0.13
Kidding per adult year (odds ratio)	140	1.03 (0.19)	136	0.96 (0.20)	0.70
Number of kids per kidding	130	1.38 (0.05)	117	1.43 (0.06)	0.58
Weight at birth (kg)	228	3.77 (0.08)	212	3.88 (0.08)	0.33
Weight (kg)	5,813	42.5 (0.26)	5,790	42.3 (0.26)	0.50
Line effect nested per month					0.002**
Mean dWD (SD)[1]	175	−0.11 (0.06)	166	−0.07 (0.06)	0.57
Mean WD (SD)[2]	169	−0.08 (0.09)	161	−0.11 (0.09)	0.77
LSCS[3]	109	4.44 (0.17)	106	4.94 (0.18)	0.04*
MY90[4]	109	256 (5.12)	106	262 (5.28)	0.43
MY250[4]	109	613 (11.6)	106	624 (11.9)	0.54
Milk fat-to-protein ratio[5]	105	0.95 (0.02)	101	1.00 (0.02)	0.07*
Log(Ig)[6]	199	1.90 (0.05)	183	1.97 (0.05)	0.30
Chest size (cm)	1,130	83.7 (0.34)	1,022	83.0 (0.34)	0.03*
Height (cm)	1,130	71.0 (0.29)	1,022	70.9 (0.29)	0.69

[1]Mean speed of growth deviation during the first year of life.

[2]Mean weight deviation during the first year of life.

[3]Adjusted SCS.

[4]Total milk yield estimation with Fleishmann method using test-day records of each in 90 or 250 DIM lactation period.

[5]Ratio of fat content to protein content calculated for the first test day in lactation (between 1 and 45 DIM).

[6]Serum immunoglobulin concentration during the first days of life.

*$0.01 < P < 0.1$; **$P < 0.01$.

censored. The Kaplan–Meier curves of the 2 lines are displayed in Figure 4. It shows a steep decline in the first few days after birth of the kids because 16.8% (74/440) of the goats died within the first month. The survival of low_LGV goats seemed slightly better during the first year, yet not significant, before curves crossed around 450 d of age.

The Schoenfeld residual analysis showed evidence of violation of proportional hazards assumption for line effect ($P = 0.01$). From the visual inspection of the residual plot (Figure 5), we can see that the residuals for the high_LGV line relative to the low_LGV line (shown as the reference line) decrease over time. The line effect was not significant during the first year, whereas the high_LGV line tended to be associated with a lower risk of being culled after 600 d of life, and more so after the second year. The Schoenfeld residual analysis showed no evidence of other factors that did not fit with the proportional hazards assumption, except for treatments ($P = 0.02$). However, no inversion of the line and treatment effect was observed. Thus, we decided not to stratify the line and treatments analysis over the different stages of life of the goats as it would not change the interpretation of the results.

The results of the multivariate Cox regression, including all significant covariates, are reported in Table 5. Significant effects ($P < 0.05$) were found for the following: line, speed of growth deviation (dWD) before 13 mo, year of birth, health treatments, and high IgG concentration. The effects of birth weight as a fixed effect, monthly WD during the first year, latent effect of mean WD during the first year over the survival after the first year, WD after the first year, normal or difficult kidding (versus no kidding), and number of kids after a kidding were tested but found not to be significant, and thus were eliminated from the model.

Some years of birth were associated with higher hazard ratio than others, especially 2021, when mortality was 3.007 times higher than in 2018. Health treatments were associated with increased hazard of culling in the following 3 mo. The average effect of line over all life stages was significant, with the high_LGV line having a decreased risk of culling (hazard ratio 0.63; CI = 0.465; 0.864).

DISCUSSION

Several studies estimated heritability of functional longevity (Castañeda-Bustos et al., 2017; Nayeri et al., 2017; Palhière et al., 2018) to be around 10% in goats. Nevertheless, there was a need to check if a hyperselection on functional longevity done on the commercial population would translate into significant differences in longevity in a common farm environment with direct

Table 4. The ANOVA testing for the difference of weight between high longevity (high_LGV) and low longevity (low_LGV) divergent goat lines[1]

	low_LGV		high_LGV		
Month of age	Weight, kg	SD	Weight, kg	SD	*P*-value
0	8.0	0.375	8.1	0.370	0.826
1	13.2	0.390	13.3	0.385	0.772
2	18.6	0.395	18.9	0.394	0.560
3	23.5	0.399	23.9	0.404	0.415
4	27.0	0.398	26.8	0.394	0.676
5	30.4	0.406	30.5	0.403	0.861
6	32.1	0.417	32.4	0.411	0.641
7	34.1	0.439	33.9	0.442	0.582
8	37.0	0.502	36.8	0.504	0.776
9	37.3	0.499	37.1	0.556	0.677
10	41.6	0.574	41.6	0.643	0.931
11	41.3	0.570	40.7	0.712	0.478
12	43.1	0.508	43.4	0.513	0.660
13	41.8	0.478	43.4	0.470	0.003*
14	40.9	0.497	42.1	0.499	0.032*
15	43.4	0.785	45.1	0.663	0.089
16	46.5	0.484	48.0	0.482	0.006*
17	46.0	0.527	46.4	0.546	0.568
18	48.5	0.847	49.2	0.777	0.525
19	48.1	0.847	48.2	0.741	0.856
20	49.6	0.816	49.9	0.792	0.763
21	49.6	0.485	50.2	0.495	0.339
24	54.7	0.643	57.2	0.585	0.001*
25	55.2	0.659	53.1	0.618	0.011*
26	55.1	0.818	53.7	0.676	0.193
28	58.8	1.114	56.9	0.821	0.157
33	60.0	0.814	58.1	0.799	0.086
34	57.5	0.778	58.1	0.715	0.605
36	64.7	0.771	65.5	0.667	0.427
37	61.9	1.057	60.2	0.753	0.177

[1]The animal was included in the model as a random effect. The line effect was nested into month of age. Results are averaged over the levels of year, gestation, and kidding.

*$0.01 < P < 0.1$.

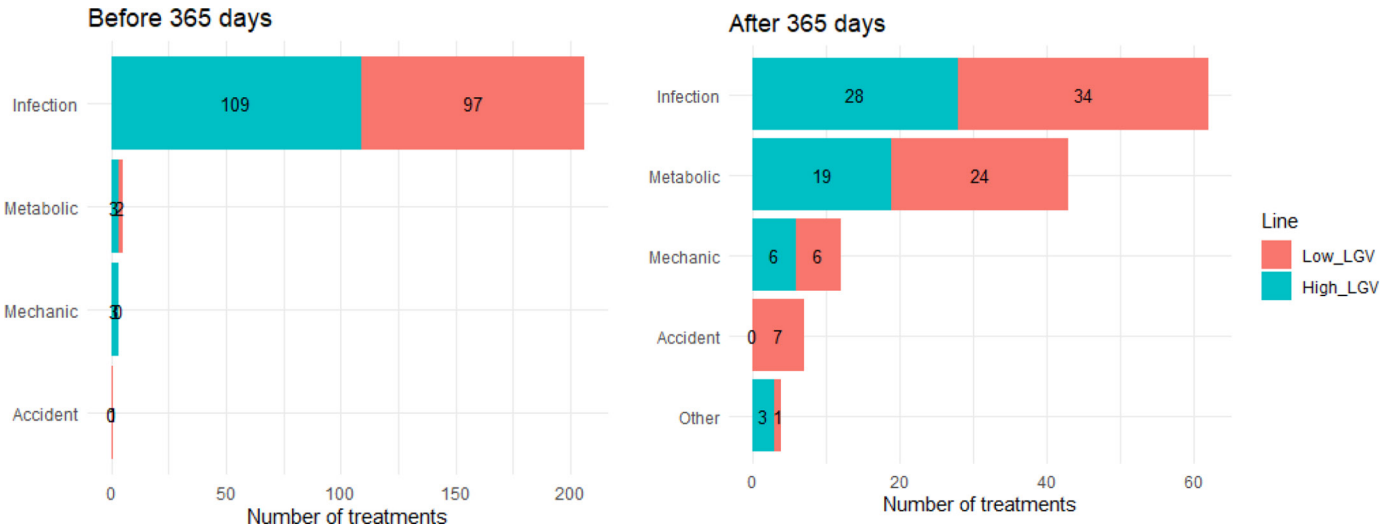


Figure 2. Distribution of treatment reasons that occurred before and after 365 d of age in the high longevity (high_LGV) and low longevity (low_LGV) lines.

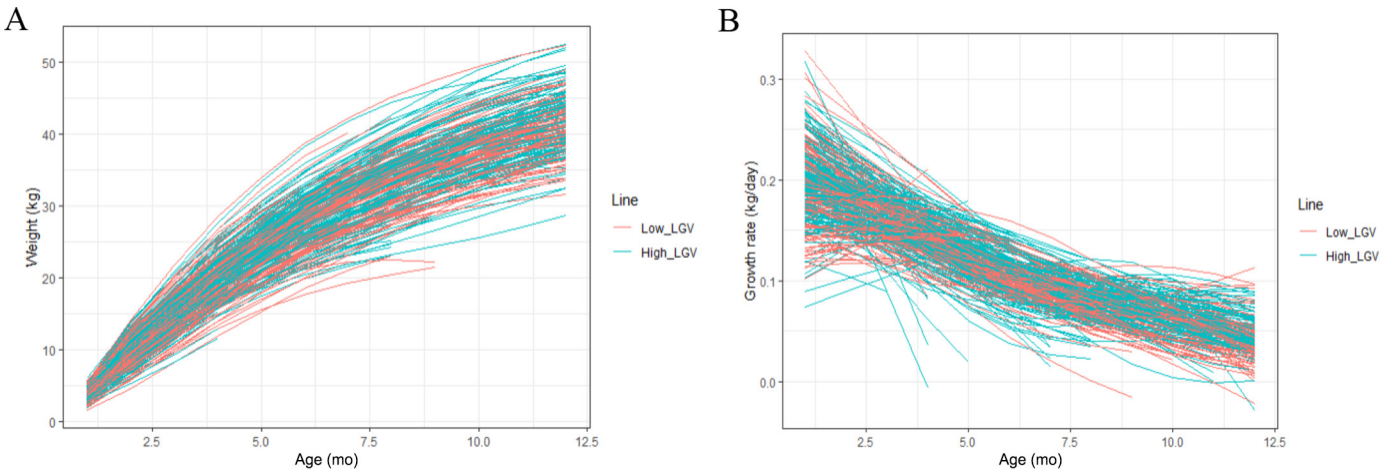


Figure 3. (A) Smoothed weight curves of the 341 goats from birth to 12 mo. (B) First derivative of the smoothed weight curves of the 341 goats from birth to 12 mo.

longevity recording. Given the differences in the relative importance of different mechanisms contributing to survival in different environments, lifespan is likely to be affected by genetics × environment interactions. Differences in functional longevity between farms will be heavily influenced by the level of challenge encountered in the different farming environments (e.g., farmer culling rules and environment harshness). Moreover, 2 animals can have the same functional lifespan, but one can receive considerably more medicinal interventions throughout its lifetime and thus be less robust. Such a selection for functional longevity was run on rabbits and led to significant difference in longevity (Garreau et al., 2010). To our knowledge, selection on longevity has never been done in dairy ruminants.

Our finding that hyperselection for functional longevity resulted in increased survival was observed in a single breed (Alpine) and in a single experimental herd over 5 yr with a management representative to that found in many commercial dairy goat farms (i.e., indoors, feeding forage and concentrate, using AI and twice day milking). According to the national performance-recording database, the average milk yield for first lactation Alpine goats over 250 d was 707 kg in 2019 (Thomas and Bourrigan, 2019). In the present study, milk yield (± SD) was 619.6 kg (± 121.2) on a 250-d basis (Fleischmann's method). In the national database, the average LSCS in Alpine goats was 5.34 (± 1.59) compared with 4.74 (± 2.05) in the present study. The survival advantage of the high_LGV line was consistent between years, even though mortality rates and environment conditions (i.e., forage quality, infectious pressure) varied.

This study showed that it is possible to get a selection response for functional longevity in goats despite a low heritability. The high_LGV median survival time was 830 d compared with 787 d for low_LGV line (difference = 43 d), showing that there was a strong delay in involuntary culling achieved by selection. This difference is, however, lower than what we estimated based on the length of productive life of the AI bucks' daughters (1,071 d for the high_LGV and 909 for the low_LGV line, difference = 162 d). That can be explained, at least to some extent, by the fact that the genetic evaluation of bucks was run only on their daughters that had a registered milk yield (i.e., the ones that survived the first unproductive year of life). Indeed, the life expectancy for goats that survived the first year was 1,498 d for the high_LGV compared with 1,097 d for the low_LGV line (difference = 401 d). The survival analysis confirmed that the line effect was not constant over the life of the animal. The 2 lines had the same survival during the first 15 mo, whereas the high_LGV line had a better survival thereafter. This finding could be explained by the fact that the environmental challenges that affect the first year (e.g., overcoming birth, dealing with milk feeding and its related health effects, building an immunocompetence) are different than those faced by adults. Survival after the first year could rely on mechanisms that are not expressed before the first year. Further, some factors that would otherwise be present throughout the life of the animal, such as malformations and inappropriate body morphology, will be culled out soon after birth. In cattle, (Pritchard et al., 2013) found a positive genetic correlation (0.31) between heifer survival and lifespan score. The relatively low correlation suggested that survival in the rearing herd and the milking period are different traits. The small number of goats included in our study did not permit calculation of genetic correla-

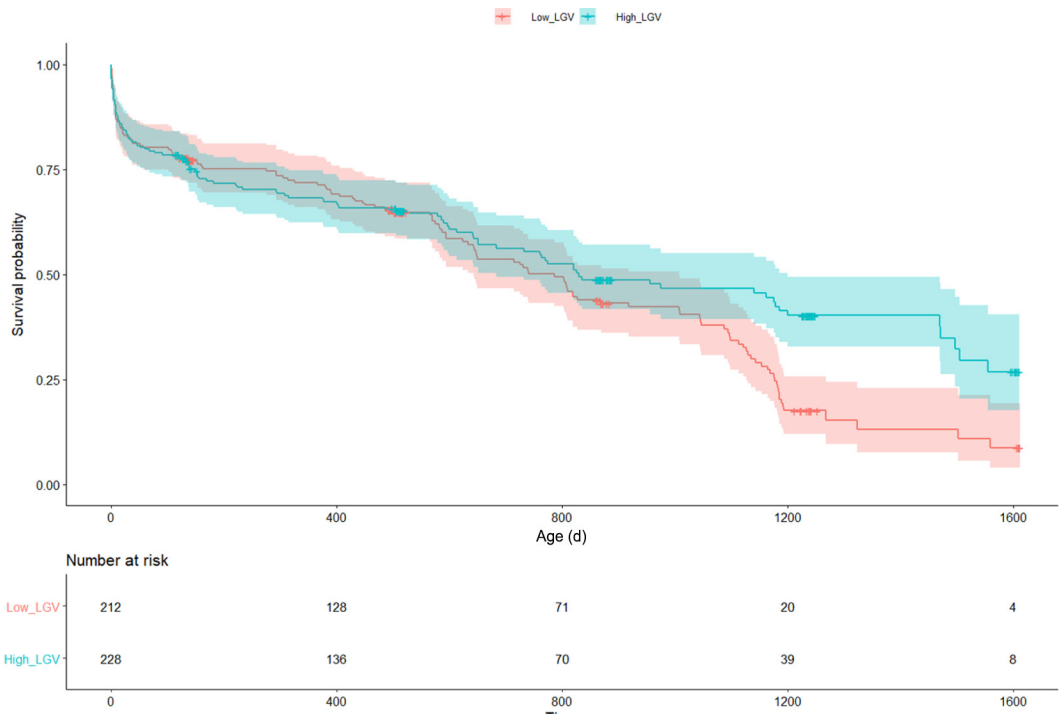


Figure 4. Plot of Kaplan–Meier curve showing survival against time for high longevity line (high_LGV) and low longevity line (low_LGV). Shaded areas represent the 95% confidence intervals calculated by Cox analysis.

tions. However, our results highlighted the need to record culling information before first kidding of goats on a national scale to address that issue. Indeed, survival at early stage of life has been shown to be heritable in sheep (Riggio et al., 2008).

Low serum immunoglobulin concentration shortly after birth was correlated with lower survival through life ($P = 0.03$). It has been shown that a lower passively acquired immunity is linked with an increase of diarrhea, lower weight gain, and increased mortality during the first month (Bekele et al., 1992; Berge et al., 2009). Here, we showed that the deleterious effect of impaired immune transfer from colostrum remained even during subsequent stages of life. In our study, all kids were given the same amount (300 mL) of heat-treated colostrum sampled from a group of kidding goats. The variability of IgG absorption could be due to a difference in IgG concentration in colostrum pools (not standardized among samples), time before ingestion (Weaver et al., 2000), heating time (Saldana et al., 2019), or difference of first milk coagulation that could affect intestinal absorption (Miyazaki et al., 2017).

First lactation milk yield was similar for both lines. This confirmed that the selection procedure resulted in differences in functional longevity (i.e., longevity corrected for milk yield). No line difference was found for the number of kiddings per adult year nor in litter size. Thus, the better survival of the high_LGV line seemed neither to be due to better production nor better fertility.

The SCS score for first lactation was higher for low_LGV than high_LGV goats. This result was consistent with the slight difference in EBV for SCS in the sire bucks that could not be avoided when choosing extreme founders. That might mean a better udder health of high_LGV goats (Poutrel and Lerondelle, 1983; Contreras et al., 1996; Jiménez-Granado et al., 2014; Rupp et al., 2019). There was no significant difference between lines concerning the number of treatments received. Indeed, despite treatment events significantly reducing survival over the 3 following months, including the treatment in the model did not affect the line effect. Although we cannot exclude the possibility that there were undetected disease events at play (affecting one line more than the other), the better survival of the high_LGV line suggested that in some way this line was more resilient to environmental perturbations. In this context, it is interesting to note that several studies found genetic correlations between functional longevity and udder traits in cows and goats. Palhière et al. (2018) found genetic correlations of functional longevity with milk SCS (from −0.29 to −0.35), rear

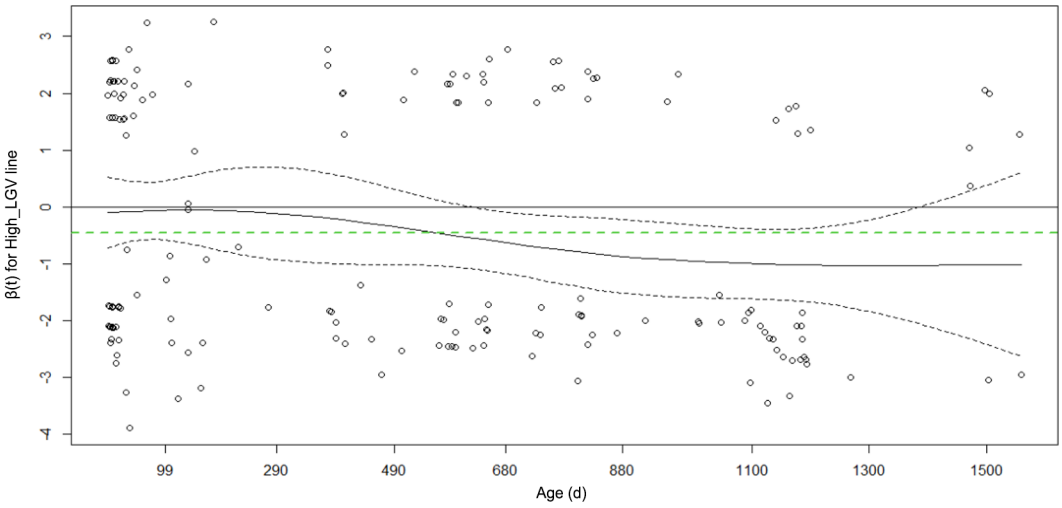


Figure 5. Plot of scaled Schoenfeld residuals against transformed event time for Cox proportional hazards model for line covariable. The effect of the high longevity line (high_LGV) compared with the low longevity line is represented. The solid curve is the smoothed LOESS curve of β(t), and broken lines represent the 95% confidence intervals. β(t) corresponds to the estimation of the hazard ratio associated with high_LGV compared with the low longevity line at age t. The green broken line corresponds to the average high_LGV line effect estimated by the Cox model. The slope suggests violation of the proportional hazards assumption for the line effect.

udder attachment, and udder floor position (from 0.17 to 0.29). Such genetic associations of functional longevity with SCS were also reported in cattle (Sasaki 2013) and in goats (Castañeda-Bustos et al., 2017).

The month-per-month survival modeling allowed us to precisely implement the effect of events that occurred at different ages of the animal, or evolving variables such as treatments and BW. A strong correlation between survival and speed of growth was found during the first year. Several studies have found that kids (or lambs) with the lowest weight have a lower chance of survival (Riggio et al., 2008; Dwyer et al., 2016; Chauhan et al., 2019) that could be partly attributed to the increased risk of hypothermia, which has been related to size as well as the individual's fat reserves (Alexander, 1962). Moreover, smaller kids are penalized in all aspects of social competition.

It is interesting that the monthly growth rate (obtained from the B-spline smoothing) was more correlated with survival than BW. As a measure, growth rate is inherently more responsive to environmental challenges than is BW per se (a strong disease or nutritional challenge can cause growth rate to shift from positive to negative, whereas the corresponding change in BW is proportionally far less due to the cumulative nature of the measure). This finding suggested that the influence of growth rate on survival is associated with ability to cope with underlying disease or stress challenges.

Table 5. Hazard ratios (HR) with 95% lower and upper CI from Cox hazard model for culling data in 440 goats of the high longevity (high_LGV) and low longevity (low_LGV) lines

Risk factor	HR	CI		*P*-value
high_LGV line vs. low_LGV	0.645	0.474	0.878	0.005
Birth year 2017 vs. 2018	1.453	0.971	2.176	0.069
Birth year 2019 vs. 2018	1.456	0.915	2.316	0.113
Birth year 2020 vs. 2018	1.072	0.576	1.996	0.826
Birth year 2021 vs. 2018	3.016	1.523	5.973	0.002
d_WD[1]	0.328	0.251	0.427	<0.001
Health treatment vs. none[2]	2.029	1.315	3.128	0.001
High IgG concentration[3]	0.687	0.492	0.960	0.028

[1]Speed of growth deviation (d_WD) is the normalized value of the first derivative of the weight curve and is implemented each month between 1 and 13 mo.

[2]Health treatment is a dummy variable = 1 if the animal received a treatment in the past 3 mo and 0 if else.

[3]Log-transformed serum immunoglobulin concentration during first days following birth [Log(IgG)] is a permanent effect over whole life. High group corresponds to a value higher than 2 and is compared with goats with values lower than 2.

Several studies reported a negative correlation between growth rate and longevity (Hou 2013) and proposed that higher growth rate implies higher oxidative stress and shorter longevity (Gabriela Jimenez, 2018). We found no differences between lines during the first year in growth rate and BW. Moreover, no carryover effect of the average growth rate during the first year on later survival was found.

The high_LGV goats were heavier during early lactation (between 12 and 16 mo). Because the body morphology records were less frequent than weighing and highly correlated with it, we did not include them in the survival analysis. However, the comparison of height and chest size between lines was of interest. No differences concerning the height at the withers was found, and high_LGV goats seemed to have a slightly wider chest ($P = 0.03$), indicating that high_LGV goats might have larger lipid reserves. In addition, the fat-to-protein ratio in milk during the first month of the first lactation was higher for the low_LGV line. This suggested that this line had a greater negative energy balance in early lactation (Bocquier and Caja, 2004), despite milk yield being similar between lines during this critical period, and no differences in litter size or litter weight. These findings taken together tended to suggest that there were different resilience capacities between the lines, with different underlying priorities for usage of body lipid reserves. This may have contributed to the differences in functional longevity between them. The argument that body fatness dynamics confer robustness and help underpin resilience responses is supported by several studies. Savietto et al. (2015) showed that rabbits selected for productive longevity had a greater capacity for resources acquisition under constrained condition than rabbits selected for reproductive intensity. In cattle, body reserves have been shown to be predictive for reproduction and susceptibility to disease; excessive BCS at calving and great loss of BCS during early lactation were related to increased health disorders (Roche et al., 2009, 2013). In dairy sheep, a divergent selection experiment for mastitis resistance was performed and showed a genetic link between susceptibility to udder infections and metabolic adaptation to energy shortage (Bouvier-Muller et al., 2018). However, the underlying mechanisms of the link between resilience, the dynamics of fat reserves, and BCS remain unclear.

The suggestion that the differences between low_LGV and high_LGV lines may be related to differences in body reserve dynamics, and thus resilience, merits further study. Studies with more intensive recording of BW, BCS and energy metabolism, as well as ingestion should be of great value to explain different lifetimes of the 2 hyperselected lines of goats.

CONCLUSIONS

Hyperselection based on functional longevity of AI bucks successfully created 2 groups of goats with different lifespans. Monitoring of the lines indicated that functional longevity-based selection was associated with resilience-related mechanisms, as evidenced by better udder health with decreasing milk cell counts. In addition, the higher BW of high_LGV goats and lower milk fat-to-protein ratio during the beginning of the first lactation suggested different resource allocation profiles between lines. Our results supported the hypothesis that functional longevity reflects the accumulated consequences of resilience and thus provides a proxy measure for resilience.

ACKNOWLEDGMENTS

The authors thank the staff of the INRAE experimental unit at Bourges, France, for technical support in producing, raising, and monitoring the animals. This work was performed in the framework of the EU H2020 SMARTER project (grant no. 772787, Castanet Tolosan, France) and the national APIS-GENE (Paris, France) funded projects ActiveGoat and Resilait. M. Ithurbide acknowledges EU H2020 (SMARTER) and APIS-GENE (Resilait) for her PhD grant. The authors have not stated any conflicts of interest.

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