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ABSTRACT

This study aims to investigate whether the variation in reproduction success, growth, and milk trajectories is associated with different adaptive strategies in the short term (response to an acute nutritional challenge), using two Alpine goat lines. A total of 382 Alpine goats (179 low longevity (**low_LGV**) and 203 high longevity (**high_LGV**)), selected for divergent functional longevity from a commercial population, were monitored for 4 years and recorded for BW, reproduction and milking performance. Every year, an average of fifty primiparous goats were exposed to a 2-d nutritional challenge in early lactation. A polynomial model was used to analyse the lifetime trajectory of lactation and BW. A piecewise model was used to analyse the individual milk yield and responses of milk components to the nutritional challenges. The statistical analysis revealed that the two lines had a similar performance for total milk yield in the first lactation, BW at birth and at first kidding, litter size and weight, kidding interval and interval from the first insemination to conception. BW trajectories revealed that low_LGV goats had a greater BW in pregnancy but then lost more weight in early lactation compared to high_LGV goats, which showed a greater BW after kidding. Milk trajectories showed that the high_LGV goats had a higher initial milk yield, an earlier but less marked lactation peak and more persistency in milk production in late lactation than low_LGV goats. Except for milk protein content, quite similar response and recovery profiles of milk yield and milk fat content were observed during the challenge for both lines. The response to the challenge was positively correlated to the initial level of milk production in early lactation but negatively correlated with milk production decline after the peak. This finding suggests that the low_LGV goats were more adapted to allocate resources to meet an expected physiological change such as gestation and lactation. However, high_LGV goats allocate more than low_LGV goats for structural mass and may better cope with an unexpected environmental change such as nutritional deficit.

Implications

Selection to improve the functional longevity in goats is becoming highly relevant and of great economic importance. In this work, we have evaluated reproduction, milk and BW performance in two Alpine goat lines selected on divergent longevity. The variation in their performance trajectories at lifetime level and to a short-term nutritional challenge were explored. This approach combining genetically divergent lines and nutritional experiments is useful to identify animal adaptative strategies under challenging environments.

Introduction

Driven by climate change and demand for animal products, livestock production is facing increasing challenges that compromise the productivity, welfare and longevity of animals (Cheng et al., 2022; Chaidanya et al., 2015). To address such challenges, genetic improvement is a potential component of climate change adaptation strategies that aim to improve adaptive capacity, and thereby secure animal production. Having animals with good potential for both productivity and longevity in the changing climate scenario is a priority for sustaining small ruminant production (Joy et al., 2020). This implies developing balanced breeding schemes that account for trade-offs and synergies between production, reproduction and health traits. In other words, we need breeding

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strategies that find a more sustainable balance between animal efficiency and resilience (Ramón et al., 2021).

Longevity, or productive lifespan, of an animal in the herd is a trait that reflects the performance of the animal and its efficiency at overcoming various challenges throughout its career. True longevity takes into account all the reasons for an animal being removed from the herd. When true longevity is adjusted for production, it gives an approximation of functional longevity (Castañeda-Bustos et al., 2014). Functional longevity refers to the ability of an animal to delay involuntary culling, which can be assumed to reflect its adaptive capacity (Rostellato et al., 2021).

Longevity has not been included in dairy goat breeding programmes but several approaches have been proposed to integrate it into the selection index for goats (Palhière et al., 2018; Ithurbide et al., 2022). Further, direct or indirect evaluation of longevity was always expected to increase the overall economic efficiency of the dairy goat industry (Scholtens et al., 2018). Different criteria calculated at the scale of the female career, such as productive lifespan, survival rate, milk persistency and somatic cell score (Rupp et al., 2019; Astruc et al., 2021), have been studied to reveal their correlations with longevity in goats. However, to date, the link between productive lifespan and adaptive capacity has rarely been studied in small ruminants. Adaptive capacity can be estimated from responses to naturally occurring environmental perturbations (Poppe et al., 2021) or, as in the present study, from responses to planned perturbations. In this context, the impact of environmental challenge on animal performance has been shown to be proportional to the deviations in performance trajectories over time (Garcia-Baccino et al., 2021).

Accordingly, the first aim of the current study was to investigate whether variation in reproduction success, growth, and milk trajectories is associated with different adaptive strategies in the short term (response to an acute nutritional challenge), using two Alpine goat lines. These lines, selected for divergent functional longevity (Ithurbide et al., 2022), were expected to increase the diversity of adaptive strategies. The second aim of the study was to quantify the differences between the two lines in long- and short-term performance trajectories, as this information is important for the design of future selection strategies and simulation of the impact of changing environments thereon.

Material and methods

Guided by the desire to enhance and integrate functional longevity into goat selection programmes, INRAE has been committed since 2016 to produce two lines of goats selected on divergent functional longevity. The experiment was carried out in accordance with the French legislation on animal experimentation and European Convention for the Protection of Vertebrates Used for Experimental and Other Scientific Purposes with experimental approval number APAFIS#8613-2017012013585646. Animals were raised at the experimental INRAE research unit P3R of Bourges (La Sapinière, Osmoy, France, Unit approval C18-174-01).

Animals

Alpine AI bucks (35) were selected from commercial populations based on the length of functional life of their daughters and used to breed two lines of Alpine goat: a high longevity (**high_LGV**) and a low longevity (**low_LGV**) lines at the INRAE experimental facility of Bourges Farm (Ithurbide et al., 2022). Sires of the two lines had a reliable (reliability $\geq$ 0.80) and extremely unfavourable or favourable EBV for functional longevity and were also required to show similar and favourable EBVs for milk production traits to avoid confounding effects from an indirect response to selection for production traits (Table 1). The experiment was conducted from 2017 until 2021, with all females born from the two lines between 2017 and 2020 raised in the same facility and fed with a ration based on lucerne hay, supplemented with concentrates.

Reproduction was seasonal and goats were inseminated at an average age of 8 months. The artificial inseminations (**AI**) were grouped in August until early September then followed by three natural matings to maximise herd fertility. Kidding ranged from January to early March. The kidding date, the difficulty of the birth, the size and the weight of the litter were recorded. During lactation, goats were milked twice a day until late October to then be dried-off for three months. Morning and evening milkings were combined to obtain the individual daily milk production. Monthly milk records were taken, and milk components analysis were performed for protein and fat content (**PC, FC**).

Lifetime growth, milk production and reproductive data

The complete dataset collected from 382 goats born from 2017 to 2020 was used to study growth performance trajectories throughout their lifetimes. Goats were weighed three to four times per month from birth to the first breeding, after that, they were weighed one time per month. A total of 7 314 BW records from 382 goats (179 low_LGV and 203 high_LGV) were included for the growth and BW trajectories analysis.

Out of these 382 goats born, 135 low_LGV and 137 high_LGV goats were considered for the insemination programme. Further, a dataset of 547 records related to reproduction events was used to assess the variation between lines in performance and reproduction success. Reproductive success was measured by the length of the interval between the first AI and the date of parturition (Freret et al., 2018). The first AI is considered fertile if the interval is between 140 and 160 days. It is considered to have failed if the interval is between 161 and 300 days. In the latter case, the second insemination is considered fertile. In the case when the interval is less than 140 days, the female is considered to have aborted. The kidding interval was measured for all the herd. The interval

Table 1
Estimated breeding values [mean (SD)] for functional longevity and milk production traits for 35 bucks that sired the high- and low-LGV Alpine goat lines.

Traits	High_LGV line bucks	Low_LGV line bucks	Contemporary bucks
EBV for functional longevity (days)	85.1 (89.3)^{a}	−108.7 (121.0)^{b}	−12.5 (122.3)^{a,b}
Length of productive life (days)	1 071 (722)^{a}	909 (651)^{b}	1 006 (697)^{c}
EBV for milk yield (kg)	2.4 (58.3)^{a}	8.5 (66.5)^{a}	−39.2 (73.8)^{a}
EBV for fat content (g/kg)	0.86 (2.87)^{a}	−0.37 (2.12)^{a}	0.37 (2.22)^{a}
EBV for protein content (g/kg)	0.13 (1.29)^{a}	0.08 (1.09)^{a}	0.14 (1.40)^{a}
Total days in milk (days)	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}

Abbreviations: LGV = longevity; EBVs = estimated breeding values.
Values within a row with different superscript letters differ significantly at $P < 0.001$.

between the first AI and the fertilising mating was also calculated for goats that had an interval between the first AI and the date of parturition greater than 160 days. After parturition, only 106 low_LGV and 109 high_LGV goats started their first lactation. A final data set consisting of 2 646 test-day milk yield records collected from 351 lactations was used to investigate the diversity of milk production and lactation curves in the Alpine goat lines during the first three lactations. The duration of lactation is 300 days and goats were required to have at least eight test-day records for production to be assessed. The Fleishmann method (Tekel et al., 2019) was used to calculate total milk production during 280 days of the first lactation. Another dataset consisting of 2 271 milk yield records, collected from 2018 to 2021 during a short-term nutritional challenge from the 96 low_LGV, and 97 high_LGV primiparous dairy goats that underwent the challenge, was used to study responses of milk production and contents of fat and protein to the nutritional challenge.

Nutritional challenge

Every year, from 2018 to 2021, almost fifty primiparous dairy goats from both lines underwent a 2-d underfeeding challenge during early lactation (mean Day In Milk (**DIM**) = 41, sd = 12.6). The design of the animal trial followed the protocol described in detail in Friggens et al. (2016). The experiment consisted of a 7-day prechallenge period, followed by a 2-day challenge period, and a 7-day postchallenge period. During the pre- and postchallenge periods, the goats received a standard ration based on lucerne hay, supplemented with concentrate. During the challenge, goats received chopped straw only. The goats had ad libitum access to feed and water throughout the experiment and were milked twice per day. Milk was sampled only from the morning milking for analysis of milk composition.

Analysis

All statistical analyses were performed using R software (RCore Team, R Foundation for Statistical Computing, 2020). Generalised linear models with random regression (lme package) were used to generate comparative descriptive statistics of repeated growth (model 1) and milk production (model 2) between the two lines. Logistic regression with animal as a random effect was performed (glmer function) to compare reproductive success between lines (model 3). The fixed effects of line, year of birth, parity, and age of the first insemination were included in the regression model.

Milk and BW trajectories throughout the lifetime were fitted using a polynomial model that makes no assumptions about the shape of the curve and combines the flexibility of fitting with mathematical simplicity. The flexibility in the model fitting depends on the degree of the polynomial used, but high-degree polynomials will tend to overfit the data because of the decline of the estimator's bias and the increases in the variance. The choice of degree of the polynomial model should appropriately consider the balance between bias and variance (Gajewicz-Skretna et al., 2021). Milk production and BW data were fitted using polynomials of 3–6° and Bayesian Information Criterion (**BIC**) was used to choose the most appropriate models, with the lower BIC values indicating a better model fit. (Schwarz, 1978). Finally, in this study, a 5° polynomial was used to fit milk production and a 3° polynomial was used to fit BW. The random effect of animal was modelled using a quadratic model that describes individual deviations in milk and BW performance. An additional analysis of variance on BW during the first pregnancy was performed to assess the difference in growth performance between the two lines in pregnancy.

Model 1

$$Y_{ij} = (\beta_0 + \beta_1 t_j + \beta_2 t_j^2 + \beta_3 t_j^3) * (\text{line}_i + \text{reproduction}_i + \text{Age-AI1}_i + \text{year}_i) + (\gamma_0 + \gamma_1 t_j + \gamma_2 t_j^2) * u_i + e_{ij}.$$

where y is the BW of goat i, and age j, β_{0-3} represent the fixed polynomial model coefficients, t is the age, line (high_LGV, low_LGV), reproduction (success, failure), age-AI1 (<8 months, >8 months), year (2017–2020) are the fixed effects of line, reproductive success, age at first insemination and year of birth, γ_{0-2} are the random regression coefficients to describes individual deviations from the mean curve, u_i is the random animal effect and e_{ij} is the random residual.

Model 2

$$Y_{ijk} = (\beta_0 + \beta_1 t_k + \beta_2 t_k^2 + \beta_3 t_k^3 + \beta_4 t_k^4 + \beta_5 t_k^5) * (\text{line}_i * \text{reproduction}_{ij} + t_k + \beta_2 t_k^2 + \beta_3 t_k^3 + \beta_4 t_k^4 + \beta_5 t_k^5) * (\text{line}_i * \text{reproduction}_{ij} + \text{Age-AI1}_i + \text{year}_{ij} + \text{parity}_{ij} + \text{litter\_size}_{ij})) + (\gamma_0 + \gamma_1 t_k + \gamma_2 t_k^2) * u_i + e_{ijk}.$$

where y is the milk production of goat i, parity j and DIM k, β_{0-5} represent the fixed polynomial model coefficients, t is DIM, line (high_LGV, low_LGV), reproduction (success, failure), age-AI1 (<8 months, >8 months), year (2017–2020), parity (for the ith parity), litter_size (1, 2+) are the fixed effects of line, reproductive success, age at first insemination, year of birth, parity and litter size, γ_{0-2} are the random regression coefficients to describes individual deviations from the mean curve, u_i is the random animal effect and e_{ijk} is the random residual.

Model 3

$$Y_{ij} = \mu + \text{line}_i + \text{age-AI1}_i + \text{year}_i + \text{parity}_{ij} + u_i + e_{ij}.$$

where y is the reproduction performance of goat i and parity j, μ is the population mean, line (high_LGV, low_LGV), age-AI1 (<8months, >8months), year (2017–2020), parity (for the ith parity), are the fixed effects of line, age at first insemination, year of birth, and parity, ui is the random animal effect and e_{ij} is the random residual.

Milk persistency in the decreasing phase of the lactation is most often defined as the measure of the decrease in production over a time interval (Cobuci et al., 2004). The persistency of milk production during late lactation was measured by the decrease in production between the 200 and 300 lactation days. The peak milk yield was measured as the maximum of individual milk production throughout lactation, the time of peak lactation was thus defined as the time when peak yield occurred. Analysis of variance with animal as a random effect, and line and parity as fixed effects, was then used to establish the difference between the two lines in terms of lactation peak and persistence.

For the milk yield and milk component responses to the nutritional challenges in the first lactation, the statistical analyses were performed using a piecewise model (see detailed description in Friggens et al., 2016). To have the net effect of the challenge on milk trajectory, the analysis of the energy-corrected milk during the challenge was performed with the same piecewise model as the milk yield and milk components and results were reported in the supplementary material S1. The piecewise model parameters characterise individual profile of response and recovery to the challenge as follows:

$$Y_i = V_1 + V_2 + V_3 + V_4 + V_5 + e_i$$

where Y_i is the milk yield of goat i, V1 is the prechallenge level, V2 is the linear slope of the response during the 2-d challenge, V3 is the linear component of the recovery, V4 is the quadratic component of the recovery, V5 is the postchallenge level and e_i is the residual error.

Table 2
Descriptive statistics of the difference in performance between high_LGV and low_LGV Alpine goat lines.

Performance	High_LGV		Low_LGV		*P*-value
	No. of observation	lsmean (SE)	No. of observation	lsmean (SE)	
BW at birth (kg)	203	3.97 (0.06)	179	3.96 (0.06)	0.74
BW at 1st kidding (kg)	124	46.2 (0.76)	113	46.7 (0.79)	0.87
Total milk yield in 1st lactation (L,280 days)[1]	101	648 (20.1)	101	651 (19.9)	0.91
Litter size	172	1.72 (0.06)	158	1.63 (0.07)	0.70
Litter weight(kg)	172	6.73 (0.11)	158	6.81 (0.11)	0.56
Reproduction success, (Odds Ratio)	254	0.87 [0.52–1.46]	241	1.31 [0.68–2.52]	0.59
kidding_interval	87	367 (3.39)	70	365 (3.78)	0.61
Interval from AI1_AIf[2]	87	30.9 (3.96)	60	29.1 (4.48)	0.74

Abbreviations: LGV = longevity; AI = Artificial Insemination; lsmean = Least-Square Mean.
[1] Total cumulate milk for the first lactation, goats that had not records in early and late lactation are not considered.
[2] Interval from the first insemination to conception for animals that failed to conceive at the first AI.

Table 3
Additive effects of line, reproductive success, age at first AI, and year on BW curve parameters of the high_LGV and low_LGV Alpine goat lines, using a polynomial model of degree three.

Item	β_0	β_1	β_2	β_3
Intercept	3.403*	6.656*	−0.374*	7.23×10^{-03}*
Line (high_LGV)	−0.020	0.291	−0.058*	3.08×10^{-03}*
Reproductive success	0.549*	−0.860*	0.023*	-9.64×10^{-03}*
Age-AI1 (>8 months)	−0.244	0.119	−0.041	2.69×10^{-03}*
Year_2018	−0.401	0.434*	−0.093*	4.01×10^{-03}*
Year_2019	−0.243	−0.465*	−0.004	2.93×10^{-03}*
Year_2020	−0.032	−1.025*	0.217*	-9.84×10^{-03}*

Abbreviations: LGV = longevity; AI = Artificial Insemination.
Intercept: Line (low_LGV), Reproductive failure, Age-AI1 (<8 months), Year_2017.
β_0, β_1, β_2 and β_3: coefficient of the polynomial model degree three.
* Significant effects of a factor, i.e. a polynomial coefficient significantly different from 0 ($P < 0.05$).

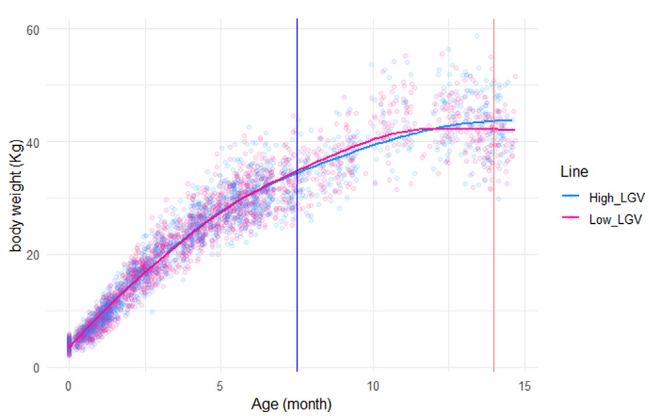

Fig. 1. Average trajectories of BW of the Alpine goat lines described by the fixed effects of a 3rd order polynomial model: high_LGV (blue) and low_LGV (pink). Vertical lines refer to the average first insemination age (blue) and the average first kidding age (red). Abbreviations: LGV = longevity.

Animal was fitted as a random effect, and line and year of challenge as fixed effects were included in the piecewise model to explore inter- and intra-line variation of response to the challenge. The animal-specific set of parameters V1 to V5 was then used to assess the correlations between parameters of the piecewise model for milk yield and milk fat and protein contents and those of polynomial lactation curves. The random coefficients of the polynomial model could be used to describe the shape of the lactation curve: γ_0 is the intercept of the curve corresponding to the initial milk yield, γ_1 corresponds to the descendant linear phase, while γ_2 corresponds mainly to ascendant quadratic phase of the lactation curve.

Results

Milk production, growth, and reproductive averages performance

As shown in Table 2, there were no significant effects of longevity line on the cumulative milk yield in the first lactation, or on BW at birth (average BW at birth was 4 kg for both lines). The average age at the first parturition was estimated at 14.5 months and BW at this age was identical for the two lines (46 kg). There was no significant effect of line on litter weight or litter size for any parity; the maximum litter size was 5 for high_LGV and 4 for low_LGV. There was no significant interaction between line and the litter size on the litter weight. The odds of being pregnant were 0.87 smaller for high_LGV goats than for low_LGV goats, but the difference was not significant (P = 0.59). The kidding interval and the interval between the first insemination and the fertilising mating were identical for both lines in goats that have a failure at the first AI.

BW trajectories

The results of fitting the polynomial model to the overall test-day data of the BW, as affected by the different levels of explanatory factors are reported in Table 3. The parameters of the polynomial models do not have a real biological explanation but could be used to describe the different parts of the BW curve: β_0 is the Intercept of the curve which corresponds to birth weight, β_1 refers to the linear part of the curve, and β_2 corresponds to the quadratic part of the curve.

There were no significant effects of line on the intercept (β_0) and the linear components (β_1) of the polynomial function. Fitted BW curves did not show significant differences between the two lines in birth BW and during the growth period (Fig. 1). However, line had a significant effect on the quadratic and third-order compo-

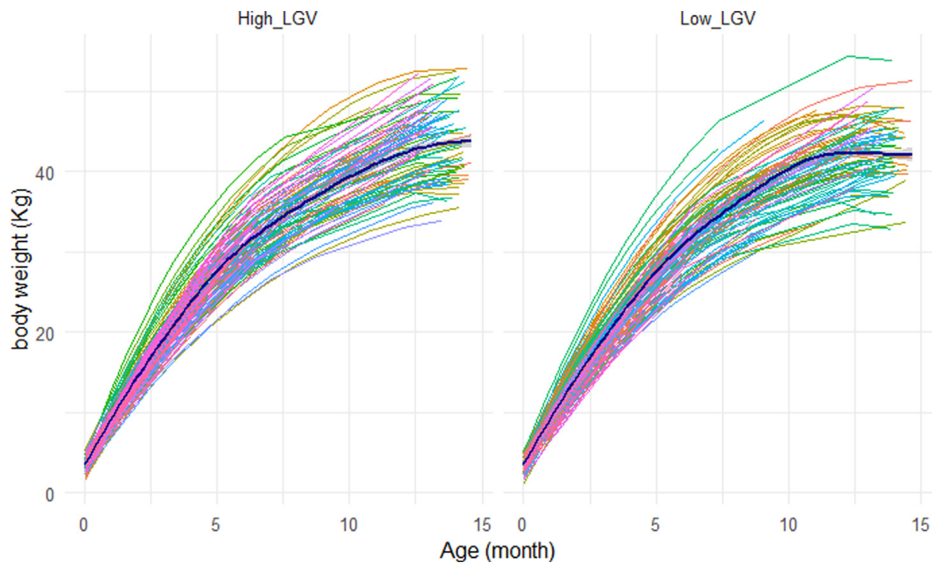

Fig. 2. Individual trajectories of BW of the Alpine goat lines described by the random effects of the polynomial model for the high_LGV and low_LGV line. Black curves refer to the average BW trajectories. Abbreviations: LGV = longevity.

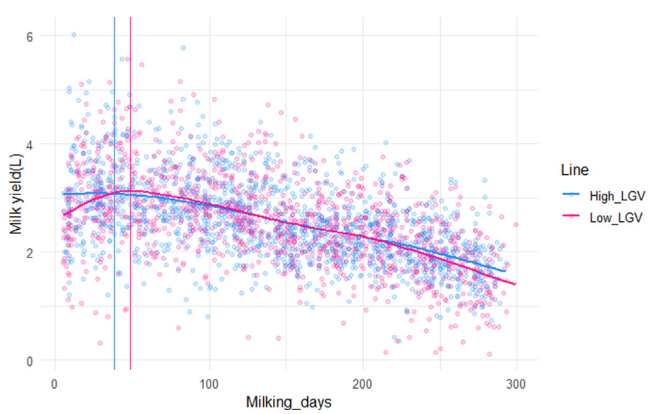

Fig. 3. Average milk yield trajectories in first lactation of the Alpine goat lines described by the fixed effects of a fifth-order polynomial model. Vertical lines refer to the lactation peak: high_LGV (blue) and low_LGV (pink). Abbreviations: LGV = longevity.

nents (β_2, β_3) of the polynomial function. These results were complemented by the analysis of variance of BW during gestation. These revealed a significant effect of line in gestation and after kidding. Low_LGV goats had a significantly ($P < 0.05$) higher BW than high_LGV goats at early gestation. Moreover, low_LGV goats had a significantly greater BW decrease from the end of gestation until early lactation compared to goats high_LGV (Fig. 1). The interactions between the line, age at the first mating, and reproduction success had no significant effect on the shape of the BW curves. The variance components of the polynomial model attributed to the random intercept were on average 0.743, while the residual variance was on average 2.257.

Individual BW curves showed a high variability relative to the average fitted curve during adult age in both lines (sd = 16.1, Fig. 2). Fitted BW curves for the two lines are shown in Figs. 1 and 2.

Milk trajectories

Parameters of lactation curve are useful to understand the underlying pattern of milk production of the two lines and to assess the effect of genetic and non-genetic factors on this pattern. The fitting of the lactation curve using the polynomial function resulted in a mean lactation curve with an initial milk yield of 2.9L and a peak yield of 3.2L occurring at day 43 (Fig. 3). The random intercept variance was 0.272, while the residual variance was 0.224. Individual lactation curves showed a high variability relative to the average fitted curve (sd = 0.8) (Fig. 4). The cumulative milk of the total lactation yield was estimated to be 650L (±20) at 280 days in the first lactation.

Estimated lactation curve parameters obtained by fitting the polynomial function to the overall test-day data of the milk production with the different levels of factors of variation considered in this study are summarised in Table 4. Differences between lines of Alpine dairy goats were found to significantly ($P < 0.05$) affect the parameters β_0, β_1, β_2, and β_3 of the fitted lactation curve. The parameter β_0 corresponds to the intercept of the lactation curve, high_LGV goats had a higher initial milk yield than low_LGV goats. An additional analysis of variance on milk peak and persistency showed a significant difference between the two lines. The time of the lactation peak was different for both lines, low_LGV goats showed a later peak time than high_LGV goats (46 vs 38 days). The decline in milk yield after the peak was also different between the two lines, high_LGV goats were significantly ($P < 0.01$) more persistent in later lactation than low_LGV goats. The persistency coefficient measured by the decrease in milk production between the 200 and 300 lactation days, showed a decrease in daily milk yield of 0.010L/day for the low_LGV goats and a decrease of 0.007L/day for high_LGV goats.

The polynomial function was fitted for the parity effect, the shape of the lactation curve was similar for the three first lactations, even though the initial level and the peak of milk production differed markedly between lactations (Fig. 5). When compared with multiparous goats, first parity goats had a significant ($P < 0.01$) lower initial level of production, by about 0.6L when compared with the third parity and about 1L when compared with the second parity. First parity goats had also a later and lower peak yield when compared with later parities, the second parity goats had the highest peak yield, about 3.5L. Differences in the shape of the lactation curve were also found for different years of birth; however, age at the first insemination and litter size had no significant effect. The interaction between line and reproductive success was significant for initial milk yield. The high_LGV pregnant goats

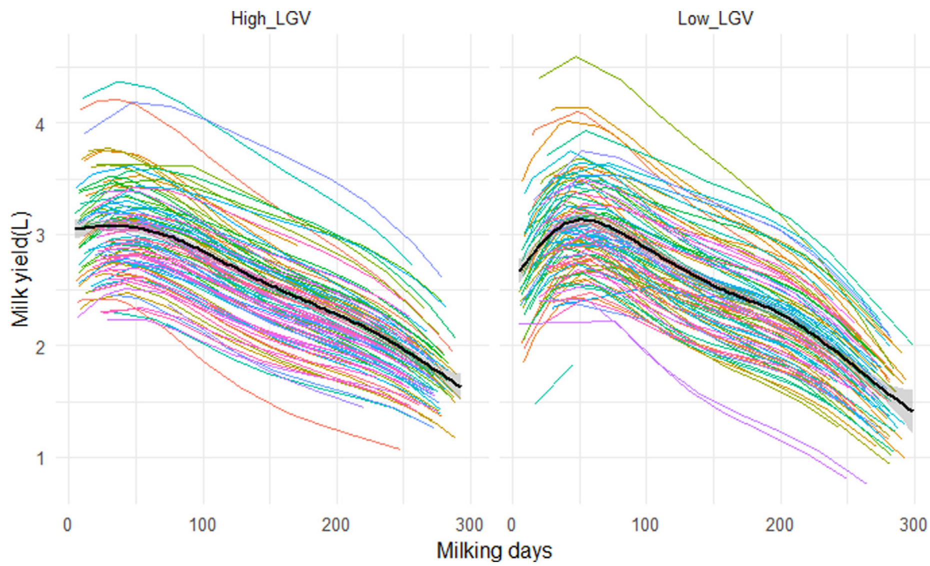

Fig. 4. Individual milk yield trajectories in first lactation of the Alpine goat lines described by the random effects of the polynomial model for the high_LGV and low_LGV line. Black curves refer to the average milk trajectories. Abbreviations: LGV = longevity.

Table 4
Additive effects of line, reproductive success, age at first AI, lactation rank, litter size, and year on lactation curve parameters of the high_LGV and low_LGV Alpine goats' lines, using a polynomial model of degree five.

Item	β_0	β_1	β_2	β_3	β_4	β_5
Intercept	2.221*	4.08×10^{-02}*	-6.82×10^{-04}	4.39×10^{-06}	-1.28×10^{-08}	1.30×10^{-11}
Line (high_LGV)	1.36*	-6.33×10^{-02}*	1.13×10^{-03}*	-8.74×10^{-06}*	3.05×10^{-08}	-3.93×10^{-11}
Age-AI1 (>8 months)	-1.63×10^{-01}	8.09×10^{-03}	-1.43×10^{-04}	1.18×10^{-06}	-4.33×10^{-09}	5.77×10^{-12}
Reproductive success	2.05×10^{-01}	-6.14×10^{-03}	1.01×10^{-04}	-5.86×10^{-07}	1.44×10^{-09}	-9.30×10^{-13}
Litter size (simple)	-2.07×10^{-01}	1.13×10^{-02}	-1.85×10^{-04}	1.21×10^{-06}	-3.49×10^{-09}	3.74×10^{-12}
Parity2	1.104*	-2.68×10^{-02}*	4.05×10^{-04}	-3.16×10^{-06}	-4.33×10^{-08}	-1.53×10^{-11}
Parity3	6.07×10^{-01}*	-3.27×10^{-02}*	4.74×10^{-04}	-2.89×10^{-06}	7.66×10^{-09}	-6.96×10^{-12}
Year_2018	-6.29×10^{-01}*	2.91×10^{-02}*	-4.35×10^{-04}	2.87×10^{-06}	-8.60×10^{-09}	9.75×10^{-12}
Year_2019	-1.99×10^{-01}	4.56×10^{-04}	-5.09×10^{-05}	6.15×10^{-07}	-2.51×10^{-09}	3.71×10^{-12}
Year_2020	1.032*	-8.16×10^{-02}*	1.52×10^{-03}*	-1.18×10^{-05}*	4.15×10^{-08}*	-5.36×10^{-11}*
Line (LGV +): Reproductive success	−1.292*	5.98×10^{-02}*	-1.09×10^{-03}*	8.47×10^{-06}	-2.97×10^{-08}	3.86×10^{-11}

Abbreviations: LGV = longevity; AI = Artificial Insemination.
Intercept: Line (low_LGV), Age-AI1 (<8months), Reproductive failure, Litter size (double), Parity1, Year_2017.
β_0, β_1, β_2, β_3, β_4 and β_5: coefficient of the polynomial model degree five.
* Significant effects of a factor, i.e. a polynomial coefficient significantly different from 0 ($P < 0.05$).

had a significantly ($P < 0.05$) lower initial milk yield than non-pregnant low_LGV goats.

Milk trajectories and responses to nutrition challenge

Line effect on variation in challenge response and recovery profiles

The trajectories of the individual profiles and the average milk yield, milk fat, and milk protein contents through the different periods of the challenge in early lactation are shown in Fig. 6. Average prechallenge values of milk yield, milk protein, and milk fat content were 1.99 (±0.47) L/d, 33.1 g/L, and 35.64 g/L. As shown in Table 5, there were no significant effects of line on the model parameters that characterise individual profiles to the challenge. The two lines showed similar response and recovery slopes in milk yield to the challenge (Fig. 6). The effect of the year on the model parameters was significant, milk response and recovery profiles vary with the year of the challenge (Fig. 6). Line and year of challenge were found to significantly ($P < 0.05$) affect milk protein content response and recovery to the challenge (V2, V3), milk protein content increased more in low_LGV goats than high_LGV goats in response to the challenge. There were no significant effects of line

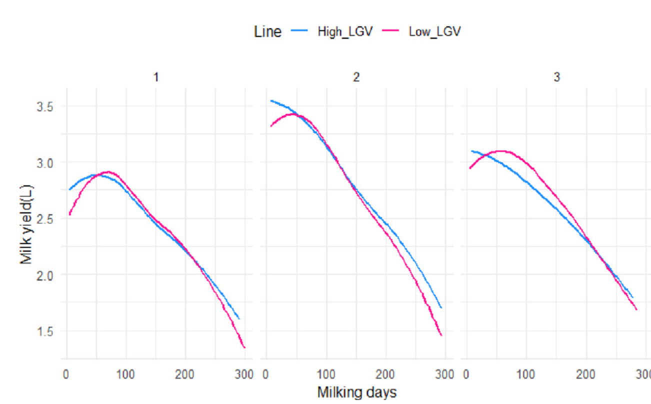

Fig. 5. Average lactation curve of the Alpine goat lines described by the fixed effects of a fifth-order polynomial model (within lactation) for the first three lactation: high_LGV (blue) and low_LGV (pink). Abbreviations: LGV = longevity.

and year of challenge on milk fat content, the challenge response and recovery slopes for milk fat content were similar for the two lines in different challenge years (Fig. 6).

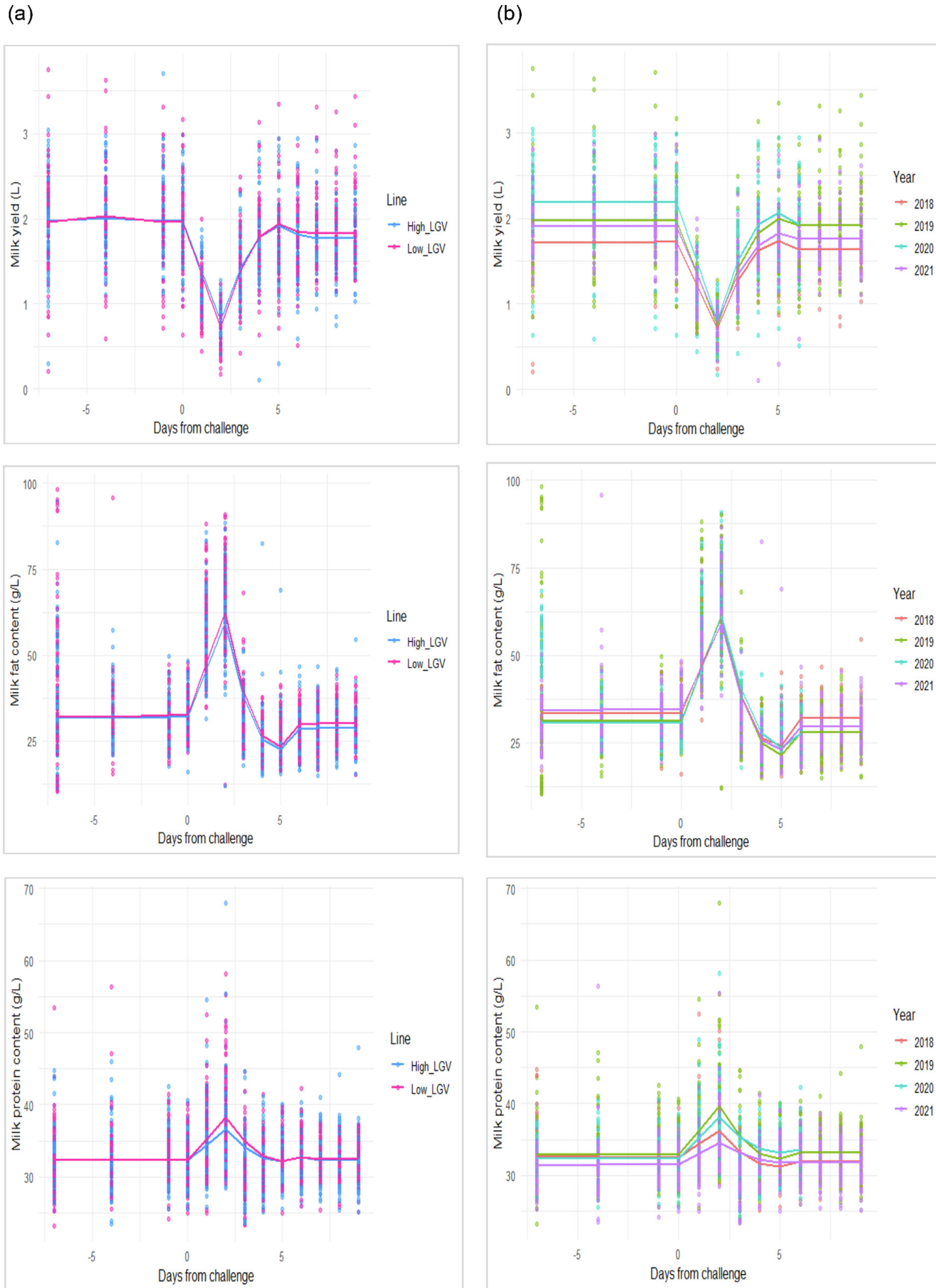

Fig. 6. Response and recovery profiles for milk yield, milk protein and fat content estimated by a piecewise model for (a) high_LGV (blue) and low_LGV (pink) Alpine goat lines and for (b) different challenge years. Abbreviations: LGV = longevity. The postchallenge profile is not completed for the year 2020 because the experiment was stopped early due to the pandemic.

Challenge responses and individual variability in milk trajectories

The correlation between the challenge response coefficients (Table 6) for milk yield and milk contents, and the full lactation curve coefficients sheds light on the relationship between the response of the animal to the challenge relative to the variation in overall milk production and the lactation curve. As expected, the results confirmed the high correlation (0.82) between the initial milk levels from the lactation curve (γ_0) and the milk level before the challenge (V1). It is noteworthy that there is a high negative correlation between the response to the challenge (parameter

Table 5
Additive effects of line and year on the piecewise model estimated parameters of the high_LGV and low_LGV Alpine goats' milk yield.

Item	V1 (prechallenge level, kg)	V2 (linear slope of response during challenge, kg/d)	V3 (linear slope of recovery postchallenge, kg/d)	V4 (quadratic slope of recovery postchallenge, kg/d/d)
Intercept	1.725*	−0.523*	0.704*	−0.115*
Line (high_LGV)	−0.026	0.291	−0.065	−0.065
Year_2019	0.253*	−0.106*	0.106	−0.011
Year_2020	0.480*	−0.199*	0.171*	−0.029*
Year_2021	0.198*	0.050	−0.015	0.007

Abbreviations: LGV = longevity.
Intercept: Line (low_LGV), Year_2018.
V1, V2, V3 and V4 are coefficients of the piecewise model describing response to a short-term nutritional challenge.
* Significant effects of a factor on that piecewise model parameter ($P < 0.05$).

Table 6
Correlations between the lactation curve coefficients and the challenge parameters in the Alpine goats.

	Milk traits								
	Milk yield			Milk fat content			Milk protein content		
Coefficients	γ_0	γ_1	γ_2	γ_0	γ_1	γ_2	γ_0	γ_1	γ_2
V1	0.82	0.37	−0.61	−0.11	−0.35	0.35	−0.27	−0.28	0.33
V2	−0.81	−0.37	0.60	−0.02	0.25	−0.22	0.03	−0.01	0.03
V3	0.79	0.40	−0.64	0.14	−0.03	−0.02	0.21	0.26	−0.33
V4	−0.79	−0.40	0.64	0.15	0.01	0.04	−0.22	−0.27	0.33

γ_0, γ_1, and γ_2: random coefficients of the polynomial model for lactation curves.
V1, V2, V3 and V4: random coefficients of the piecewise model describing response to a short-term nutritional challenge.

V2) and the intercept (γ_0) of the lactation curve ($R = -0.81$), animal responses to the challenge seem to be negatively correlated to their initial milk production. The correlations of the response to the challenge parameter (V2) with the descendant linear phase (γ_1) were highly negative ($R = -0.37$). However, they were highly positive ($R = 0.60$) with the ascendant quadratic phase (γ_2). Correlations with milk fat and protein contents were not significant (Table 6).

Discussion

The purpose of this study was to identify the differences in performance trajectories between two lines of Alpine goats from a commercial population that have been selected for divergent functional longevity. The main idea was to look at the link between the variation in individual performance trajectories and the responses to short-term nutritional perturbation, to improve our understanding of the adaptive capacity of the two lines. Environmental conditions are likely to affect resource availability and compromise the form and extent of the trade-offs that develop in animal populations. Thus, the adaptive capability of the animal, in terms of production and reproduction to overcome the direct and indirect impact of adverse environmental conditions throughout llifetime, may be affected by the selection environment (Joy et al., 2020). Consequently, the trajectories of productive traits are of particular interest, providing an integrated picture of the animal's adaptive capacity and the adaptive responses to environmental change.

In this context, a number of studies of Alpine goat performance have been reported that highlight the potential of the breed. The mean birth weights in this study (4 kg) were higher than those reported by Đuričić et al. (2021) and Gaddour et al. (2012) for Alpine goats (3.46 kg, 3.66 kg). Birth weight of kids is an important indicator of its potential for growth and survival, it had a positive correlation with subsequent weight gain and has been deemed a principal risk factor for kids' viability and survival that is crucial for the profitability of goat farms (Ceyhan et al., 2022). However, no difference in birth weight and litter weight was found between high_LGV and low_LGV kids in this study. Indeed, Ithurbide et al. (2022) found no effect of birth and litter weights on the survival of these animals. BW at the first insemination and kidding were also similar in the different lines.

The estimate of the BW curve parameters of the goats did not show any significant difference between the lines from birth to the first insemination. The mean weight at the first insemination was 32.6 kg (sd = 0.4). However, the effect of the line on BW was significant from the first insemination until early lactation. Low_LGV goats had a greater BW during early gestation but then lost more weight from later gestation into early lactation, compared to high_LGV goats which showed a greater BW after the kidding. It seems that low_LGV goats allocate more to body reserves during the gestation followed by a greater mobilisation of body reserves peripartum. Therefore, safeguarding reproductive function (Friggens, 2003) seems to be a priority for the low_LGV goats, although this did not translate into significant differences in reproductive performance. Despite increased gestation and lactation requirements around the parturition, high_LGV goats maintained an increased growth rate during gestation and lactation. This increase in BW may suggest that high_LGV goats allocate more resources to growth, which may be a factor in them having a greater longevity. Low energy intake in late pregnancy combined with high energy outflow via parturition requirements and milk production is associated with a negative energy balance (Kinoshita et al., 2018). Consequently, more body reserves gain in pregnancy may explain animal strategies to support the nutritional demands peripartum and in early lactation. It seems that low_LGV goats prioritise body reserves mobilisation in late gestation to safeguard reproduction which may suggest that low_LGV goats were better adapted to cope with the expected physiological change around parturition. However, more resource allocation to growth during gestation could suggest that high_LGV use their structural mass to better respond to other life functions under unexpected perturbations.

Several models of lactation curves have been developed as one of the available tools for analysing the performance of dairy animals, mainly because milk production is the most important factor affecting nutritional requirements (Pulina et al., 2005). In the same way, the pattern of milk production is a reference tool that can be used to identify animals with steady production throughout the lactation and those with a substantial decline after a high level of production until the peak (Takma et al., 2009). Thus, better quantification of the lactation curve can be used as a tool for better management and selection. A simple polynomial model was used in this study to characterise the variability in the performance trajectories throughout the lifetime of two lines of Alpine goats that have been selected for divergent functional longevity. This model makes no assumptions about the shape of the lactation curve. Thus, it does not introduce bias into the quantification of the relationship between milk production performance and response to short-term nutritional perturbations.

In the present study, lactations lasted 280d on average, for a cumulate total production of 650L (±20) of milk. Thomas et al. (2021) reported an average milk yield of 719 kg over 250 days for the first lactation in Alpine goats. An average total production of 964.1 kg of milk was also reported (Arnal et al., 2018). First parity goats had a lower initial level of production, later and lower peak yield, when compared with multiparous goats. However, Arnal et al. (2018) and León et al. (2012), reported that primiparous goats have higher persistency, earlier peak, and lower total milk production, compared to multiparous goats.

Our results found that age at the first insemination and the litter size had no effect on the lactation shape and milk production. Rojo-Rubio et al. (2016) demonstrated in their study that litter size had a significant effect on all the parameters of the lactation curve, this effect was attributed to the hormonal effect during pregnancy and to the greater stimuli that more kids exert compared to only one when suckling maternal milk (Salvador and Martínez, 2007). The non-significant effect of littersize shown in our study could be explained by the uniform intensity of udder stimulation when milking goats, which is not the case when more kids suckle the udder. Goats that kidded youngest (9–10 months) were reported to have a lower milk production level but higher persistency (Arnal et al., 2018). In our study, the age of the first insemination ranged from 7 to 10 months which corresponds to the youngest age in the study of Arnal et al. (2018), and that could explain the non-significant effect of the age of the insemination on the lactation curve coefficients. The shape of the lactation curve was not significantly affected by the reproductive status except for the initial milk yield, which was significantly (P < 0.05) lower for concomitantly pregnant high_LGV goats than non-pregnant low_LGV goats. Given that persistency is the degree of maintenance of the milk yield after reaching the maximum daily milk yield (Cobuci et al., 2004), animals with low persistency presented a higher peak of lactation and a steeper curve. High persistency animals that presented a slow rate of decline could be better suited to future efficient production systems (Cole and Null, 2009; Siqueira et al., 2017). Thus, the high_LGV goats showed better milk persistency profiles than low_LGV goats with similar total milk quantities over the lactation. In fact, better milk production in early lactation reflects a good metabolic balance around parturition and suggests that high_LGV goats had a better capacity to acquire resources in early lactation.

BW and milk trajectories taken together tend to suggest a different energy allocation profile for the two goats' lines. The decline on BW in late gestation and early lactation combined with lower initial milk production and the later lactation peak may suggest that low_LGV goats gain more body reserve in pregnancy to safeguard future reproduction. It seems that low_LGV goats were more adapted to allocate resources to anticipate their expected physiological change after the conception. The increase in growth rate which suggests a greater allocation of resources to more structural mass, with better persistency at the end of lactation could be considered as an indicator of greater longevity of high_LGV goats and maybe a better response to unexpected environmental change. Furthermore, the high_LGV line was found to have better survival after the first kidding, whereas both lines had the same survival during the first 15 months (Ithurbide et al., 2022).

Friggens (2003) reported that mammals evolved the strategy of the priority to safeguarding reproductive investment by the accumulation of body lipid reserves in pregnancy. Acquisition capacity and allocation pattern, reflecting the priorities of the females throughout life, are expected to be modified by their genetic potential (Arnau-Bonachera et al., 2018). Thus, animals that anticipate their physiological change after conception and allocate more to safeguard reproduction may decrease their ability to safeguard life functions such as growth, which gives them a better structural mass for reacting to unforeseen perturbations.

The differences observed between the two lines in milk and BW trajectories lead to the hypothesis of a difference in acquisition and allocation strategy between high and low longevity goats. In the sense of determining the difference between the two lines in terms of resource allocation, the study of the response of the two lines to a nutritional challenge was an asset. The piecewise mixed model was performed to characterise individual profiles during prechallenge, the challenge, and postchallenge periods.

Relative to the prechallenge period, the nutritional challenge resulted in a reduction in milk yield and an increase in the milk fat and protein content. The recovery from the challenge was proportional to the response slope from the challenge. The nutritional challenge occurred in early lactation, and the average response and the recovery profiles of milk yield and milk fat content were quite similar for both lines during the different challenge years but line was found to significantly (P < 0.05) affect milk protein content response and recovery to the challenge. In a similar study, Huau et al. (2020) reported significant differences in beta-hydroxybutyrate response profiles following a nutritional challenge in early lactation between the two lines suggesting a greater dependence on body reserves and metabolic stress in low_LGV goats at the end of gestation and a strong mobilisation of body reserves for high_LGV goats following the nutritional challenge. Although no significant line differences were found in milk yield response and recovery slopes, the correlation between the indicator parameters of the lactation curve and those of the challenge showed a positive correlation between the response to the challenge and the ascending phase (γ_2) of the lactation curve. The level of milk production in early lactation (γ_0) was negatively correlated to the slope of the response to the challenge. Hence, the response to the challenge was negatively correlated with the decline of milk level after the lactation peak (γ_1). Accordingly, milk persistency and initial yield were strongly correlated with the slope of the response to the challenge. This finding indicates that milk yield and milk component responses to the challenge could be in part predictable from prechallenge levels. Friggens et al. (2016) also found that the size of the response to an externally applied challenge is related to the initial level of animal performance. Individual performance patterns through lifetime and in the short term were relevant to show the variability in the population in allocation during normal conditions and in response to perturbation. This has been found in other studies, in cattle, pigs, and poultry (Nguyen-Ba et al., 2020; Poppe et al., 2021).

If it seems necessary to select lines to improve functional longevity, it should also be important to preserve the diversity of the population where each animal has its particular strategy for allocation and survival. Individual heterogeneity in adaptive capacity and trade-offs has been shown to be important for system or population-level resilience (Nussey et al., 2007), and this will be increasingly important in agro-ecological livestock systems (Ducos et al., 2021). The findings of the present study, taken together, suggest that there are differences in adaptive capacity between the high longevity and low longevity goats. However, measures of feed intake would be needed to confirm this difference between acquisition and allocation mechanisms.

Conclusion

This study showed that goats selected for low longevity allocate more resources to body reserves during pregnancy to safeguard reproduction. However, high longevity goats allocate more resources to structural mass and had greater milk production persistency in late lactation. This finding supports the idea that high-functional longevity goats were better adapted to respond to unexpected perturbations. Although there were no significant differences between the lines in response to short-term nutritional challenge in early lactation, response-recovery profiles were correlated to some aspects of the goats' lifetime performance trajectories.

Supplementary material

Supplementary material to this article can be found online at https://doi.org/10.1016/j.animal.2023.101004.

Ethics approval

All the experimental procedures followed the French legislation on animal experimentation and the European Convention for the Protection of Vertebrates Used for Experimental and Other Scientific Purposes with experimental approval number APAFIS#8613-2017012013585646.

Data and model availability statement

None of the data was deposited in an official repository. The data sets that support the findings of this study are available from the corresponding author upon request.

Declaration of Generative AI and AI-assisted technologies in the writing process

The authors did not use any artificial intelligence-assisted technologies in the writing process.

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Declaration of interest

The authors declare that there is no conflict of interest in this study.

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