

SMARTER

SMAll RuminanTs breeding for Efficiency and Resilience

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G×E interaction for the resource use efficiency related phenotypes

Georgios Arsenos^{1*}, Sotiria Vouraki¹, Stergios Priskas¹, Angeliki Argyriadou¹, Vasileia Fotiadou¹, Rachel Rupp², Gilles Lagriffoul³, Jean-Michel Astruc³, Flavie Tortereau², Dominique Hazard², Christel Marie-Etancelin², Lawal Agboola², Marjorie Chassier³, Apolline Bailly-Salins⁴

¹AUTH

²INRAE

³IDELE

⁴Capgènes

* Deliverable leader – Contact: arsenosg@vet.auth.gr

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About the SMARTER research project

SMARTER will develop and deploy innovative strategies to improve Resilience and Efficiency (R&E) related traits in sheep and goats. SMARTER will find these strategies by: i) generating and validating novel R&E related traits at a phenotypic and genetic level ii) improving and developing new genome-based solutions and tools relevant to the data structure and size of small ruminant populations, iii) establishing new breeding and selection strategies for various breeds and environments that consider R&E traits.

SMARTER, with help from stakeholders, chose several key R&E traits, including feed efficiency, health (resistance to disease, survival) and welfare. Experimental populations will be used to identify and dissect new predictors of these R&E traits and the trade-off between animal ability to overcome external challenges. SMARTER will estimate the underlying genetic and genomic variability governing these R&E related traits. This variability will be related to performance in different environments, including genotype-by-environment interactions (conventional, agro-ecological and organic systems) in commercial populations. The outcome will be accurate genomic predictions for R&E traits in different environments across different breeds and populations. SMARTER will also create a new cooperative European and international initiative that will use genomic selection across countries. This initiative will make selection for R&E traits faster and more efficient. SMARTER will also characterize the phenotype and genome of traditional and underutilized breeds. Finally, SMARTER will propose new breeding strategies that utilise R&E traits and trade-offs and balance economic, social and environmental challenges.

The overall impact of the multi-actor SMARTER project will be ready-to-use effective and efficient tools to make small ruminant production resilient through improved profitability and efficiency.

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1 Summary

Selection for improved feed efficiency of small ruminants is an important breeding objective towards increasing the sustainability of the sector. Feed efficiency proxies, which are easy to measure, have been identified in Task 1.1 of the SMARTER project. However, future breeding strategies for such traits should take into account potential genotype by environment (G×E) interactions that may exist due to the diversity of small ruminant production systems. Therefore, the objective of Deliverable 1.4 (Task 1.4) was to investigate G×E interactions for feed efficiency phenotypes (identified in Task 1.1) in sheep and goats. These include (i) milk yield and composition of Lacaune dairy sheep reared intensively in Greece vs semi-extensively in France (AUTH, INRAE & IDELE), (ii) body weights and growth traits at different ages of Romane meat lambs reared under intensive vs extensive conditions (INRAE), (iii) feed intake and residual feed intake (RFI) of Romane meat lambs fed with a concentrate diet vs a forage-based diet (INRAE), and (iv) residual energy intake (REI) of Alpine and Saanen dairy goats reared under intensive vs extensive conditions (IDELE, INRAE & Capgènes).

Regarding the Lacaune sheep study, a total of 2,000 ewes from four intensive farms in Northern Greece and 4,859 ewes from 186 semi-extensive farms in Southern France that were daughters or granddaughters of the same rams were used. Milk yield and composition records (n=1,658) in Greece were collected within the framework of SMARTER project, whereas respective records (n=7,166) in France were extracted from the existing national genetic database. In the case of Romane meat sheep, the first study included a total of 8,619 lambs (born from 79 common rams) that were reared in two experimental farms following different farming systems (intensive and extensive); background data for lamb body weights and growth traits were assessed. The second study included 332 Romane male lambs from two divergent lines on RFI (RFI- and RFI+) that were phenotyped partly within SMARTER for feed intake and RFI under both concentrate and forage-based diets. Finally, in the study of dairy goats, 977 Alpine and 1,211 Saanen primiparous goats from 14 commercial and one experimental farm were used; REI records (n=4,461 and 3,119 for Alpine and Saanen, respectively) were collected within SMARTER. Genetic parameters, including genetic correlations between the studied traits under different environmental conditions, were estimated with univariate and bivariate analyses.

Results suggested (i) no G×E interactions for milk yield and protein content and some degree of interaction for fat content of Lacaune ewes reared in Greece and France, (ii) no G×E interactions for birth weight of Romane lambs reared under intensive and extensive conditions (further research is needed to provide reliable results for the rest of the traits), (iii) significant differences for feed intake and RFI between the RFI- and RFI+ Romane lambs (RFI- lambs ate less concentrate and forage and were more efficient than RFI+ lambs) indicating no evidence of important G×E between genetic line and diet, and (iv) possible G×E interactions for REI of Alpine and Saanen dairy goats reared in intensive and extensive farming systems.

2 Introduction

Improving feed efficiency of small ruminants is a desirable breeding goal to maximize farm profitability, increase productivity and reduce environmental impact. Genetic selection for feed efficiency traits using and combining data from animals reared under different conditions (countries, environments and/or farming systems) could increase progress and benefit breeding programmes. Specifically, such an approach would increase the number of selected candidates, thus resulting in a higher selection intensity (Banos and Smith, 1991; Fitzmaurice et al., 2021).

However, small ruminant farming is characterised by great diversity in terms of aims, farming systems and resources. Farming systems vary from fully extensive to intensive ones, characterised by different management and feeding practices. Moreover, available feed resources, their quality and climatic conditions vary by geographical region (Arsenos et al., 2021). Therefore, to implement successful breeding programmes towards increasing feed efficiency, it is important to investigate whether differences in selection responses could be expected depending on animal rearing and environmental conditions (Berry and Crowley, 2013). The latter is defined as genotype by environment (G×E) interactions.

Several studies have investigated G×E interactions for residual feed intake in dairy and beef cattle (Durunna et al., 2011; Yao et al., 2017; Kenny et al., 2018; Puilet et al., 2021). Most of these studies suggested some extent of G×E, and therefore, that sire re-ranking might be expected. However, relevant literature in small ruminants is scarce. Moreover, G×E interactions for other traits that could be used as proxies of feed efficiency have not been investigated.

Taking into consideration the issues above, part of the H2020-SMARTER project was to study the feasibility of genetic evaluation and selection for feed efficiency indicators in sheep and goats reared under different conditions. Specifically, the objective of this deliverable was to investigate G×E interactions for feed efficiency proxies that were identified in Task 1.1; such proxies include milk yield and composition, body weight, and feed intake. In this regard, new and existing datasets from AUTH, INRAE, Capgènes and IDELE were used. Specifically, in the present report, the following case studies are presented:

- Lacaune dairy sheep reared in Greece and France – AUTH (new data), INRAE & IDELE (background data)
- Romane meat sheep – INRAE
 - extensive vs intensive (background data)
 - concentrate vs hay (new data)
- Alpine and Saanen dairy goats: extensive vs intensive – IDELE, INRAE & Capgènes (new data)

3 Lacaune dairy sheep reared in Greece and France – AUTH, INRAE & IDELE

The objective of this study was to investigate the feasibility of genetic evaluation and selection for feed efficiency indicators, namely milk yield and composition (identified in Task 1.1) in purebred Lacaune sheep reared intensively in Greece and semi-extensively in France.

3.1 Materials and methods

3.1.1 Animals and farms

A total of 2,000 Lacaune ewes from four intensive farms in Northern Greece and 4,859 Lacaune ewes from 186 semi-extensive farms in Southern France were selected for the study (Figure 1).

Selected ewes in Greece were all born after artificial insemination using semen of imported Lacaune rams (n=14) from France. During the study period, they were in their first or second parity and were fed a total mixed ratio consisting of alfalfa silage, alfalfa hay and high level of concentrates. Following quality control of recorded data (as described in section 3.1.2), 1,658 ewes were included in the study. Selected ewes in France were genetically related to those in Greece through 6 common sires and 11 common grandsires and were in their first to seventh parity during the study period. All studied French farms reared at least five ewes genetically related to ewes in Greece. The French data were extracted from the national genetic database where they were stored for genetic evaluation purposes; they were not collected specifically in SMARTER.

Overall, a total of 6,517 ewes from Greece and France that were daughters or granddaughters of the same rams were used in the study. A combined pedigree file was created for the Greek and French populations. This file included 26,547 animals, 2,738 sires and 17,361 dams.

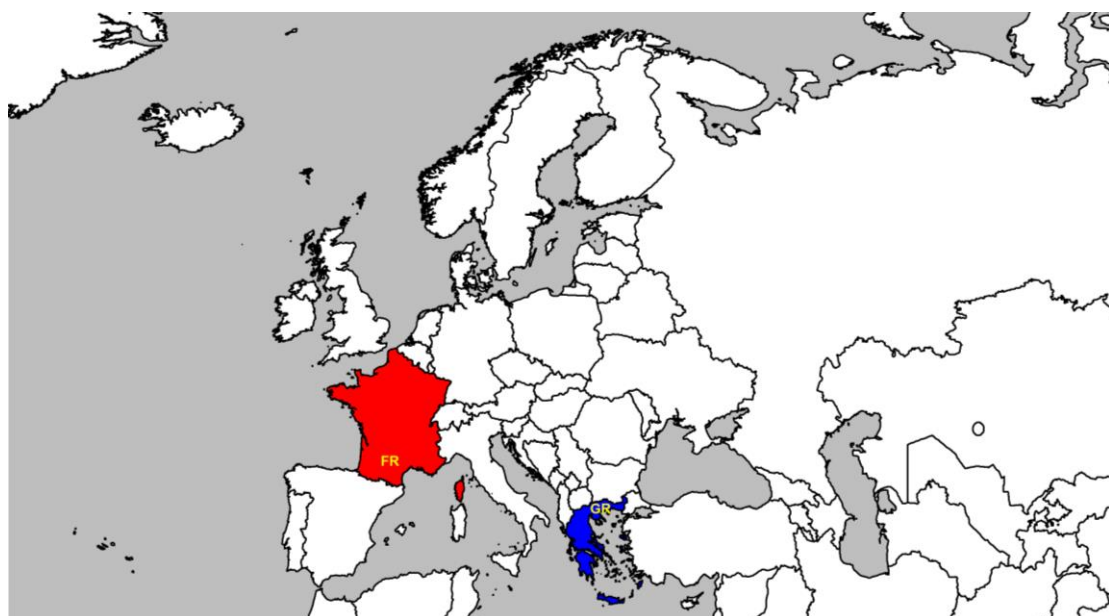


Figure 1. Map illustrating the regions in Greece and France where the studied farms were located.

3.1.2 Phenotypic data collection and editing

In Greece, individual animal recording was performed during the milking periods of years 2021 and 2022; 548 and 1,452 ewes were monitored during 2021 and 2022, respectively. Monitoring of each animal started after lamb weaning (approximately 35 days post-partum) and lasted for five months. Specifically, individual ewe milk yield was recorded monthly (5 records per animal) with volumetric milk meters (Figure 2). Moreover, milk samples (3 monthly samples per animal in early lactation) were collected in 50 ml tubes to assess chemical composition; fat, protein, lactose, and solids-non-fat (SNF) content. Milk samples were transported to the laboratory at 4° C, and milk composition was determined with Near Infrared Spectroscopy using a DA 7250 NIR analyser (PerkinElmer, Waltham, Massachusetts, USA).

Individual animal daily milk yield was calculated according to the official A4 method of the International Committee of Animal Recording (ICAR, 2016). Then, the total milk yield in the milking period was calculated using the Fleishmann method of ICAR (ICAR, 2016). A minimum of three valid monthly records (>0.2 kg of milk) for each ewe was required to calculate milk yield per milking period reducing the number of ewes included in the study to 1,658. The respective milk components content was estimated as the arithmetic mean of individual monthly records weighted for milk yield. A total of 1,658 milking period records were obtained. Then, quality control of milk composition records was implemented based on biological limits set for each trait. These limits set 120, 92, 43, and 90 records of fat, protein, lactose, and SNF content, respectively, as missing values.



Figure 2. Milk yield recording of Lacaune dairy ewes in Greece.

In France, a total of 7,166 milking period records corresponding to years 2019, 2020, 2021, and 2022 from 1,670, 1,521, 1,900, and 499 ewes, respectively were obtained from the national genetic database (CTIG, Centre de Traitement de l'Information Génétique, Paris). Specifically, records included milking period milk yield, fat content and protein content, which were calculated from individual animal monthly records (five and three records for milk yield and milk components content, respectively), as described in the case of Greece.

Based on the above, the combined dataset from the two countries included 8,822 milking period records. Moreover, additional data were available regarding age at lambing, length of milking period, and days from lambing to first sampling in both countries; number of lambs born from each ewe was also available in France. Finally, the combination of monthly records used to calculate the average content of milk components for each milking period was defined.

Characteristics of the final datasets from Greece and France and relationship of studied phenotypes with other variables are presented in Table 1 and Appendix Figures S1-S12, respectively).

Table 1. Characteristics of datasets from Greece and France.

Characteristic	Greece	France
Study period	2021-2022	2019-2022
Number of ewes	1,658	4,859
Number of records	1,658	7,166
Type of records	Single	Multiple
Number of first parity records	858	4,047
Number of second parity records	800	2,564
Number of third and above parity records	0	555
Milking period length in days (SD)	168.7 (17.72)	168.8 (38.94)
Age at lambing in months (SD)	20.4 (6.00)	20.5 (10.65)
Days from lambing to first sampling (SD)	34.2 (6.66)	51.5 (11.82)

3.1.3 Collection of climatic data

Mean temperature and relative humidity during the studied milking period(s) were collected from the database of the NASA Power Project. These traits were used to define mean temperature-humidity index (THI) according to the following formula described by Finocchiaro et al. (2005):

$$THI_m = T_m - [0.55 \times \left(1 - \frac{RH_m}{100}\right)] \times (T_m - 14.4)$$

where:

THI_m = mean daily temperature-humidity index;

T_m = mean daily temperature ($^{\circ}$ C);

RH_m = mean daily relative humidity (%).

3.1.4 Data analysis

Combined data from Greece and France were considered in a series of statistical analyses. Descriptive statistics of studied phenotypes and climatic data were performed using R statistical package “psych”. Mixed linear models were used to identify environmental factors with significant effects on the studied traits with R statistical package “lme4” (Bates et al., 2015). Specifically, the effects of farm, year, parity, age at lambing, number of lambs born, milking period length, days from lambing to first sampling, and combination of monthly records used to calculate the weighted average of milk components content were tested.

(Co)variance components of milk production traits were estimated in a series of univariate and bivariate analysis using the ASReml software version 4.2 (Gilmour et al., 2021; Gilmour and Thompson, 2021). The following model was used to analyse milk yield within-country:

$$Y_{ijklm} = \mu + F_i + Y_j + P_k + b1 * M + b2 * A + b3 * D + L_l + A_m + e_{ijklm}$$

Where:

Y_{ijklm} = milk yield of animal m;

μ = overall population mean;

F_i = fixed effect of farm (4 levels in Greece and 186 levels in France);

Y_j = fixed effect of year (2 levels in Greece and 4 levels in France);

P_k = fixed effect of parity (2 levels in Greece and 7 levels in France);

b_1 = regression coefficient on milking period length M (days);

b_2 = regression coefficient on age at kidding A (months);

b_3 = regression coefficient on days from lambing to first sampling (days);

L_i = fixed effect of number of lambs born (2 levels);

A_m = random additive genetic effect of animal m ;

e_{ijklm} = random residual effect

In the case of France, the random permanent environmental effect was also fitted in the above model to account for repeated records. For within-country analysis of milk components content, the same model was used after including the fixed effect of the combination of monthly records used to calculate the weighted average of the milking period (11 levels). Bivariate analyses were also implemented using the above model with an additional fixed effect of country.

Trait heritability, repeatability and genetic correlations were calculated based on the corresponding variance and covariance values after convergence.

Estimated breeding values (EBVs) of common sires and grandsires were derived from within-country analyses of traits, and their reliability was calculated using the following formula proposed by Jamrozic et al. (2000):

$$Rel = 1 - \frac{PEV}{\sigma_A^2}$$

Where:

PEV = prediction error variance of EBV;

σ_A^2 = additive genetic variance of the trait.

Pairwise correlations between EBVs for the studied traits were subsequently calculated. These correlations were adjusted for reliability according to the method of Calo (Calo et al., 1973) to derive an approximate estimate of the genetic correlation between traits in the two countries as described below:

$$r_g = \frac{\sqrt{\sum_{i=1}^n \rho_{i,EBV} \times \sum_{i=1}^n \rho_{i,EBV}'}}{\sum_{i=1}^n \rho_{i,EBV} \times \rho_{i,EBV}'} \times r_{EBV,EBV}'$$

Where:

r_g = approximate genetic correlation between two traits;

$\rho_{i,EBV}$ = the reliability of the EBV for one trait;

$\rho_{i,EBV}'$ = the reliability of the EBV for the other trait;

$r_{EBV,EBV'}$ = Pearson correlation between the EBVs for the two traits.

Standard error for the above approximate genetic correlations was calculated using the following formula proposed by Onyiro et al. (2018):

$$SE = \sqrt{\frac{1 - r_g^2}{n - 2}}$$

Where:

SE = standard error of approximate genetic correlation between two traits;

r_g = approximate genetic correlation between two traits;

n = number of common sires and grandsires with records.

3.2 Results

3.2.1 Descriptive statistics

Descriptive statistics of the studied phenotypes and climatic data in Greece and France are presented in Tables 2 and 3, respectively. Mean milk yield and fat content were similar between the two countries, whereas protein content was higher in France. Mean lactose and SNF content that were only available in Greece were 5.08% and 12.09%, respectively (Table 2). Differences were reported between the two countries regarding climatic parameters during the studied milking periods. Specifically, mean temperature and THI were higher and relative humidity was lower in Greece compared to France (Table 3).

Table 2. Descriptive statistics of milk production traits per country.

Phenotype	Country	N	Mean	SD	Min	Max
Milk yield (kg/animal/milking period)	Greece	1,658	362.58	149.62	37.9	865.66
	France	7,164	329.96	98.48	13.6	836.00
Fat content (%)	Greece	1,538	6.16	0.81	3.93	9.37
	France	7,145	6.77	0.92	2.87	10.00
Protein content (%)	Greece	1,566	4.48	0.48	2.94	6.54
	France	7,166	5.52	0.52	3.97	8.04
Lactose content (%)	Greece	1,615	5.08	0.20	3.19	6.65
SNF content (%)	Greece	1,568	12.09	0.60	10.09	14.73

SNF = solids-non-fat; SD = standard deviation.

Table 3. Descriptive statistics of climatic parameters during the studied milking periods per country.

Trait	Country	N	Mean	SD	Min	Max
Mean temperature (° C)	Greece	1658	14.35	4.51	0.51	20.53
	France	7166	9.32	3.55	0.56	24.96
Relative humidity (%)	Greece	1658	63.67	5.99	54.47	78.40
	France	7166	79.85	6.67	47.23	93.38

THI	Greece	1658	14.21	3.70	2.16	19.00
	France	7166	9.77	3.21	1.22	22.08

THI = temperature-humidity index.

3.2.2 Genetic parameters

Estimates of heritability for the studied phenotypes and genetic correlations between traits in the two countries are presented in Table 4; repeatability estimates of the traits in France are also reported. Statistically significant ($P < 0.05$) similar heritability estimates were reported for milk yield and fat content in Greece and France. Heritability of protein content was higher in France compared to Greece; a low borderline significant estimate was found. Significant low heritability estimates were reported for lactose and SNF contents in Greece.

Bivariate analyses of studied traits from the two countries produced high standard errors, which could be potentially attributed to the limited links between the animals reared in Greece and France. Therefore, the approximate genetic correlations derived based on the correlation between EBVs of common sires and grandsires according to Calo et al. (1973), are presented. Results showed a strong genetic correlation for milk yield and protein content and a relatively high correlation for fat content between animals raised in the two countries, suggesting no and limited G×E interactions, respectively.

Table 4. Heritability (h^2), repeatability [®] and genetic correlations between studied phenotypes in Greece and France with respective standard errors in parenthesis.

Trait	Country	h^2	r	Genetic correlations
Milk yield (kg/animal/milking period)	Greece	0.19 (0.09)*		0.86 (0.13)*
	France	0.24 (0.05)*	0.41 (0.02)*	
Fat content (%)	Greece	0.30 (0.13)*		0.59 (0.21)*
	France	0.34 (0.05)*	0.40 (0.02)*	
Protein content (%)	Greece	0.19 (0.10)		0.88 (0.12)*
	France	0.52 (0.02)*	0.52 (0.02)*	
Lactose content (%)	Greece	0.10 (0.05)*		
SNF content (%)	Greece	0.14 (0.07)*		

*Indicates statistically significant estimates ($P < 0.05$); SNF = solids-non-fat.

3.3 Conclusions

In the present study, the feasibility of genetic evaluation and selection for feed efficiency indicators, namely milk yield and composition in purebred Lacaune sheep reared intensively in Greece and semi-extensively in France, was evaluated. Genetic correlations for the studied traits between animals raised in the two countries indicate no evidence of G×E interactions for milk yield and protein content. In the case of fat content in which a moderate genetic correlation was detected, some degree of sire re-ranking could be expected. Overall, results suggest that a joint genetic evaluation of Lacaune sheep in Greece and France is feasible. Breeding strategies should be tailored to the needs and conditions in each country subject to accurate and systematic recording of phenotypes of individual animals to improve feed efficiency.

4 Romane meat sheep: extensive vs intensive and concentrate vs hay - INRAE

Two studies have been conducted on interactions between genetics and environment. In the first study, two connected experimental INRAE flocks were analysed, and the environment was defined at the farming system level. The second study involved two divergent lines selected on Residual Feed Intake in the Romane breed.

4.1 Materials and methods

4.1.1 Animals and farms – Study 1

Two INRAE experimental farms manage a Romane flock. One experimental farm is located in Bourges (centre of France), and the other one is located in La Fage, in the Roquefort area (Figure 3).



Figure 3. Location of the two INRAE experimental farms with Romane flocks.

Both farms manage the Romane flocks with different farming systems. In Bourges, the system can be qualified as more intensive, with indoor periods. In La Fage, animals are bred outdoors 365 days a year and fed on rangelands.

Common Romane rams have been used in both experimental farms. For this study, a total of 8,619 Romane lambs born from 79 sires were analysed.

4.1.2 Phenotypes – Study 1

The analyses focus on suckling lambs (lambs fed artificially were retrieved from the dataset). Lambs are weighed on a regular basis from birth to slaughter. Because of the group management, body weights on a given day correspond to different ages for the lambs. Therefore, body weights at given ages were calculated from true body weights. Growth (Average daily gains; ADG) were calculated from these body weights.

A total of 16 traits were analysed: 3 observed body weights (birth weight, weaning weight and slaughter weight), 6 calculated body weights at different days of age (P15, P30, P60, P90, P120 and P150), and 7 growth traits (ADG between birth and 30 days of age, between 30 and 60 days of age, between 90 and 120 days of age, between 120 and 150 days of age, between birth and weaning and between weaning and slaughter).

4.1.3 Data analyses – Study 1

After descriptive statistics, genetic analyses were performed for all traits. Early-life traits are usually analysed with complex genetic models, including direct and maternal genetic effects. These more complex models require large datasets with dams phenotyped as lambs to reach significant results.

Descriptive statistics were performed considering all the datasets and within each dataset. The significance of fixed effects was assessed, particularly for the farm effect.

Genetic analyses were performed considering the common dataset. All genetic analyses were performed using the ASReml software version 4.2 (Gilmour et al., 2021; Gilmour and Thompson, 2021). First, univariate analyses were performed within each farm in order to check whether maternal effects (genetic and permanent environment) were significantly different from zero. Results from univariate models were used to define which random effects had to be considered in bivariate analyses.

Then, bivariate analyses were performed, considering one trait but defining it as two different traits depending on the farm. Genetic correlations were estimated between the two farms for the analysed traits.

4.1.4 Animals and farms – Study 2

A total of 332 Romane males belonging to two divergent lines selected on residual feed intake were considered in the analyses.

Briefly, the divergent selection started in 2014, and animals involved in this study were born from 2019 to 2022 and belonged to 3rd and 4th generation of selection. Animals belonging to the efficient line or less efficient line are referred as RFI- and RFI+, respectively.

Each year, around 100 male lambs born from planned matings are controlled from 90 to 140 days of age under a concentrate diet (as presented in (Tortereau et al., 2020)). During a 6-weeks period of control, lambs are weighed at the beginning and at the end of the control period, and ultrasounds are performed at the end of the control to measure backfat thickness (BFT-US) and muscle depth (MD-US). During all the control periods, concentrate intake is recorded through automatic concentrate feeders (ACF). Male lambs are then controlled under a total mixed diet (2/3 forage + 1/3 concentrate), with similar phenotypes being recorded: feed intake, body weights, and body composition traits (BFT and MD at the end of the control period). Because fewer individuals can access automatic forage feeders (AFF) than ACF (Weisbecker et al., 2020), male lambs were split into two groups for this control under a total mixed diet. The first group was tested during 6 weeks from 5 to 7 months old, and the second group was tested during 6 other weeks, from 7 to 9 months old.

Under a concentrate diet, the individual RFI was estimated as the residual of the multiple linear regression of ADFI on ADG, E-BFT, and E-MD to account for production requirements and on the metabolic BW at the end of the test ((E-W)0.75) to account for maintenance requirements (proc reg; SAS Institute Inc., Cary, NC, USA). The year was added as a fixed effect, and the feed conversion ratio (FCR) was calculated as the ratio ADFI/ADG. Under a forage diet, the individual RFI was estimated with a similar model, including an additional fixed effect of the control period within each year.

Among the 332 studied animals phenotyped under a concentrate diet, 255 were also phenotyped under the forage-based diet.

4.1.5 Phenotypes – Study 2

Traits analysed in this second study are traits recorded under both diets: Daily feed intake (g/d) and residual feed intake (g/d). Under the forage diet, concentrate and forage were provided separately, so intakes are calculated separately. Water intake was also available.

4.1.6 Data analyses – Study 2

In order to identify potential interactions between the genetic line and the diet, we estimated the line effect for all studied traits thanks to a linear model accounting for the year, series of control, and line effect. A phenotypic correlation was also estimated between concentrate intake recorded in the first period and forage intake recorded in the second period.

4.2 Results

4.2.1 Study 1

4.2.1.1 Descriptive statistics

Descriptive statistics are given in Table 5. All traits are significantly different between both farms. Lambs born in UEP3R are heavier than lambs born in La Fage, whatever the age at weighing. Similarly, their growth is higher than the growth of lambs born in La Fage.

Table 5. Summary statistics for the traits recorded in lambs reared in extensive (Ext) or intensive (Int) farms.

Traits ¹	n		Mean		SD		Min ²		Max ²		LS Means ²		Farm effect ⁴
	Ext ³	Int ³	Ext	Int	Ext	Int	Ext	Int	Ext	Int	Ext	Int	
BW (hg)	5171	3435	385.51	422.75	91.39	86.11	90.00	100.00	700.00	821.90	357	372	***
WW (hg)	4183	2881	2123.02	2368.99	472.43	525.46	610.00	770.00	3920.00	5280.00	1951	2550	***
SWT (hg)	987	1052	3986.83	3929.66	250.44	440.66	2710.00	2110.00	5010.00	6260.00	3563	3713	***
P15 (hg)	4387	3117	745.16	808.07	162.78	153.27	40.00	336.60	1739.62	1675.95	756	770	***
P30 (hg)	4319	3068	1109.86	1187.06	238.71	242.72	289.74	423.33	1921.54	2218.27	1089	1123	***
P60 (hg)	4222	2990	1750.88	2180.39	358.25	407.72	544.71	717.14	3000.19	3758.55	1667	2069	***
P90 (hg)	4114	2349	2335.34	3212.72	477.89	483.74	706.89	702.29	6579.71	4842.13	2263	3141	***
P120 (hg)	3750	2344	3072.39	3984.00	653.86	555.99	1016.39	650.18	5930.00	5899.79	3210	3524	***
P150 (hg)	2918	1093	3438.21	4655.65	682.60	881.36	1169.64	2425.29	5450.00	8063.00	3626	4045	***
G0_30 (g/d)	4319	3068	237.66	252.55	64.53	65.37	7.80	1.62	451.79	557.29	226	237	***
G30_60 (g/d)	4222	2990	211.31	330.04	56.31	69.94	21.26	42.58	470.59	567.74	196	319	***
G60_90 (g/d)	4059	2310	193.48	317.81	68.70	65.27	1.83	19.70	472.70	570.56	206	326	***
G90_120 (g/d)	3706	1767	243.93	282.69	106.78	78.80	2.58	6.70	715.94	488.30	200	320	***
G120_150 (g/d)	2751	897	205.57	269.30	116.36	111.77	0.39	1.94	684.52	875.13	231	249	***
G_suck (g/d)	4168	2877	214.62	296.52	50.58	62.16	30.95	62.22	656.50	529.78	205	293	***
G_fat (g/d)	1020	994	321.93	326.92	80.54	75.25	96.02	23.08	550.00	632.67	323	289	***

¹BW= birth weight; WW= weaning weight; SWT= slaughter weight; P15, P30, P60, P90, P120, P150 = body weights at 15, 30, 60, 90, 120, 150 days of age, respectively; G0_30, G30_60, G60_90, G90_120, G120_150, G_suck, G_fat = average daily gain

between birth and 30 days of age, between 30 and 60 days of age, between 90 and 120 days of age, between 120 and 150 days of age, between birth and weaning and between weaning and slaughter, respectively; ² Min, minimum; Max, maximum; LS Means, least squares means; ³ Ext.: extensive farming conditions; Int.: intensive farming conditions; ⁴ *: $p < 0.05$; NS: non-significant.

4.2.1.2 Univariate genetic analyses

Results of univariate analyses performed within each farm are presented in Table 6.

Direct heritabilities were always significantly different from zero except for slaughter weight of lambs born in La Fage. Maternal genetic effects and the permanent environmental effect of the dam were not different from zero for many traits. Therefore, bivariate analyses will often include only direct genetic effects.

Table 6. Estimates of direct and maternal heritabilities and permanent effect of the dam on body weights and growth traits.

Trait	Farm	Animal (h^2) ²	Maternal genetic (m^2) ²	Dam env. (c^2) ²	Total variance
BW	Sap	0.22 (0.05)	0.1 (0.04)	0.2 (0.04)	5205.8 (158.52)
	Laf	0.17 (0.04)	0.16 (0.03)	0.1 (0.02)	5803.9 (156.34)
WW	Sap	0.13 (0.05)	0.09 (0.04)	0.15 (0.04)	103510 (3105.7)
	Laf	0.18 (0.04)	0.04 (0.03)	0.14 (0.02)	93338 (2467.8)
SWT	Sap	0.09 (0.06)	0 (0)	0.04 (0.06)	77407 (3520.6)
	Laf	0.02 (0.04)	0 (0)	0 (0)	43292 (1968.7)
P15	Sap	0.07 (0.03)	0.09 (0.04)	0.19 (0.04)	6099.5 (171.8)
	Laf	0.2 (0.04)	0.06 (0.03)	0.07 (0.02)	7555.8 (199.98)
P30	Sap	0.08 (0.03)	0.09 (0.04)	0.19 (0.04)	23019 (658.21)
	Laf	0.1 (0.03)	0.1 (0.03)	0.12 (0.03)	19896 (508.01)
P60	Sap	0.12 (0.04)	0.09 (0.04)	0.17 (0.04)	84886 (2500.2)
	Laf	0.11 (0.03)	0.12 (0.03)	0.1 (0.03)	53947 (1427.7)
P90	Sap	0.18 (0.06)	0.03 (0.04)	0.16 (0.04)	133530 (4401.7)
	Laf	0.29 (0.05)	0.02 (0.02)	0.13 (0.02)	133220 (3788.7)
P120	Sap	0.13 (0.05)	0.11 (0.05)	0.13 (0.05)	158290 (5219.3)
	Laf	0.17 (0.04)	0 (0)	0.02 (0.02)	118300 (2979)
P150	Sap	0.27 (0.1)	0.22 (0.09)	0.09 (0.08)	199080 (5614.4)
	Laf	0.17 (0.04)	0 (0.02)	0 (0)	199080 (5614.4)
G0_30	Sap	0.09 (0.04)	0.1 (0.04)	0.18 (0.04)	2536.4 (72.96)
	Laf	0.1 (0.03)	0.1 (0.03)	0.12 (0.03)	2210.7 (56.45)
G30_60	Sap	0.17 (0.05)	0.02 (0.03)	0.17 (0.04)	3494.2 (102.74)
	Laf	0.16 (0.04)	0.09 (0.03)	0.05 (0.02)	2281.9 (58.82)
G60_90	Sap	0.19 (0.05)	0 (0)	0.12 (0.03)	2770.9 (90.01)
	Laf	0.23 (0.04)	0 (0)	0.05 (0.02)	626.2 (93.68)
G90_120	Sap	0.09 (0.05)	0 (0)	0.12 (0.04)	3744.3 (131.11)
	Laf	0.14 (0.03)	0 (0)	0.04 (0.02)	6589 (163.06)
G120_150	Sap	0.26 (0.1)	0 (0)	0.08 (0.06)	7736.8 (405.53)

	Laf	0.09 (0.03)	0 (0)	0 (0)	6551.1 (180.06)
G_suck	Sap	0.14 (0.05)	0.09 (0.04)	0.14 (0.04)	2491.6 (75.01)
	Laf	0.18 (0.04)	0.06 (0.03)	0.13 (0.02)	1403 (37.27)
G_fat	Sap	0.11 (0.07)	0 (0)	0.26 (0.06)	2099.8 (101.47)
	Laf	0.16 (0.08)	0 (0.03)	0 (0)	2230.5 (106.04)

¹BW= birth weight; WW= weaning weight; SWT= slaughter weight; P15, P30, P60, P90, P120, P150 = body weights at 15, 30, 60, 90, 120, 150 days of age, respectively; G0_30, G30_60, G60_90, G90_120, G120_150, G_suck, G_fat = average daily gain between birth and 30 days of age, between 30 and 60 days of age, between 90 and 120 days of age, between 120 and 150 days of age, between birth and weaning and between weaning and slaughter, respectively; h^2 , m^2 , c^2 = proportion of phenotypic variance attributed to the additive genetic, maternal genetic, and permanent environment of the dam effects, respectively;

4.2.1.3 Genetic correlations estimated between contrasted environments

Genetic correlations were estimated between traits recorded in UEP3R and traits recorded in La Fage.

Genetic correlations were estimated between direct genetic effects and maternal genetic effects when fitted in the model (Table 7).

Standard errors were always very high in comparison with the estimates, so the results are not very reliable. Only for birth weight can we conclude that there are no GxE interactions for direct effect, and limited interactions might exist for the maternal genetic effect.

Table 7. Genetic correlations (rg) for direct and maternal effects (standard errors).

Variables ¹	rg - direct	rg - maternal
BW	0.97 (0.07)	0.85 (0.31)
WW	-0.02 (0.18)	0.67 (0.47)
SW	0.95 (0.87)	ne
P15	0.52 (0.18)	0.07 (0.47)
P30	0.39 (0.25)	0.36 (0.54)
P60	0.19 (0.25)	0.66 (0.59)
P90	0.21 (0.21)	ne ²
P120	0 (0.19)	ne ²
P150	-0.02 (0.21)	ne ²
G_suck	0.4 (0.25)	0.35 (0.52)
G0_30	0.31 (0.18)	ne ²
G30_60	-0.07 (0.21)	ne ²
G60_90	0 (0.25)	ne ²
G90_120	-0.22 (0.3)	ne ²
G120_150	-0.23 (0.22)	ne ²
G_fat	0.22 (0.39)	ne ²

¹BW= birth weight; WW= weaning weight; SWT= slaughter weight; P15, P30, P60, P90, P120, P150 = body weights at 15, 30, 60, 90, 120, 150 days of age, respectively; G0_30, G30_60, G60_90, G90_120, G120_150, G_suck, G_fat = average daily gain between birth and 30 days of age, between 30 and 60 days of age, between 90 and 120 days of age, between 120 and 150 days of age, between birth and weaning and between weaning and slaughter, respectively; ne = not estimated.

4.2.2 Study 2

The effect of the genetic line is estimated under two contrasted diets (Table 8).

Table 8. Lsmeans of feed intake and residual feed intake phenotyped under two contrasted diets.

Diet	Trait	Line effect	LS Means RFI+	LS Means RFI-
Concentrate 100% ad libitum	Average daily feed intake (g/j)	***	2124	2001
Concentrate 100% ad libitum	Residual feed intake (g/j)	***	+68.2	-62.9
Forage-based	Average daily feed intake of concentrate (g/j)	NS	691	693
Forage-based	Average daily feed intake of forage (g/j)	***	1200	1120
Forage-based	Average daily water intake (g/j)	NS	5886	5783
Forage-based	Residual feed intake (g/j)	***	+36	-15

As expected, the lines have highly different RFI and feed intake during C-diet – with a difference of 123 g/d of concentrate's intake and 131.1 g/d of RFI. It is noticeable that the difference is also highly significant during the M-diet with 80 g of forage intake between lines and 0.041 of RFI (in UFV).

At the phenotypic level, the correlation between concentrate intake recorded under the 100% concentrate diet, and forage intake recorded under the forage-based diet is 0.22.

4.3 Conclusions

In the Romane breed, GxE interactions were difficult to assess through genetic correlations between two experimental farms with different farming systems (intensive vs extensive). Only reliable results could be obtained for birth weight with no GxE interactions for the direct genetic effect and very low GxE interactions for the maternal genetic effect.

Moreover, we compared animals from two divergent lines selected on residual feed intake under a concentrate diet and successively fed with a concentrate-based diet and a forage-based diet. Significant differences were observed between the RFI- and RFI+ animals, with RFI- also eating less forage than RFI+ animals and being more efficient. The phenotypic correlation estimated between concentrate intake and forage intake is moderate but positive. If GxE exist, they should not be too important.

5 Alpine and Saanen goats: extensive vs intensive – INRAE & IDELE & Capgènes

5.1 Materials and methods

5.1.1 Animals and housing

The experiment was performed in 14 commercial farms and one INRAE Experimental Farm (INRAE, P3R, Bourges, France) between 2019 and 2021 in the framework of Smarter (T1.2 & T1.4). A total of 2,188 (977 Alpine and 1,211 Saanen) primiparous dairy goats were phenotyped for feed efficiency.

Feed intake was recorded 4 times during the lactation: 2 times at the beginning of the lactation (between 0 and 60 days in milk (DIM) and between 60 and 90 DIM), around the reproduction (between 210 and 260 DIM) and at the end of the lactation (between 240 and 280 DIM). A total of 7,580 records (4,461 and 3,119 for Alpine and Saanen, respectively) were included in the dataset.

Animals were fed with different forages and concentrates, depending on the breeder. On each test day, feed intake was determined by weighing the total ration distributed and that wasted by trained staff from the milk recording organisms. The forage quantity was measured by weighing all the offered forage, with a scale, at the batch or farm level (not individually). For concentrates, the quantity was measured either individually with automatic feeders or manually in the milking parlour or at the batch level by weighing all the offered concentrates, depending on the farm. Thus, for farms without individual distribution of concentrates, the individual feed intake was the average feed intake of the batch to which the animal belongs (83% of the dataset). For farms with individual distribution of concentrate, the individual feed intake was the average feed intake of the batch to which the animal belongs for forage, plus the individual intake of concentrate (17%). Dry matter intake (DMI) was thus estimated from the information indicated on the concentrate labels and from forage analysis, for each animal and each test day. Energy Intake (EI) was estimated by multiplying DIM and energy concentration. Nutritional feed quality was recorded for each forage and each concentrate, and energy content was given by INRAE (Agabriel, 2010). Test day milk recording data (milk yield, fat, and protein contents) were also measured at the same time as the feed intake control.

The chest width (CW) was used as a proxy of the body weight and was measured one time during the lactation (about 150 DIM). No measurements for body condition scores were performed.

In each farm, the percentage of concentrate and dehydrated (PCD) distributed in each test day ration was estimated, and then the mean PCD by farm was calculated to characterize the farming system as extensive (PCD <35%) or intensive (PCD ≥ 35%).

To solve model convergence problems, only goats from sires with offspring in both systems and with 2 or more test day records were kept. The final dataset comprised 1,908 (103 Alpine data and 405 Saanen goats) and 1,876 test day records (256 and 296 Alpine and Saanen goats, respectively) in extensive and intensive farming systems, respectively. Characteristics of extensive and intensive farming systems are reported in Table 9.

Table 9. Characteristics of data used for GXE study of Alpine and Saanen farms in French extensive and intensive systems. Edits consisted in keeping the most connected animals to ensure convergence.

Characteristic	Extensive	Intensive
Number of farms	6	9
Number of goats before edits	869	1,319
After edits	508	552
Number of records before edits	3,118	4,462
Number of records after edits	1,908	1,876
Type of records	Multiple	Multiple

5.1.2 Data analysis

Residual Energy Intake (REI), was estimated as the residual of a linear regression model (1):

$$DEI = \beta_0 + \beta_1 \times MY + \beta_2 \times FC + \beta_3 \times PC + REI \quad (1)$$

Where, DEI is the daily energy intake (expressed in Unité Fourragère Lait unit (UFL)), β_0 is the intercept, β_1 is the regression coefficient for MY (milk yield), β_2 and β_3 are the regression coefficients of FC and PC (fat and protein contents). REI has been estimated for two breeds in commercial flocks: Saanen and Alpine.

Genetic parameters have been estimated for REI between two systems, using WOMBAT software, with the following animal linear models:

$$Y = \text{Breed} + \text{Flock} + \text{Camp} + \text{Htd} + \text{PhSt} + a_n + \text{perm}_p + e$$

Where, Y is the observation vector for REI, Breed is the fixed effect of the breed, Flock is the fixed effect of the flock, Camp is the fixed effect of the lactation campaign, Htd is the fixed effect of the herd test day, PhSt is the fixed effect of the physiological stage. The random effects included in the model were the additive genetic effect of the animal (a_n), the permanent environmental effect (perm_p) and the residual (e).

To estimate genetic correlations between the two different farming systems we used a two-traits model.

5.2 Results

5.2.1 Descriptive statistics

Descriptive statistics of the studied phenotypes in extensive and intensive farming systems are presented in Table 10. Mean milk yield and REI were similar between the two systems.

Table 10. Descriptive statistics of the percentage of concentrate and dehydrated (PCD), milk yield and residual energy intake (REI) traits per farming system.

Phenotype	Systems	N	Mean	SD	Min	Max
REI	Extensive	1,908	-0.11	0.26	-1.09	1.03
	Intensive	1,876	-0.02	0.29	-0.89	0.71
PCD (%)	Extensive	1,908	31.6	5.2	3.54	45.7
	Intensive	1,876	45.9	9.9	8.53	61.1
Milk yield (kg)	Extensive	1,908	3.15	0.78	0.70	6.10
	Intensive	1,876	3.25	0.96	0.70	7.20

SD = standard deviation.

5.2.2 Genetic parameters

Estimates of heritability for REI and genetic correlation between traits in the two farming systems are presented in Table 11; repeatability estimates are also reported.

Results showed similar heritability of REI in the two farming systems and a high genetic correlation in the two French farming systems, suggesting possible G×E interaction. However, bivariate analyses of the REI traits from the two French farming systems produced high standard errors for the genetic correlation, which could be potentially attributed to the limited number of animals recorded and the structure of the dataset.

Table 11. Heritability (h^2), repeatability (r) and genetic correlation between residual energy intake (REI) in extensive and intensive systems with respective standard errors in parenthesis.

Trait	Systems	h^2	r	Genetic correlation
REI	Extensive	0.10 (0.06)	0.28 (0.07)	0.55 (0.59)
	Intensive	0.08 (0.05)	0.12 (0.05)	

5.3 Conclusions

In the present study, the genetic parameters of REI were evaluated in two different farming systems (extensive vs intensive). Genetic correlation between goats raised in the two farming systems seems to indicate a possible G×E interaction for REI. This value should be confirmed since high standard errors were produced in the present study. However, if such a G×E interaction exists, it should be taken into consideration in future breeding programs.

6 Summary of genetic correlations

All estimated genetic correlations of feed efficiency phenotypes between animals reared in different environmental conditions from the above studies are summarised in Table 12.

Table 12. Genetic correlations of feed efficiency phenotypes between sheep and goats reared in different environmental conditions.

Trait ¹	Breed	Environments	Genetic correlations
Milk yield (kg/animal/milking period)	Lacaune	Greece vs France	0.86 (0.13)*
Fat content (%)	Lacaune	Greece vs France	0.59 (0.21)*
Protein content (%)	Lacaune	Greece vs France	0.88 (0.12)*
Birth weight (hg)	Romane	Intensive vs Extensive	0.85 (0.31)*
Weaning weight (hg)	Romane	Intensive vs Extensive	0.97 (0.07)*
P15 (g/day)	Romane	Intensive vs Extensive	-0.02 (0.18)
P30 (g/day)	Romane	Intensive vs Extensive	0.39 (0.25)
P60 (g/day)	Romane	Intensive vs Extensive	0.19 (0.25)
P90 (g/day)	Romane	Intensive vs Extensive	0.21 (0.21)
P120 (g/day)	Romane	Intensive vs Extensive	0.00 (0.19)
P150 (g/day)	Romane	Intensive vs Extensive	-0.02 (0.21)
G0_30 (g/day)	Romane	Intensive vs Extensive	0.31 (0.18)
G30_60 (g/day)	Romane	Intensive vs Extensive	-0.07 (0.21)
G60_90 (g/day)	Romane	Intensive vs Extensive	0 (0.25)
G90_120 (g/day)	Romane	Intensive vs Extensive	-0.22 (0.3)
G120_150 (g/day)	Romane	Intensive vs Extensive	-0.23 (0.22)
G_fat (g/day)	Romane	Intensive vs Extensive	0.22 (0.39)
G_suck (g/day)	Romane	Intensive vs Extensive	0.4 (0.25)
Residual energy intake	Alpine & Saanen	Intensive vs Extensive	0.55 (0.59)

¹P15, P30, P60, P90, P120, P150 = body weights at 15, 30, 60, 90, 120, 150 days of age, respectively; G0_30, G30_60, G60_90, G90_120, G120_150, G_suck, G_fat = average daily gain between birth and 30 days of age, between 30 and 60 days of age, between 90 and 120 days of age, between 120 and 150 days of age, between birth and weaning and between weaning and slaughter, respectively; *Indicates statistically significant estimates ($P < 0.05$).

7 Conclusion

The present deliverable focused on investigating G×E interactions for feed efficiency phenotypes that were identified in Task 1.1. Specifically, four studies were conducted to assess (i) milk yield and composition of Lacaune dairy sheep reared intensively in Greece vs semi-extensively in France, (ii) body weights and growth traits of Romane meat lambs reared under intensive vs extensive conditions, (iii) feed intake and residual feed intake (RFI) of Romane lambs (divergent lines for RFI) fed with a concentrate diet vs a forage-based diet, and (iv) residual energy intake (REI) of Alpine and Saanen dairy goats reared in intensive vs extensive farming systems. In Lacaune dairy sheep, genetic correlations for milk yield and protein content suggested no G×E interactions across countries and farming systems. However, some degree of interaction was found for fat content, indicating that sire re-ranking could be expected. In Romane meat lambs reared under different farming systems, no strong evidence of G×E interactions was found for birth weight; however, further research is needed for the rest of the studied traits. Likewise, for feed intake and RFI of Romane lambs, no important interaction was detected between genetic lines and diets (concentrate vs forage). In Alpine and Saanen dairy goats, genetic correlations for REI suggest that G×E interactions may exist, but further research is needed to confirm this result. Overall, joint genetic evaluations for feed efficiency indicators of sheep and goats reared in contrasted environments are feasible. However, breeding strategies should be tailored to the needs and conditions in each country and farming system, depending on animal species and selected feed efficiency phenotype and subject to accurate and systematic recording of individual animals.

8 Deviations or delays

Deviations per partner are described below:

- AUTH: A total of 2,000 Lacaune ewes reared in Greece were selected for the study as initially foreseen in the DoA. However, following quality control of milk yield and composition records 1,658 animals were included in the analysis.
- INRAE: The second study in Romane meat sheep focuses on 332 animals, because a hundred lambs, phenotyped in 2018 were not considered. These animals were fed a total mixed ration so forage and concentrate intake could not be measured separately. In 2019, new feeders were available so we could separate concentrate intake and forage intake. We focused on these data in this deliverable.
- IDELE, INRAE & Capgenes: A total of 6,124 dairy goats (3,180 Saanen and 2,582 Alpine) were phenotyped for the study as initially foreseen in the DoA. However, only 2,188 primiparous goats (1,211 Saanen and 977 Alpine) were kept for this study and following quality control REI records only 1,060 goats (701 Saanen and 359 Alpine) were included in the analysis.
The season vs out of season breeding study could not be conducted due to the imbalance of data between the two breeding seasons.

9 Acknowledgements

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11 Appendix

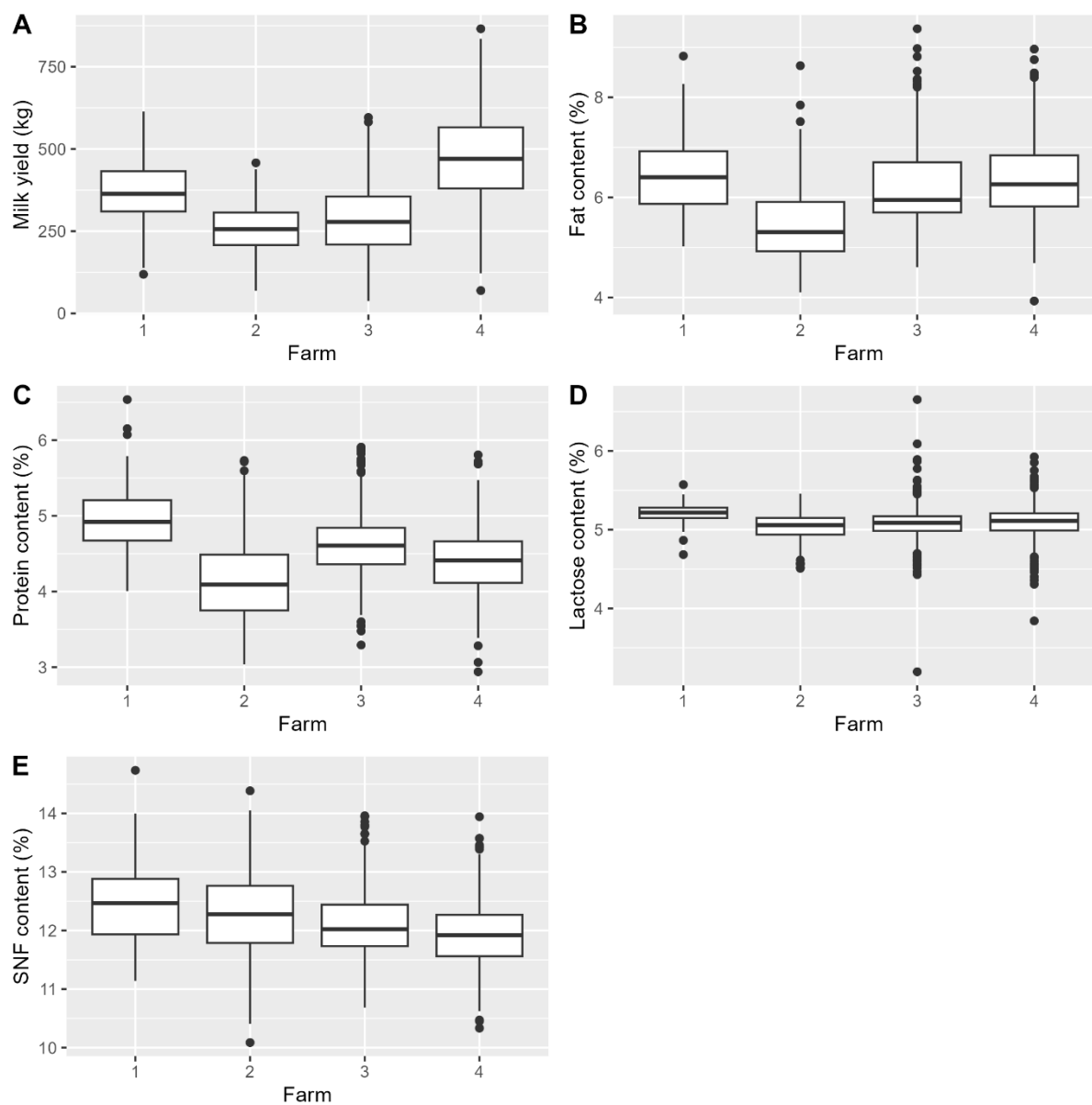


Figure S1. Relationship (box and whisker plots) of milk production traits with studied farms in Greece.

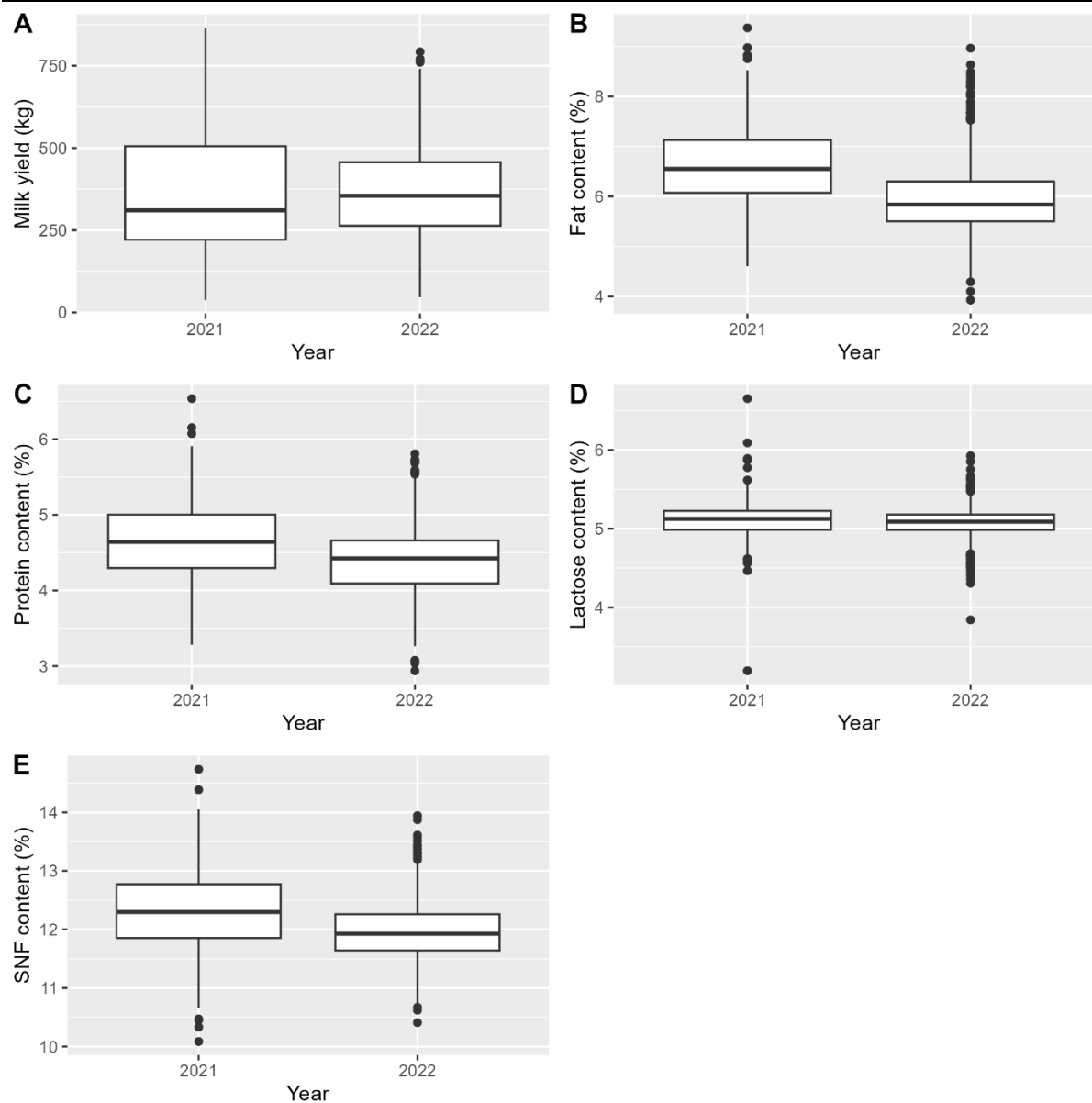


Figure S2. Relationship (box and whisker plots) of milk production traits with studied years in Greece.

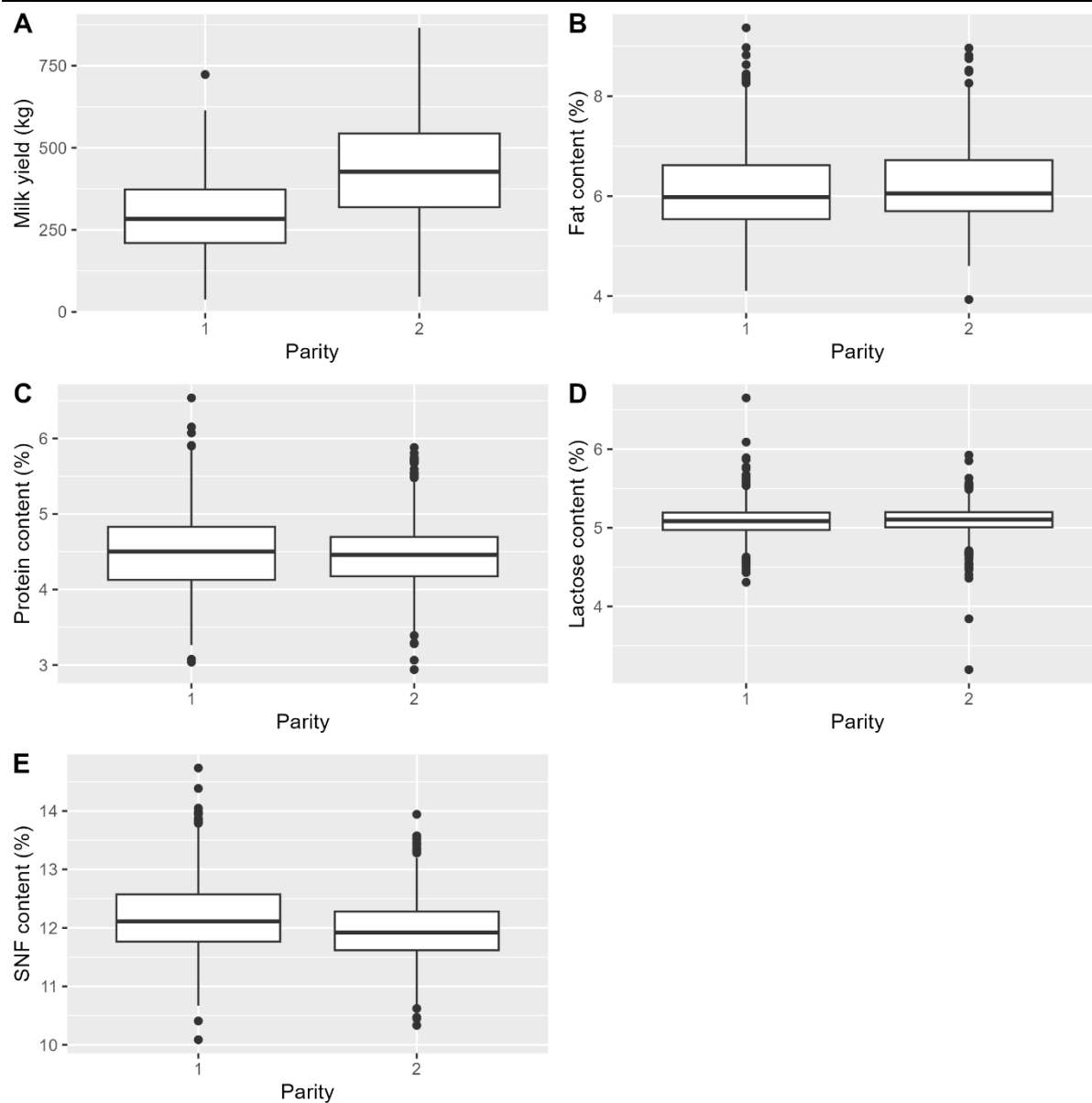


Figure S3. Relationship (box and whisker plots) of milk production traits with parity of studied Lacaune ewes in Greece.

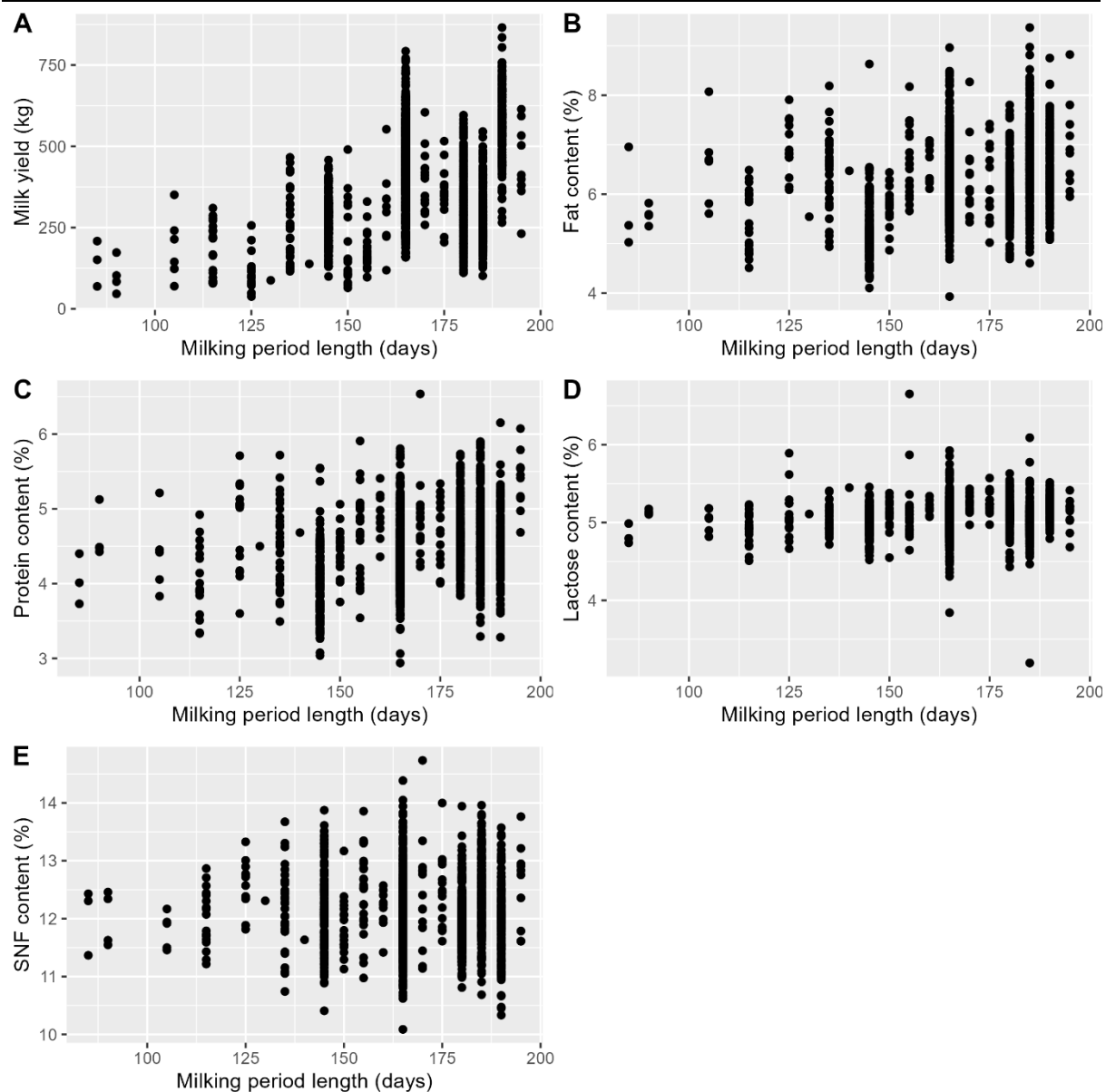


Figure S4. Relationship (scatterplots) of milk production traits with milking period length of studied Lacaune ewes in Greece.

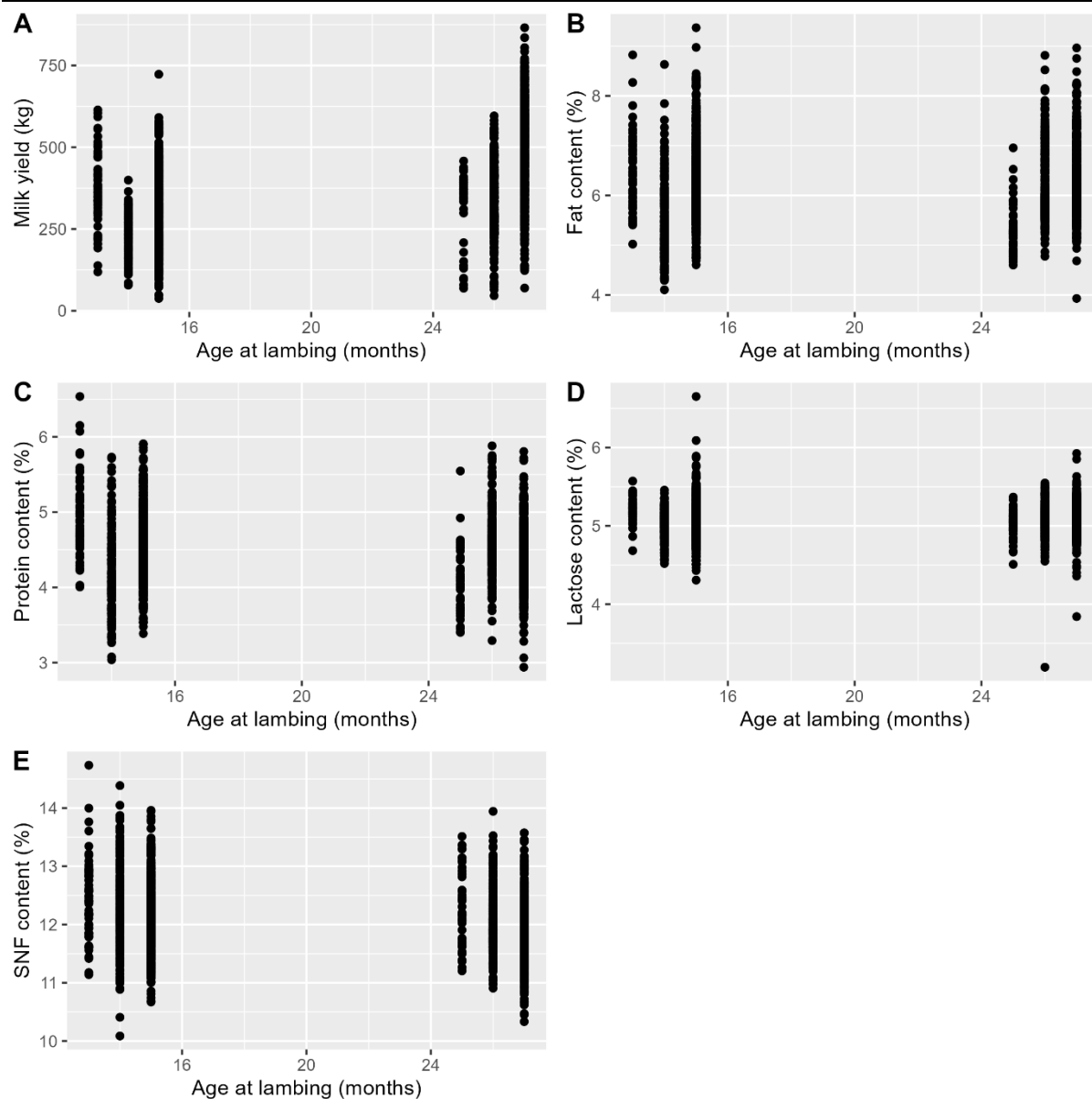


Figure S5. Relationship (scatterplots) of milk production traits with age at lambing of studied Lacaune ewes in Greece.

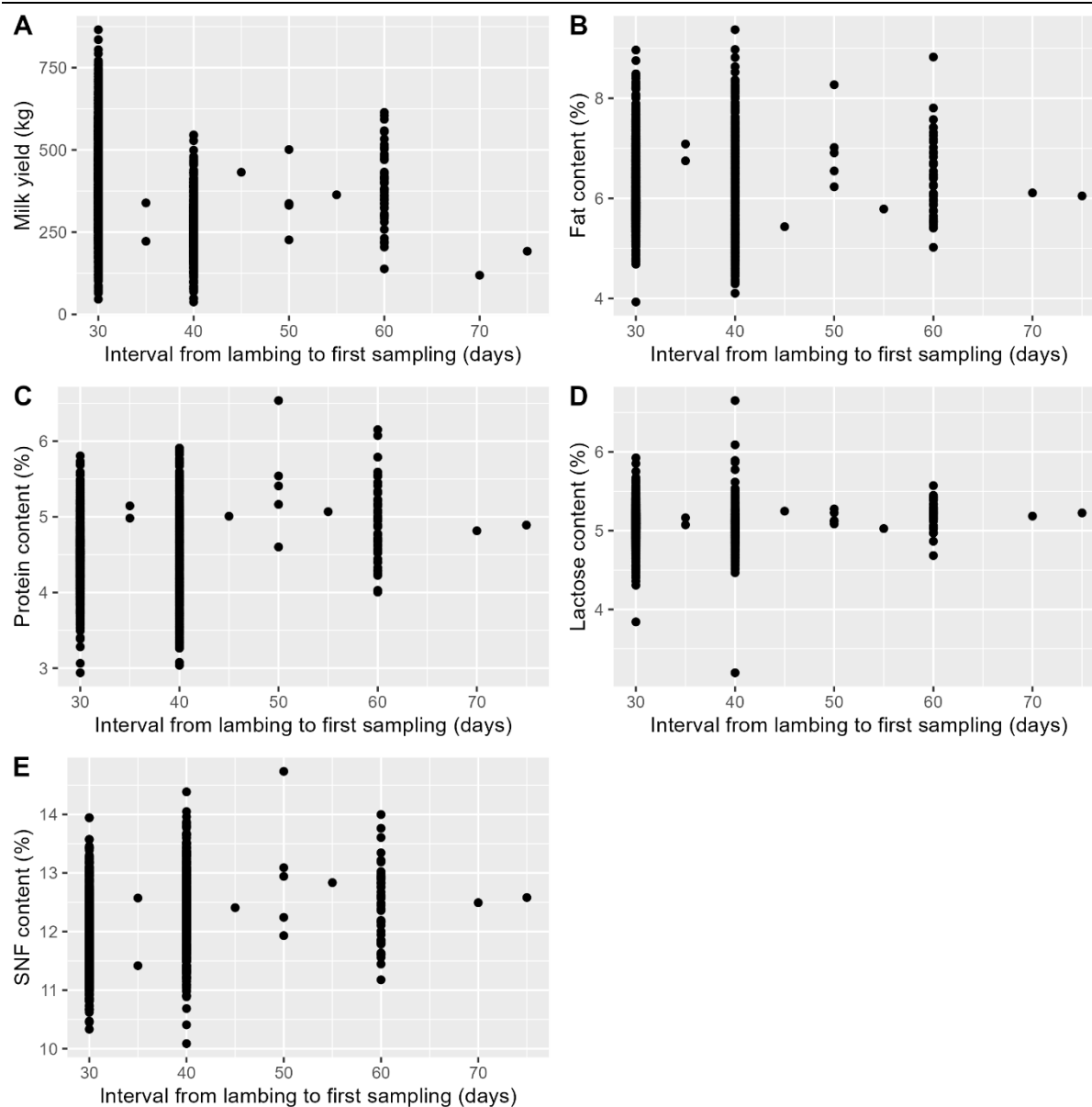


Figure S6. Relationship (scatterplots) of milk production traits with days from lambing to first sampling of studied Lacaune ewes in Greece.

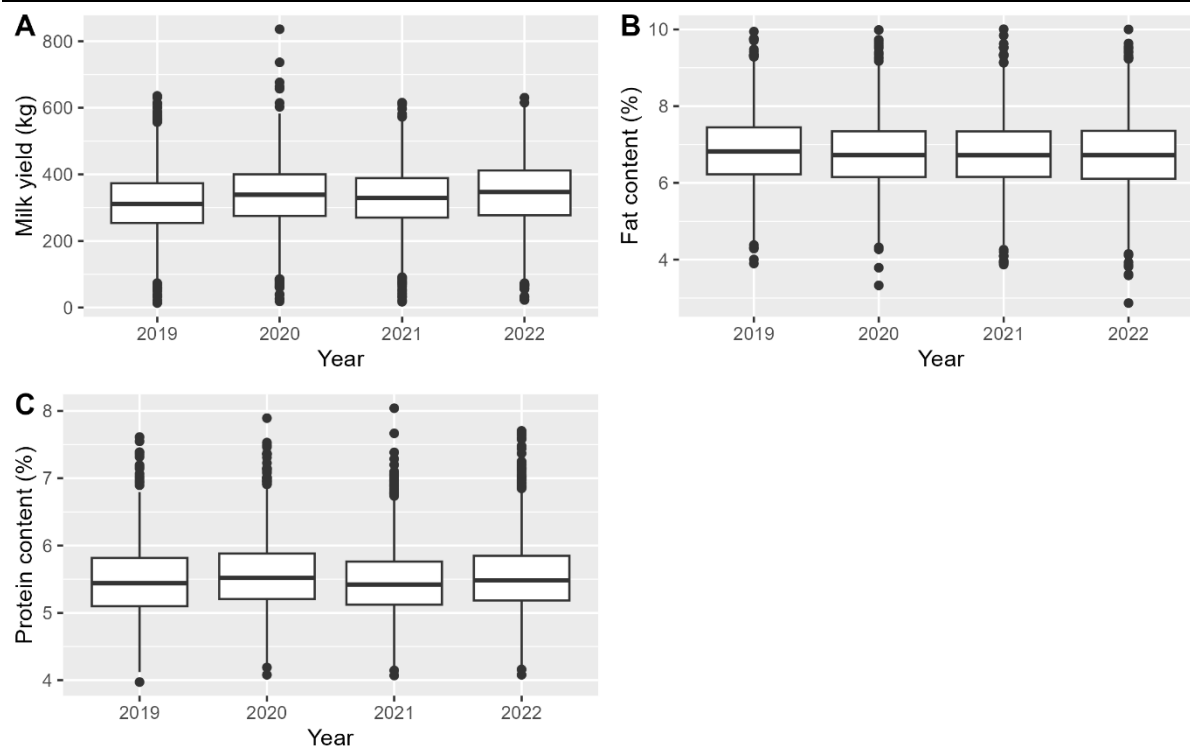


Figure S7. Relationship (box and whisker plots) of milk production traits with studied years in France.

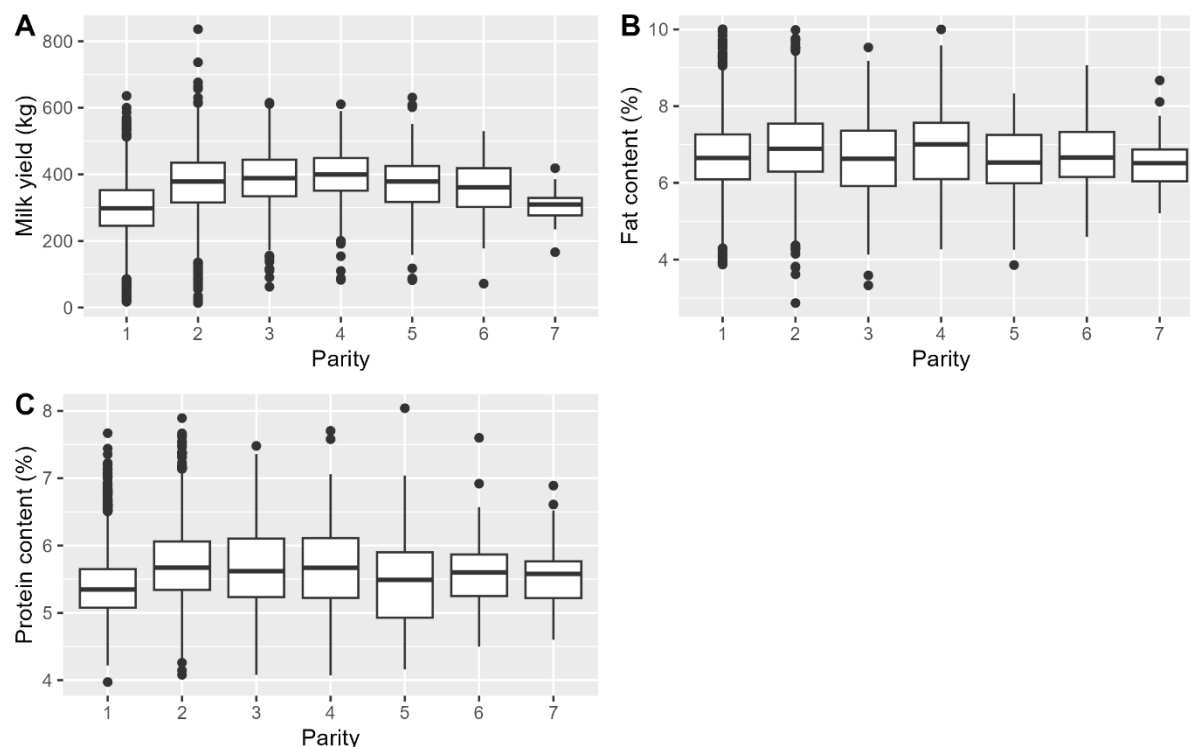


Figure S8. Relationship (box and whisker plots) of milk production traits with parity of studied Lacaune ewes in France.

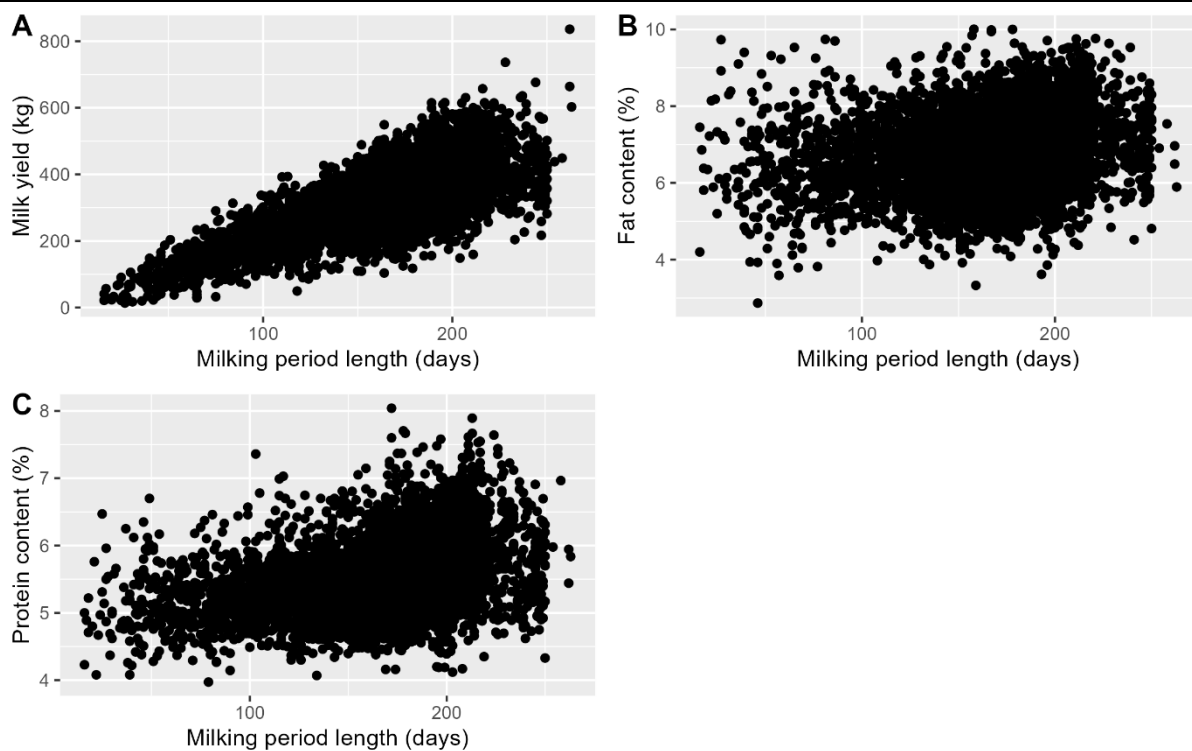


Figure S9. Relationship (scatterplots) of milk production traits with milking period length of studied Lacaune ewes in France.

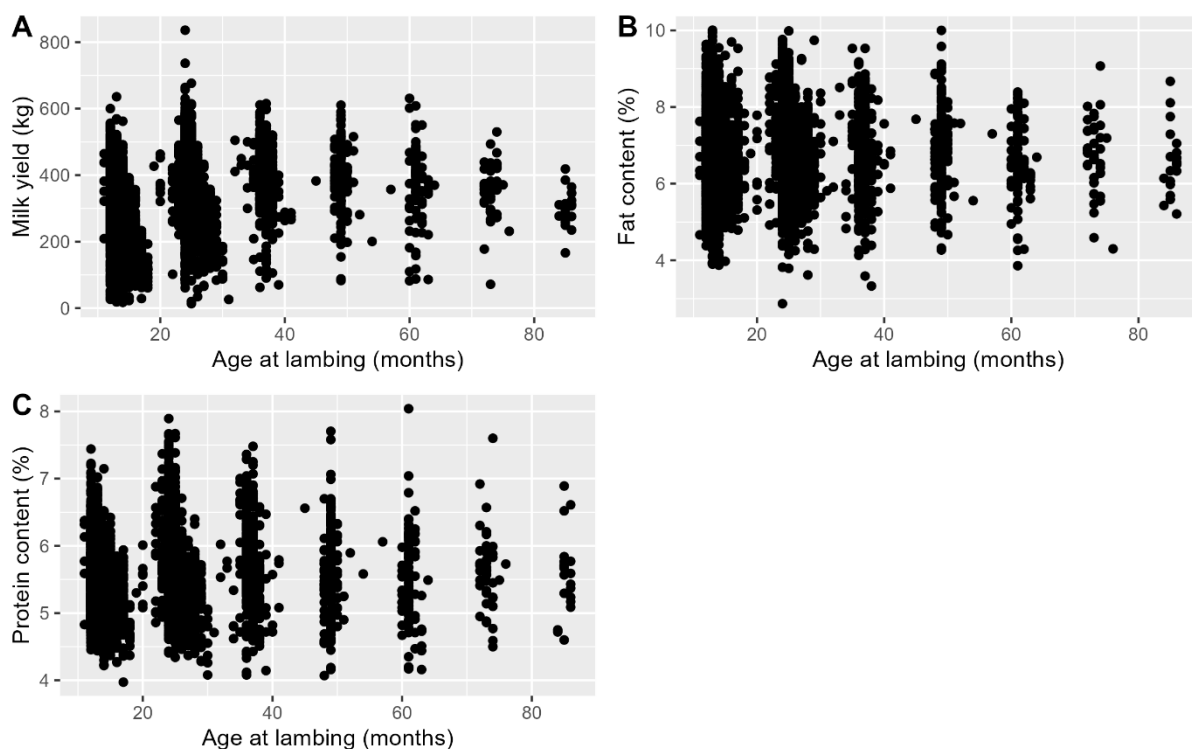


Figure S10. Relationship (scatterplots) of milk production traits with age at lambing of studied Lacaune ewes in France.

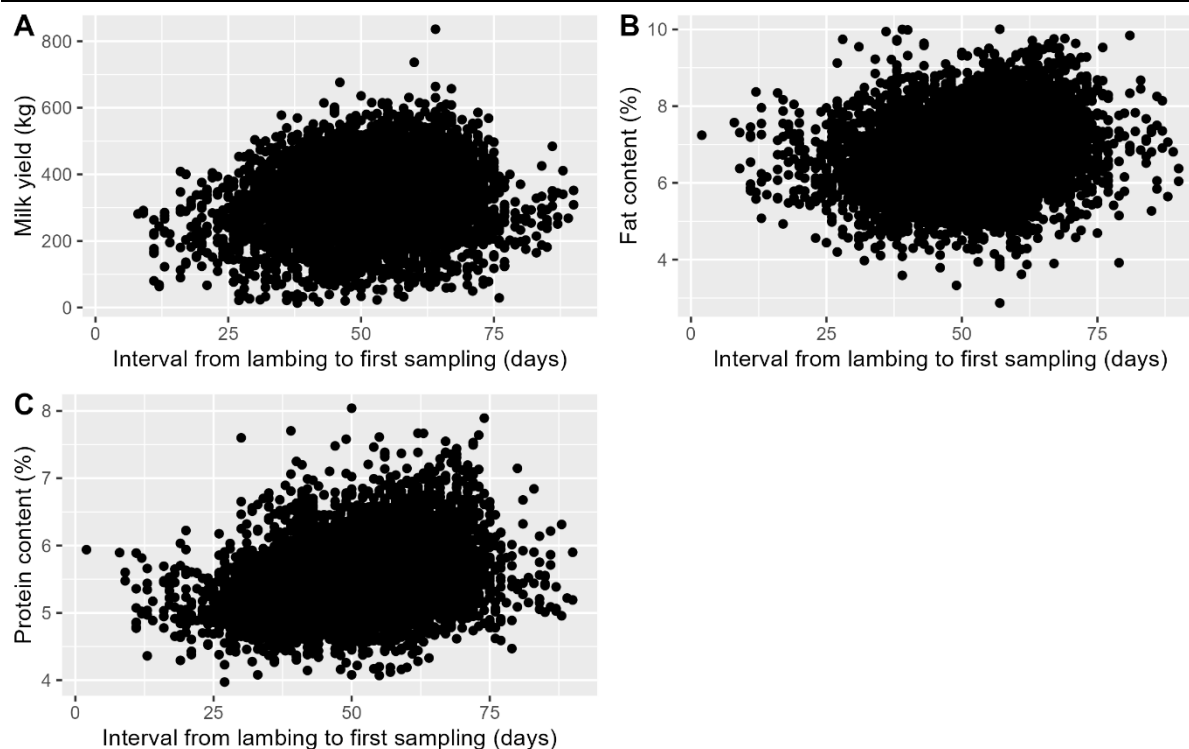


Figure S11. Relationship (scatterplots) of milk production traits with days from lambing to first sampling of studied Lacaune ewes in France.

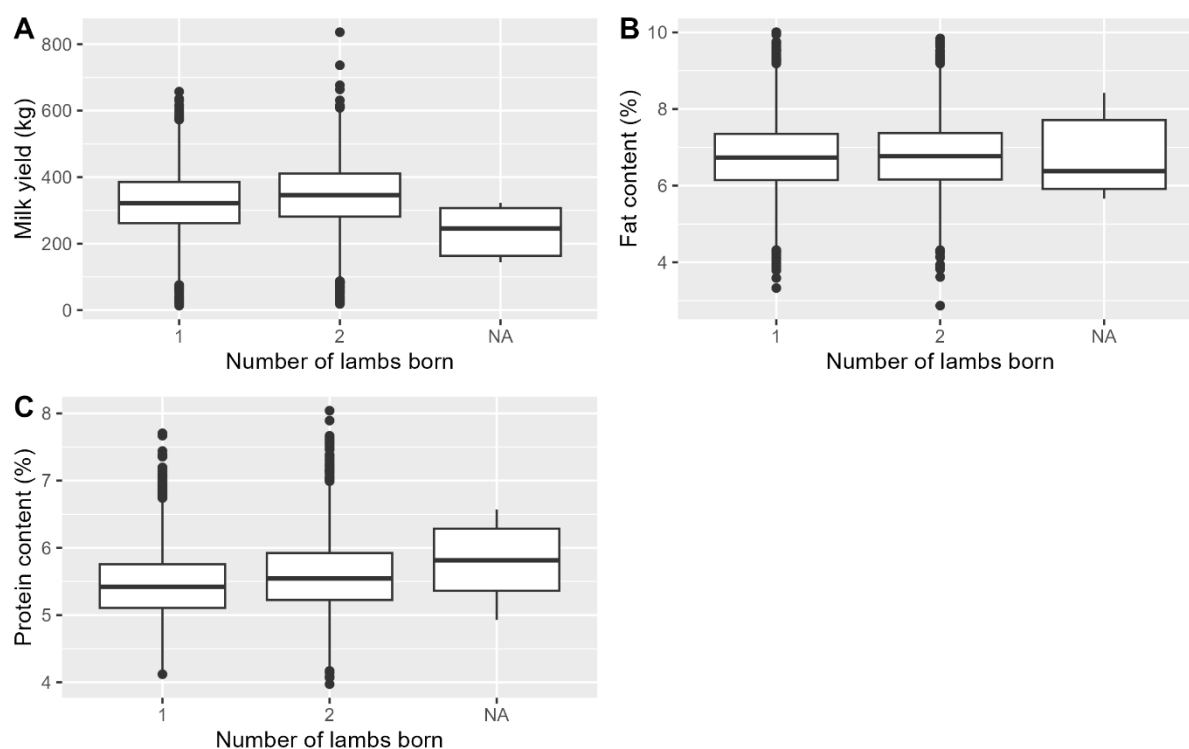


Figure S12. Relationship (box and whisker plots) of milk production traits with number of lambs born from studied Lacaune ewes in France.