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Opportunities and limits of commercial farm data to study the genetic determinism of feed efficiency throughout lactation in dairy sheep

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ABSTRACT

The collective economic and environmental interest of the whole dairy sheep sector is to reduce feed costs and the negative impact of milk production on the environment. Thus, this study focused on the characterisation and genetic selection potential of feed efficiency in the Lacaune breed. Estimates for feed efficiency in dairy ewes are limited, mainly due to a lack of individual feed intake measurements in the sheepfold or in the pasture. We estimated the genetic parameters for two approximated (not entirely based on individual data) feed efficiency traits (lactation feed conversion ratio (**LFCR**) and residual energy intake (**REI**)) and daily milk yield (**DMY**) at different stages of lactation and throughout lactation. The accuracy of the efficiency traits was first evaluated on samples from Lacaune dairy ewes that were monitored individually, especially for their feed intake. Then, feed efficiency estimation methods were applied on eight commercial farms corresponding to 4 680 Lacaune dairy ewes over two milk lactations (30 854 records). Animals were collectively (for a large part of feed intake) or individually (for milk performance and dynamics of body fat reserves) monitored at different lactation stages. The heritabilities of LFCR and REI were estimated over lactations at 0.10 ± 0.01 and 0.11 ± 0.01, respectively. High genetic correlations were observed between the two efficiency traits and milk production traits, with a genetic correlation between LFCR and DMY of 0.74 ± 0.04 and between REI and DMY of −0.79 ± 0.04. A strong influence of environmental factors such as farm, year of milk production and lactation stage affected the genetic link between REI and milk production traits. Efficiency values observed in early lactation when animals were bred in the sheepfold were less genetically correlated with values obtained later in lactation when animals were grass-fed. However, individual characterisation of feed efficiency remains difficult due to the collective feeding context in dairy ewe farms.

Implications

Dairy sheep breeders are increasingly interested in selecting efficient animals, and aim to buy less concentrate while maintaining their milk production and becoming more self-sufficient. The calculation of feed efficiency requires precise individual measures that are unavailable on commercial farms, especially for feed intake. On-farm approximated feed efficiency traits are heritable in dairy sheep. Feed efficiency is mainly genetically linked to milk yield and is also strongly influenced by the environmental effects of commercial farms. The results of this study encourage breeders to continue their phenotyping efforts, particularly at individual level, in order to approach ewe efficiency.

Introduction

Improving animal feed efficiency has economic (feed costs) and environmental (reduces methane emissions) importance for sheep production (Paganoni et al., 2017; González-García et al., 2020). Sheep that are more feed-efficient decrease their methane and carbon dioxide production. The way animals use feed as efficiently as possible without compromising their production is also a desirable characteristic for the adaptability of animals to cope with variations in feed resources in quantity and/or quality. Feed conversion ratio, i.e., the ratio of animal production to resources, and residual

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feed intake (**RFI**), i.e., the difference between actual and expected performance of feed intake, are the two most common indicators used to estimate feed efficiency (Koch et al.,1963; Marie et al., 2002; González-García et al., 2020). Under experimental conditions, González-García et al (2020) observed individual phenotypic variability in the RFI of Lacaune dairy ewes fed individually. Routinely recording large-scale feed intake data at the individual level are costly and difficult to achieve in dairy sheep commercial farms. This is mainly due to the collective feeding system, which is based on the needs of an average ewe in the flock. Moreover, 84% of French dairy sheep production is located in mountainous regions, where ewes graze rangelands all or part of the year (Lagriffoul et al., 2016; Hassoun et al., 2018). These breeding conditions limit the possibility of recording individual feed consumption. In animal insemination centres, the feed consumption of males is usually not individually recorded either (Hassoun et al., 2018). The present study was part of the European project H2020 **SMARTER** (SMAll RuminanTs breeding for Efficiency and Resilience, 2018–2023), which aims to evaluate feed efficiency phenotypes that are measurable in commercial farms. The project, which focuses on small ruminants such as dairy sheep, investigates the efficiency of animals in diverse environments with the goal of evaluating the possibility of a genetic selection of feed efficiency traits.

Several studies in dairy cattle using different estimation methods and populations have shown that feed efficiency traits have low (0.04 ± 0.08) to moderate (0.36 ± 0.17) heritability (review by Brito et al., 2020); thus, genetic improvement can be considered. To our knowledge, no heritability for feed efficiency traits and their genetic correlations with economically important traits have been assessed in dairy ewes.

The objectives of this study were to propose measurable feed efficiency phenotypes, using both collective and individual data, and to estimate their relevance to consider genetic selection in dairy ewes. The data were focused on lactating Lacaune dairy ewes in an on-farm collective feeding context. Our decision was to express the quantities of feed consumed in net energy due to the differences in feeding systems between farms and evolution in the feed values over time. Thus, we proposed net energy feed efficiency for lactating ewes as a new trait. First, the accuracy and reliability of these traits were evaluated using INRAE experimental data by comparing classical feed efficiency traits based on individual performances to our proposed traits. Then, genetic parameters for proposed feed efficiency traits, including genetic correlations with milk production traits, were estimated.

Material and methods

Commercial farms

In the framework of the European SMARTER project, data were collected from eight French Lacaune dairy sheep farms during two milk production years from September 2019 to September 2021. After data editing, 30 854 records for all the traits studied from 4 680 ewes (including 30% of primiparous ewes) were available in the commercial farms' dataset. On average, the ewes had 7 ± 3 records ranging from 1 to 12 for the whole testing period. These flocks had two methods of harvesting fodder (hay for three farms and silage for five farms), they all used an automatic concentrate feeder in the milking parlour (individualised monitoring of concentrate consumption), and they had the same mating period (animal insemination between June and July) for grouped lambing in autumn.

Milking started one month after lambing, just after the lambs weaning. The sheep feeding management strategies were established at the first milk test day (i.e., two months after lambing) depending on the average dairy requirements of ewes that had been inseminated at the end of the previous lactation, which represent the majority of the flock. The diet was based on the average ewe requirements and increased up to 110% for the energy and 130% for the protein requirements. This strategy made it possible to cover part of the energy and protein requirements of high milk-producing ewes (Hassoun et al., 2018). Such a practice leads to underfeeding the highest milk-producing ewes (few in number) and to overfeeding low- and mid-producing ewes. The established diet did not substantially change until one month before grazing to avoid penalising the milk production of primiparous ewes (which start mating one month later) and ewes bred by natural mating, including in the milking flock over time. However, the amount of concentrates could be different according to the level of milk production or the fattening condition. Depending on the commercial farms studied, ewes started grazing 4–6 months after the average lambing date of the inseminated flock.

Phenotypes

Milk production traits

Dairy performances of each ewe were measured during the morning milking with a target of a six-monthly test day. The daily milk yield (**DMY**, L/d) was estimated by correcting the morning milk yield for the evening and morning differences using the ratio between the total volumes of milk produced by the whole flock at two milkings (ICAR, 2018). Protein and fat content (g/L) were quantified (mid-infrared predicted) from samples taken each morning test day. The standardised milk yield (**SMY**, L/d) proposed by Bocquier et al. (1993) was calculated at each test day as follows:

$$\begin{aligned}\mathrm{SMY} = {} & \mathrm{DMY} \\ & \times (\mathrm{Fat\_Content} \times 0.0071 + \mathrm{Protein\_Content} \times 0.0043 + 0.2224).\end{aligned}$$

The net energy of one litre SMY (unité fourragère lait (**UFL**)/d) was calculated as SMY × 0.71 (Hassoun and Bocquier, 2007). In the French feeding system for ruminants, energy requirements are based on the net energy unit for lactation (UFL), where one UFL is the net energy requirement for lactation equivalent to one kg of standard air-dried barley (Jarrige et al., 1986).

Body reserve dynamics

Five body condition scores (**BCS**) were measured on each ewe with the following target physiological stages: 30 days before lambing, at the end of suckling (30 days after lambing), at the first milk test day, and 30 days before and after mating. These stages correspond on average to −30, 30, 50, 180 and 240 days related to lambing, respectively. The data were recorded at fixed dates on farms. An interval from 30 to 60 days was defined around each BCS target physiological stage as follows: −60 to 0, 0 to 30, 30 to 80, 150 to 210 and 210 to 270 days related to lambing. The data recorded during these time intervals were assigned to the corresponding physiological stages; outside these intervals, they were removed.

The BCS was evaluated by palpation of the lumbar region according to the 6-point scale proposed by Russel et al. (1969), ranging from 0 (emaciated) to 5 (very fat), with 0.25-point intervals. Body condition was scored by a single trained evaluator. Evaluators were previously trained to harmonise the scoring and make the comparison possible between evaluators.

Due to missing data, a longitudinal imputation method was applied to the BCS data. This imputation was applied per farm and was dedicated to ewes with at least two actual BCSs, i.e., 35% of the dataset. The method used was the copyMean method implemented by Genolini and Falissard (2011) in the kml package of R software combining trajectory-based and mean-based imputation methods to predict intermittent (in the middle of a trajectory) and monotonic (at the beginning or end of a trajectory) missing data. The imputation accuracy was quantified by taking a sample of ewes from the commercial farms' dataset having all BCSs (n = 3 840 records corresponding to 2 996 ewes). An individual random degradation of three BCSs on 20% of the ewes in the sample was performed, and then, imputation was applied to the artificially degraded BCS data. The protocol was repeated 30 times. Imputed data were highly correlated with actual data (cor = 0.79). Only 20% of individuals had a difference of more than 0.25 point between imputed and actual data, and 4% had a difference of more than 0.5 BCS point difference.

The variation in BCS (BCS_Δ), meaning the difference between two successive scores, was converted into net energy ($BSC_\Delta e$, UFL/d) according to the following formula (Hassoun et al., 2018):

$$BCS_\Delta e = \left(-0.43 \times BW \times \frac{BCS_\Delta}{Day_\Delta}\right) \times 0.956$$

where BCS_Δ is the BCS variation between two periods and Day_Δ is the duration (in days) between the same two periods. $BSC_\Delta e$ was calculated three times: between the end of suckling and the first test day ($BSC_\Delta e1$ with $BSC_\Delta 1$), between the first test day and before mating ($BSC_\Delta e2$ with $BSC_\Delta 2$) and between before and after mating ($BSC_\Delta e3$ with $BSC_\Delta 3$) on the imputed data.

BW, maintenance and growth energy requirements

Without weights, a parity-dependent reference BW was assigned to all ewes, i.e., 65 kg for primiparous and 75 kg for multiparous according to the expertise of technicians. The choice of setting an average BW for individuals was a strong assumption. The maintenance energy requirement (UFL/d) was calculated as 0.033 × metabolic BW ($BW^{0.75}$) (Hassoun and Bocquier, 2007), which increased by 10% when ewes were grazing (De Boissieu et al., 2019). Because primiparous lambs are lambed at one year old, they still have growth requirements. We set a standard average daily gain of 80 g/d. The daily growth energy requirement (UFL/d) was calculated as (average daily gain/100) × 0.26 (Hassoun and Bocquier, 2007).

Feed intake

On each test day, a feeding survey was conducted to calculate individual DM intake. The total amount of each forage and concentrate fed to the whole or a part of the flock was weighed or visually estimated by the breeder with an experienced technician and sampled for DM content determination. The systems used on farms do not allow for individualised feed distribution, especially for forage, so a strong assumption that all ewes consume the same amount of feed was made. To calculate individual DM intake, the total amount of DM was divided by the number of ewes per farm assuming a 10% refusal for forages offered *ad libitum* (De Boissieu et al., 2019), and individual concentrate fed at the milking parlour was added. No refusals were considered for all concentrates. For the grazing part, De Boissieu et al. (2019) proposed an ingestion estimate at pasture according to the time of presence per ewe, i.e., 2 h = 0.4 kg DM, 4 h = 0.8 kg DM, 6 h = 1 kg DM. The individual daily energy intake (**DEI**, UFL/d) was calculated by multiplying the individual DM intake by the energy density (from technical references or forage analysis) of the feed in the diet on each test day.

Feed efficiency traits

On each test day, the lactation feed conversion ratio (**LFCR**) and residual energy intake (**REI**) were calculated and considered lactation net energy feed efficiency traits. The LFCR was calculated as follows:

$$LFCR = \frac{SMYe}{DEI - (Maintenance\_energy + Growth\_energy) + BCS_\Delta e}$$

The REI was estimated as the residual of multiple linear regression of DEI on DMY, fat content, protein content to account for production requirements, BCS_Δ to account for body reserve dynamics and BW to account for maintenance requirements. Depending on the test day, BCS_Δ changed accordingly ($BCS_\Delta 1$ for test day 1, $BCS_\Delta 2$ from test day 2 to test day 5 and $BCS_\Delta 3$ for test day 6). The LFCR trait reflected the part of feed energy inputs provided and body reserves used to produce milk, whereas REI represented the difference between the feed energy provided and the theoretical feed energy intake estimated from the production level, dynamic fat reserves and BW of animals. Based on the LFCR and REI definitions, efficient animals had an upper LFCR but negative REI values. According to data available from commercial farms, strong assumptions on several traits (by setting an average BW or dividing the proportion of collective feeding by the number of ewes) were issued. A validation step was then necessary to discern the greater or lesser impact of these assumptions.

Validation of the feed efficiency traits from experimental data

Since individual phenotypes of commercial farms data were missing (BW, collective feed) or incomplete (BCS, SMY) for some ewes, the impact of these partial data on feed efficiency traits had to be evaluated. For this purpose, individual data collected at the La Fage INRAE experimental farm were used. In total, 287 Lacaune dairy ewes (including 32% of primiparous ewes) were individually monitored during nine milk production years (2008–2013 and 2017–2019) for their dairy performances (SMY), BW, BCS, and DEI (based on weighing of feed distributed and refused in individual troughs). All measurements were collected once a week (BW, BCS, SMY) or four times per week (DEI) over a period of 3–4 months after suckling (i.e., lactation months 2–5), corresponding to 2 146 lactations. In the experimental dataset, feed efficiency traits were calculated weekly. On average, the ewes had 8 ± 7 feed efficiency records over the whole testing period, ranging from 1 to 28 records per ewe. The BCS_Δ considered a time step of one month around the efficiency measure. To mimic the on-farm SMARTER available data, each variable, BW, BCS_Δ, SMY and DEI, one at a time or several at once, was averaged for each lactation month and year and was applied to each ewe of the batch (n = 2 146). LFCR and REI were calculated from these simplified average variables, and the results were compared to the corresponding actual individual LFCR and REI. To observe the effect of average milk performance, the SMY effect was considered in the REI regression model, whereas in the commercial farm REI model, milk was separated from its components. Actual and simplified REI regressed DEI on SMY, BCS_Δ and BW in the experimental dataset. To assess the reliability of the feed efficiency traits, statistical deviation indicators such as R^2, RMSE and bias were computed between simplified and actual results with R software. Then, an error rate was calculated between the actual efficiency results and the results provided by the set of SMARTER-type simplifications classified into two or three classes. This validation step from the experimental dataset adjusted the treatment of the missing data in the commercial farms' dataset.

Statistical analysis

In the commercial farms' dataset, feed efficiency traits calculated at each test day were linked to a month of lactation. Only data from month 2 to month 7 were kept, i.e., the exclusive milking period, and extreme months (month 1 and month 8) were not analysed due to the low number of ewes. Analyses were performed on 30 854 records for 4 680 dairy ewes over the two lactations. To determine the environmental factors affecting LFCR and REI, analyses of variance were performed with the packages car, lme4 and lmerTest implemented in R software. First, at each lactation month, fixed environmental effects and interaction terms were included in a linear model and selected using Fisher's tests (P-value <0.05). The environmental factors selected were retained as fixed effects for the genetic analyses. At each stage of lactation, the heritabilities of DMY, LFCR and REI were estimated with univariate analyses with WOMBAT software (Meyer, 2007) using the REML method and a six-generation pedigree including 17 267 animals. The single trait animal model used for the estimation of heritabilities was:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Za} + \mathbf{Wp} + \mathbf{e} \tag{1}$$

where $\mathbf{y}$ is the vector of observations for the three traits across six lactation months, and $\mathbf{X}$ is the incidence matrix relating environmental fixed effects ($\mathbf{b}$) to the individuals. The same fixed effects were considered for each trait and lactation month, with parity (1/2/3/4+), litter size (single/multiple), lambing period (start/end) according to parity, mating mode (animal insemination/return/natural breeding) and flock (n = 8) interacting with dairy years (2019–2020/2020–2021). $\mathbf{Z}$ is the design matrix allocating observations to the vector of random additive genetic effects ($\mathbf{a}$) normally distributed ($N(\mathbf{0}, \mathbf{A}\ \sigma_a^2)$) with $\mathbf{A}$ being the genetic relationship matrix based on pedigree, $\mathbf{W}$ is the design matrix allocating observations to the vector of random permanent environmental effects ($\mathbf{p}$) ($N(\mathbf{0}, \mathbf{I}\ \sigma_p^2)$) and $\mathbf{e}$ is the vector of random normal errors ($N(\mathbf{0}, \mathbf{I}\ \sigma_e^2)$), with $\mathbf{I}$ being the identity relationship matrix. The heritability (h^2) and repeatability (t) of a trait were calculated as

$$h^2 = \frac{\sigma_a^2}{\sigma_a^2 + \sigma_p^2 + \sigma_e^2} \text{ and } t = \frac{\sigma_a^2 + \sigma_p^2}{\sigma_a^2 + \sigma_p^2 + \sigma_e^2}$$

The model used for bivariate analysis between records at two lactation stages for each feed efficiency trait was:

$$\begin{bmatrix} \mathbf{y}_1 \\ \mathbf{y}_2 \end{bmatrix} = \begin{bmatrix} \mathbf{X}_1 & 0 \\ 0 & \mathbf{X}_2 \end{bmatrix} \begin{bmatrix} \mathbf{b}_1 \\ \mathbf{b}_2 \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_1 & 0 \\ 0 & \mathbf{Z}_2 \end{bmatrix} \begin{bmatrix} \mathbf{a}_1 \\ \mathbf{a}_2 \end{bmatrix} + \begin{bmatrix} \mathbf{W}_1 & 0 \\ 0 & \mathbf{W}_2 \end{bmatrix} \begin{bmatrix} \mathbf{p}_1 \\ \mathbf{p}_2 \end{bmatrix} + \begin{bmatrix} \mathbf{e}_1 \\ \mathbf{e}_2 \end{bmatrix} \tag{2}$$

where $\mathbf{y}_1$ and $\mathbf{y}_2$ are vectors of observations for traits 1 and 2, respectively, $\mathbf{b}_1$ and $\mathbf{b}_2$ are vectors of environmental fixed effects as defined in the univariate model and $\mathbf{X}_1$ and $\mathbf{X}_2$ are associated incidence matrices. $\mathbf{a}_1$ and $\mathbf{a}_2$ are vectors of random additive genetic effects, $\mathbf{Z}_1$ and $\mathbf{Z}_2$ are associated incidence matrices, $\mathbf{p}_1$ and $\mathbf{p}_2$ are vectors of random permanent environmental effects, $\mathbf{W}_1$ and $\mathbf{W}_2$ are the associated incidence matrices, and $\mathbf{e}_1$ and $\mathbf{e}_2$ are vectors of random residuals. The random effects are assumed to follow a normal distribution and feature the following variance–covariance structure:

$$\begin{matrix} a \\ Var[p] = \\ e \end{matrix} \begin{bmatrix} \begin{matrix} \sigma_{a_1}^2 & \rho_1\sigma_{a_1}\sigma_{a_2} \\ \rho_1\sigma_{a_1}\sigma_{a_2} & \sigma_{a_2}^2 \end{matrix} & 0 & 0 \\ 0 & \begin{matrix} \sigma_{p_1}^2 & \rho_2\sigma_{p_1}\sigma_{p_2} \\ \rho_2\sigma_{p_1}\sigma_{p_2} & \sigma_{p_2}^2 \end{matrix} & 0 \\ 0 & 0 & \begin{matrix} \sigma_{e_1}^2 & \rho_3\sigma_{e_1}\sigma_{e_2} \\ \rho_3\sigma_{e_1}\sigma_{e_2} & \sigma_{e_2}^2 \end{matrix} \end{bmatrix}$$

with $\sigma_{a_1}^2$ and $\sigma_{a_2}^2$ being the additive genetic variances of traits 1 and 2 with ρ_1 being the additive genetic correlation between them, $\sigma_{p_1}^2$ and $\sigma_{p_2}^2$ being the permanent environmental variances of traits 1 and 2 with ρ_2 being the permanent environmental correlation between them, and $\sigma_{e_1}^2$ and $\sigma_{e_2}^2$ being the residual variances of traits 1 and 2 with ρ_3 being the residual correlation between them.

To analyse the effect of the lactation stage, all lactation month data were merged, and a linear mixed animal model was constructed (see Supplementary Table S1). The use of adjusted means estimated by the emmeans package implemented in the R software provided a comparison of the average response between different levels of lactation months. On this dataset, the heritabilities of DMY, fat content, protein content, LFCR and REI and the genetic correlations between each pair of traits were estimated with univariate and bivariate analyses. The models used for these estimations were the same as those above, with the addition of a lactation stage effect interaction with all fixed environmental effects.

Results and discussion

Validation of the feed efficiency traits from experimental data

The descriptive statistics of the studied traits from the experimental dataset are presented in Table 1. The actual values of LFCR and REI were 0.88 ± 0.31, ranging from 0.24 to 1.97, and 0 ± 0.49 UFL/d ranging from −1.50 to 1.47 UFL/d, respectively. The statistical deviation indicators (R^2, RMSE, bias) comparing the actual LFCR and REI with the simplified ones calculated with the average BW, BSC_Δ, SMY or DEI are presented in Table 2. The accuracy evaluation showed a different influence of the zootechnical performances depending on the efficiency trait. Using the fixed average BW had a low impact on the estimation of LFCR with minimal error (RMSE = 0.04, R^2 = 0.98). In this case, a stronger individual bias (−0.33) was obtained for a difference of 19 kg from the fixed BW value. When the average BCS_Δ was used, the error in predicting LFCR was increased (RMSE = 0.24, R^2 = 0.41). An underestimation of the BCS_Δ of −0.3 points resulted in a bias of −0.79, while an overestimate of + 0.3 points of BCS_Δ led to a larger bias of 1.34. The average SMY also had a stronger impact on the LFCR results, with a decrease in R^2 to 0.61 and a concomitant increase in RMSE to 0.20 and individual bias from −1.24 to 0.57. The greatest underestimation of SMY (−1.1 L) led to a bias of −1.24, whereas the greatest overestimation (+1.4 L) led to a smaller bias of 0.57. When the averaged DEI was used, the impact was as strong as for the SMY variable with an adjustment quality and residuals of the same order (RMSE = 0.22, R^2 = 0.56). For the REI trait, BW and BCS_Δ were the simplified variables that had the least impact on this trait. Nevertheless, average BW seemed to have a greater effect on REI than on LFCR traits, with a lower R^2 of 0.93, a higher RMSE of 0.10 UFL/d but with a similar scale of individual bias. Using the average BCS_Δ had the least effect on REI (RMSE = 0.05 UFL/d, R^2 = 0.98 and individual biases from −0.20 to 0.20). The accuracy of REI estimation with the average SMY was higher than that for LFCR regarding the R^2 (0.81 and 0.61, respectively) and RMSE but with a larger bias scale. Using an average DEI had the largest impact on REI (R^2 = 0.10, RMSE = 0.37 UFL/d) and led to a reclassification of ewes compared to the original data. Although the expected value of the mean of REI was equal to zero, individual biases were the largest (from −1.40 to 1.51). Averaging BW, BCS_Δ and DEI (model 5 in Table 2) did not reduce the important impact of DEI on the REI trait. Since BW, BCS_Δ and DEI were more difficult to phenotype on farms than SMY, having only information on individual milk performance to predict efficiency was not accurate enough (R^2 = 0.19, RMSE = 0.29 for LFCR and R^2 = 0.16, RMSE = 0.34 UFL/d for REI).

The classification of ewes based on simplified results of efficiency traits, instead of the actual results (model 6 in Table 2) into two classes (LFCR: <1, ≥1; REI: <0, ≥0), led to a classification error rate of 19% for LFCR and 43% for REI. In this classification, ewes whose efficiency was close to that of the batch average had the most misclassifications. Building the classification with three classes (LFCR: ≤0.8, 0.8–1.2, ≥1.2; REI: ≤−0.25, −0.25–0.25, ≥0.25) led to an error rate of 32% for LFCR and 50% for REI. In this classification, the middle class was well predicted, with 62% of the animals well classified for LFCR and 68% classified for REI. The rather good prediction for average values of feed efficiency traits

Table 1
Descriptive statistics of BW (kg), BCS$_\Delta$, SMY (L/d), DEI (UFL/d) and feed efficiency traits (LFCR, REI (UFL/d)) from the experimental Lacaune dairy sheep dataset.

Trait, unit	Nb. of records	Mean	SD	Min.	Max.
BW (kg)	2 146	71	10	46	99
BCS$_\Delta$	2 146	−0.02	0.21	−0.80	0.60
SMY (L/d)	2 146	2.3	0.6	0.2	4.5
DEI (UFL/d)	2 146	2.7	0.5	1.2	4.3
LFCR	2 146	0.88	0.31	0.24	1.97
REI (UFL/d)	2 146	0	0.49	−1.50	1.47

Abbreviations: BCS$_\Delta$ = variation in body condition score; SMY = standardised milk yield; DEI = daily energy intake; UFL = unité fourragère lait; LFCR = lactation feed conversion ratio; REI = residual energy intake.

Table 2
Statistic deviation indicators comparing actual and simplified LFCR and REI results of data from the experimental Lacaune dairy sheep dataset.

Trait, unit	Simplified variables used	Nb. of records	R^2	RMSE	Bias[1]
LFCR	[1] LFCR with fixed average BW	2 142	0.98	0.04	0 [−0.33; 0.30]
	[2] LFCR with fixed average BCS$_\Delta$	2 143	0.41	0.24	0.04 [−0.79; 1.34]
	[3] LFCR with fixed average SMY	2 118	0.61	0.20	−0.01 [−1.24; 0.57]
	[4] LFCR with fixed average DEI	2 125	0.56	0.22	0.01 [−0.79; 1.31]
	[5] LFCR with fixed average BW, BSC$_\Delta$ and DEI	2 146	0.19	0.29	0.06 [−0.71; 1.48]
	[6] LFCR with BW fixed to 75 kg and fixed average DEI	2 126	0.56	0.22	0 [−0.99; 1.28]
REI, UFL/d	[1] REI with fixed average BW	2 146	0.93	0.10	0 [−0.36; 0.29]
	[2] REI with fixed average BCS$_\Delta$	2 146	0.98	0.05	0 [−0.20; 0.20]
	[3] REI with fixed average SMY	2 146	0.81	0.17	0 [−0.65; 0.60]
	[4] REI with fixed average DEI	2 146	0.10	0.37	0 [−1,40; 1,51]
	[5] REI with fixed average BW, BSC$_\Delta$ and DEI	2 146	0.16	0.34	0 [−1.37; 1.59]
	[6] REI with BW fixed to 75 kg and fixed average DEI	2 146	0.09	0.38	0 [−1.43; 1.42]

Abbreviations: BCS$_\Delta$ = variation in body condition score; SMY = standardised milk yield; DEI = daily energy intake; LFCR = lactation feed conversion ratio; REI = residual energy intake; UFL = unité fourragère lait.

[1] Average bias and range of individual bias.

was linked to the use of average energy intake and requirements. However, the interest of genetic selection is to be able to distinguish extreme individuals. Classification of ewes based on the proposed feed efficiency traits would be of interest for a given collective feeding system.

Levels of milk production, intake and body reserve phenotypes of ewes on the experimental farm were consistent with those of ewes on commercial farms (Tables 1 and 3). Moreover, ewes on the experimental farm were genetically well connected to the commercial farm population through artificial insemination rams. This allowed us to extend the scope of the results obtained on feed efficiency traits from experimental farms to the commercial farm population.

For the estimation of feed efficiency traits, the validation test showed that the average BCS$_\Delta$ had a higher impact on the LFCR trait than on REI. Average BW did not generate a lot of inaccuracy, compared to milk production (SMY) and feed resources (DEI). Milk production and quality could be individually phenotyped more easily than DEI, so collective feeding remained the main limitation to calculating feed efficiency. Some studies have highlighted that individual feed intake and group feed intake data were not the same, both phenotypically and genetically. In pigs, Gao et al. (2021) studied the genetic correlation between DM intake measured individually and in pens of 10 pigs. They found a genetic correlation of 0.23 over the whole test period between the two DM intake traits, showing that they were two different traits. However, this very low correlation also may indicate the presence of a strong genotype-by-environment interaction. In beef cattle, Cooper et al. (2010) studied estimated genetic values for feed intake using several practices of BW gain and feed intake. Animals were assigned to pens containing up to nine steers. They also found a low-rank correlation of 0.15 between individual and collective pen feed intake

Table 3
Descriptive statistics (mean ± SD) for dairy traits, body reserve dynamics, intake and feed efficiency traits during lactations from the commercial Lacaune dairy sheep farm dataset.

Trait, unit	Lactation month 2	Lactation month 3	Lactation month 4	Lactation month 5	Lactation month 6	Lactation month 7	All data
Nb. of records	4 574	5 521	5 595	5 696	4 880	4 588	30 854
Nb. of ewes	3 863	4 251	4 098	4 285	3 822	3 491	4 680
DMY, L/d	2.9 ± 0.7	2.6 ± 0.6	2.2 ± 0.6	1.8 ± 0.5	1.5 ± 0.5	1.1 ± 0.4	2.04 ± 0.81
Fat content, g/L	61.6 ± 9.6	64.8 ± 9.4	71.0 ± 9.6	77.0 ± 10.8	82.0 ± 12.8	85.9 ± 13.3	73.6 ± 13.9
Protein content, g/L	50.5 ± 3.9	53.8 ± 4.6	58.7 ± 5.5	63.3 ± 6.1	66.4 ± 6.6	68.3 ± 7.6	60.1 ± 8.6
BCS	2.77 ± 0.30	2.55 ± 0.27			2.88 ± 0.24	2.91 ± 0.25	2.81 ± 0.30
BCS$_\Delta$	0.00 ± 0.23[1]	0.17 ± 0.27[2]	0.17 ± 0.27[2]	0.17 ± 0.27[2]	0.17 ± 0.27[2]	0.02 ± 0.18[3]	0.12 ± 0.27
DEI, UFL/d	2.8 ± 0.3	2.7 ± 0.3	2.5 ± 0.3	2.3 ± 0.3	2.3 ± 0.3	2.3 ± 0.3	2.5 ± 0.4
LFCR	0.94 ± 0.23	0.97 ± 0.24	1.00 ± 0.24	1.01 ± 0.29	0.92 ± 0.32	0.74 ± 0.32	0.93 ± 0.29
REI, UFL/d	0.14 ± 0.29	0.05 ± 0.33	−0.05 ± 0.29	−0.08 ± 0.30	−0.05 ± 0.27	0.00 ± 0.30	0.00 ± 0.31

Abbreviations: DMY = daily milk yield; BCS = body condition score; BCS$_\Delta$ = body condition score variation; DEI = daily energy intake; UFL = unite fourragère lait; LFCR = lactation feed conversion ratio; REI = residual energy intake.

[1] BCS$_\Delta$ between the end of suckling and the first test day (BSC$_\Delta$1).

[2] BCS$_\Delta$ between the first test day and before mating (BSC$_\Delta$2).

[3] BCS$_\Delta$ before and after mating (BSC$_\Delta$3).

data. Adding individual weight gain to the collective feed intake data increased the rank correlation to 0.32. This difficulty with collective feeding was accompanied, on commercial dairy sheep farms, by the problem of only knowing the amount of feed offered. To overcome these problems, there were individual gauges for cattle with weighing (Spurlock et al., 2012; Manafiazar et al., 2013; Li et al., 2017) or predicting DM intake (Ledinek et al., 2016; Köck et al., 2018; Huhtanen et al., 2020), and for goats, there was a trial of collective weighing on feed that was offered and refused (Chassier et al., 2022). Tools such as sensors for estimating feeding activity at the animal level have been tested, generally in dairy cows, and marketed (Dela Rue et al., 2020). The use of automatic troughs that individually recognise each animal is only possible under experimental conditions in dairy sheep and can allow monitoring only a small number of animals (González-García et al., 2020; Ledda et al., 2023). The measure of DEI on experimental farm cannot be easily propagated and compared to the one estimated in commercial farms.

On-farm feed efficiency traits and factors of variation

Descriptive statistics of feed efficiency traits and their components during lactations from the commercial farms dataset are provided in Table 3. Milk yield progressively decreased over lactation from 2.9 ± 0.7 L/d to 1.1 ± 0.4 L/d at the end of lactation (−40%). The milk components (fat and protein content) had an opposite dynamic, as they increased by 35–40% from the beginning to the end of lactation. During the period between suckling and the first test day (lactation month 2), the body reserves did not, or rarely, change (0.00 ± 0.23 average BCS_{Δ}). BCS increased from 2.77 in the first month to 2.91 in the seventh month of lactation, except in the third month where BCS decreased by 0.22 point. On average, during lactation, ewes had a BCS of 2.81 ± 0.30, and they reconstituted their body reserves with a BCS_{Δ} of 0.12 ± 0.27. With feed energy inputs relatively stable during lactation (2.3 ± 0.3 to 2.8 ± 0.3 UFL/d), LFCR averages were close to 1, except at month 7 with 0.74 ± 0.32. Regarding REI mean values, animals appeared to be inefficient at lactation month 2 (0.14 ± 0.29 UFL/d). For other stages of lactation, the REI values were close to 0, with average values ranging from −0.08 to 0.05 UFL/d.

All environmental fixed effects (parity, litter size, mating mode and lambing period) included in multiple linear models were globally significant for all stages of lactation for the LFCR trait but not for the REI trait, e.g., parity was only significant at lactation months 2, 5, 6 and 7. The adjustment quality explained by R^2 was from 0.30 to 0.49 for LFCR and from 0.67 to 0.81 for REI. An analysis of variance highlighted that flock interaction with year significantly affected the variability of the two feed efficiency traits the most (85 to 99% of the R^2 model per lactation month). Estimated means adjusted for the month of lactation showed a reversal of the feed efficiency trend from the fourth lactation month. Two patterns could be observed depending on the trait. For the LFCR trait, values had a linear evolution between lactation months 2 and 4 from 0.94 to 0.99, and then values decreased over time from 0.95 to 0.73 between months 5 and 7. Adjusted means estimated for REI dropped from months 2 to 4 (from 0.16 to −0.06) and appeared to be similar during the last three months of the testing period.

Heritabilities of daily milk yield and feed efficiency traits at each lactation month

The heritability estimates of DMY, LFCR and REI at each lactation stage from the commercial farms dataset are presented in Fig. 1. Estimated heritabilities for DMY were low and relatively stable during lactation (from 0.15 ± 0.03 to 0.19 ± 0.03). Estimated heritabilities for approximated feed efficiency traits were low for LFCR (ranging from 0.08 ± 0.02 to 0.14 ± 0.03) and were low to moderate for REI depending on the lactation stage (ranging from 0.09 ± 0.02 to 0.21 ± 0.03). On the second month of lactation, the heritability of LFCR was the lowest, while for REI, it was the highest (0.08 ± 0.02 vs 0.21 ± 0.03, respectively). Longitudinal genetic analysis in dairy cattle with daily or monthly data presented heritabilities of the same order for a similar testing period. Liinamo et al. (2015) in Nordic Red dairy cattle showed the highest estimated heritability in the first two and last two lactation months for REI and the energy conversion efficiency ratio and very low heritabilities during the middle of lactation from months 3 to 6. In the study of Spurlock et al. (2012) in Holstein cows in the USA with precise individual feed intake measures, heritabilities of energy balance decreased over time. Varied trends in heritability estimates of the RFI trait were found by Tempelman et al. (2015) analysing data from three countries, and Li et al. (2017) for Holstein cows with increasing values during lactation.

Genetic correlations between months of lactation for feed efficiency traits

Phenotypic and genetic correlations between each stage of lactation for LFCR and REI traits estimated from the commercial farms dataset are presented in Table 4. Phenotypic correlations between lactation stages were overall higher for the LFCR trait than for REI. Between two successive lactation months, genetic correlations were high for each feed efficiency trait (ranging from 0.85 ± 0.08 to 1 ± 0.06). The longer the time between two measurements of feed efficiency, the lower the genetic correlations. Feed efficiency traits were more correlated in mid-lactation, e.g., 1 ± 0.06 between months 3 and 4 and 0.91 ± 0.09 between months 3 and 5 for LFCR. These highest genetic correlations in mid-lactation can be partly explained by the use of the same BSC_{Δ} data in the calculations for the feed efficiency traits. Feed efficiency traits at the beginning of the milking season (month 2) seemed to be slightly correlated with the same traits at the end of lactation, particularly with month 6 of lactation (0.16 ± 0.19 for LFCR, 0.32 ± 0.12 for REI). This low specific genetic correlation made it possible to distinguish the periods in the sheepfold when diets changed little and the periods on the pasture when feed intake estimation was less precise and milk production dropped. In dairy cattle, Li et al. (2017) reported that RFI in middle and late lactation were genetically highly correlated with each other and have low correlations with RFI in early lactation.

Given the relatively low genetic correlation between the beginning and the end of lactation (corresponding to periods of sheepfold or grazing), it is unclear when to measure feed efficiency traits. The economic interest in feed efficiency is greater during the sheepfold period than during the grazing period, when feed costs are lower. Moreover, estimates of feed efficiency traits would be more robust due to the stable energy intake during the indoor period (De Boissieu et al., 2019). Fisher (2017) suggested calculating feed efficiency in dairy cattle from 2.5 lactation months to avoid rapid changes in energy supply and requirements in early lactation. In addition, in dairy ewes, Hassoun et al. (2018) suggested starting to calculate intake capacity when it stabilises, i.e., between weeks 4 and 6 after lambing. This allows us to exclude the suckling period and the drop in milk production when the lambs were weaned.

Genetic parameters over the whole lactation for milk production traits and feed efficiency traits

For feed efficiency and milk production traits, estimates of heritabilities and of 2 by 2 phenotypic and genetic correlations from the commercial farms dataset are presented in Table 5. The heri-

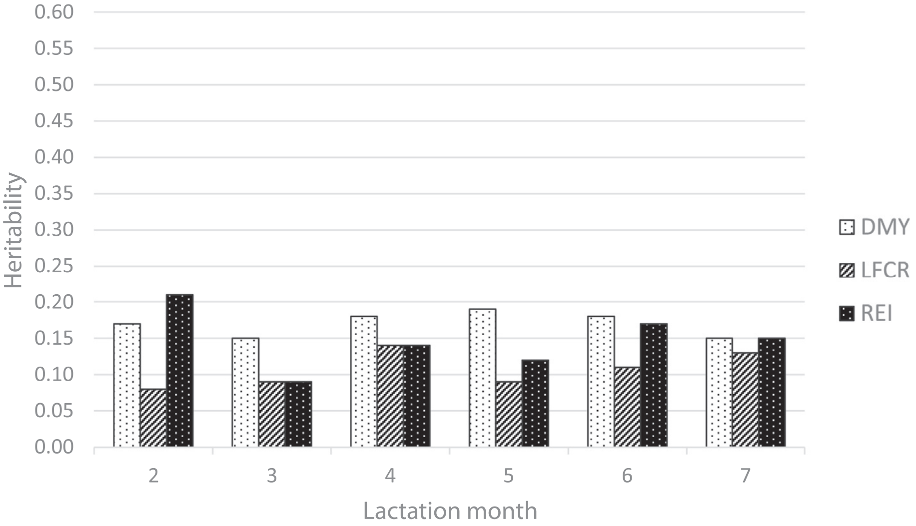

Fig. 1. Heritability estimates for traits DMY, LFCR and REI over lactation months 2–7 from the commercial Lacaune dairy sheep farm dataset (SE of estimates varied between 0.02 and 0.03 for all traits). Abbreviations: DMY = daily milk yield; LFCR = lactation feed conversion ratio; REI = residual energy intake.

Table 4
Phenotypic (above the diagonal) and genetic (below the diagonal) correlations (±SE) between each lactation month for LFCR (A) and REI (B) traits from the commercial Lacaune dairy sheep farm dataset.

(A)

	Lactation month 2	Lactation month 3	Lactation month 4	Lactation month 5	Lactation month 6	Lactation month 7
Lactation month 2	_	0.42 ± 0.01	0.30 ± 0.02	0.31 ± 0.01	0.14 ± 0.02	0.16 ± 0.02
Lactation month 3	0.90 ± 0.11	_	0.51 ± 0.01	0.42 ± 0.01	0.31 ± 0.01	0.21 ± 0.02
Lactation month 4	0.76 ± 0.13	1 ± 0.06	_	0.54 ± 0.01	0.44 ± 0.01	0.25 ± 0.02
Lactation month 5	0.58 ± 0.15	0.91 ± 0.09	0.94 ± 0.06	_	0.49 ± 0.01	0.35 ± 0.02
Lactation month 6	0.10 ± 0.19	0.75 ± 0.12	0.66 ± 0.10	0.97 ± 0.07	_	0.48 ± 0.01
Lactation month 7	0.46 ± 0.17	0.53 ± 0.14	0.54 ± 0.12	0.67 ± 0.13	0.91 ± 0.08	_

(B)

	Lactation month 2	Lactation month 3	Lactation month 4	Lactation month 5	Lactation month 6	Lactation month 7
Lactation month 2	_	0.42 ± 0.01	0.05 ± 0.02	0.26 ± 0.02	0.06 ± 0.02	0.11 ± 0.02
Lactation month 3	0.83 ± 0.09	_	0.27 ± 0.02	0.19 ± 0.02	0.17 ± 0.02	0.10 ± 0.02
Lactation month 4	0.42 ± 0.13	0.82 ± 0.11	_	0.34 ± 0.01	0.35 ± 0.02	0.28 ± 0.02
Lactation month 5	0.36 ± 0.12	0.61 ± 0.14	0.86 ± 0.08	_	0.19 ± 0.02	0.17 ± 0.02
Lactation month 6	0.24 ± 0.12	0.73 ± 0.13	0.59 ± 0.10	0.96 ± 0.09	_	0.47 ± 0.01
Lactation month 7	0.59 ± 0.11	0.60 ± 0.13	0.67 ± 0.10	0.52 ± 0.13	0.95 ± 0.05	_

Abbreviations: LFCR = lactation feed conversion ratio; REI = residual energy intake.

tabilities of the three milk production traits were low (0.16 ± 0.02 for DMY) to moderate (0.36 ± 0.02 for fat content and 0.43 ± 0.02 for protein content). DMY was highly correlated with their quality components (−0.50 ± 0.05 with fat content and −0.62 ± 0.05 with protein content). Heritabilities related to approximated feed efficiency traits were low (0.10 ± 0.01 for LFCR, 0.11 ± 0.01 for REI) over the whole lactation period. The heritabilities of the numerator and denominator of the LFCR trait were estimated separately with values of 0.12 ± 0.02 and 0.03 ± 0.008, respectively. A similar heritability was found for the LFCR trait (0.10 ± 0.04) from the experimental dataset presented in Table 1, with individual feed intake measurements. In dairy cattle, studies using similar traits on whole lactation reported higher heritability estimates of LFCR-type traits, with 0.16 ± 0.01 (Hurley et al., 2018) in Holstein-Friesian cows from an estimate of pasture intake and 0.20 (Parke et al., 1999) and 0.25 ± 0.03 (Manafiazar et al., 2016) in Holstein cows from the amount of feed weighed. Köck et al. (2018) found similar heritability results in the efficiency ratio during lactation on Austrian farms, with environmental diversity and predicted DM intake, from 0.09 ± 0.03 to 0.11 ± 0.04 depending on the cattle breed

Table 5
Estimates of heritabilities ± SE (on the diagonal), phenotypic (above the diagonal) and genetic correlations ± SE (below the diagonal) among feed efficiency and milk production traits from the commercial Lacaune dairy sheep farm dataset.

	DMY	Fat content	Protein content	LFCR	REI
DMY	0.16 ± 0.02	−0.23 ± 0.01	−0.36 ± 0.01	0.76 ± 0.003	−0.44 ± 0.01
Fat content	−0.50 ± 0.05	0.36 ± 0.02	0.51 ± 0.01	0.12 ± 0.01	0.15 ± 0.01
Protein content	−0.62 ± 0.05	0.65 ± 0.03	0.43 ± 0.02	−0.08 ± 0.01	0.30 ± 0.01
LFCR	0.74 ± 0.04	0.11 ± 0.07	−0.18 ± 0.07	0.10 ± 0.01	−0.65 ± 0.004
REI	−0.79 ± 0.04	0.46 ± 0.06	0.75 ± 0.04	−0.63 ± 0.06	0.11 ± 0.01

Abbreviations: DMY = daily milk yield; LFCR = lactation feed conversion ratio; REI = residual energy intake.

(Fleckvieh, Brown Swiss or Holstein). The estimated heritability of REI in our study was higher than that reported in the Holstein-Friesian cattle breed (0.07 ± 0.02) (Hurley et al., 2018). The heritability of the RFI trait in dairy cattle was 0.20 ± 0.03 in Manafiazar et al. (2016) and varied from 0.01 ± 0.05 to 0.27 ± 0.12 in the review from Brito et al. (2020). Although approximate traits were used in our study, their heritabilities were lower or sometimes close to than those of studies using more precise individual phenotypes.

Repeatabilities over lactations of dairy production traits (0.51 for DMY, 0.45 for fat content and 0.54 for protein content) were higher than for efficiency traits (0.34 for LFCR and 0.22 for REI). In each month, the repeatability of the efficiency traits was of the same order (from 0.15 to 0.30 for LFCR and from 0.14 to 0.29 for REI). These results for feed efficiency traits were close to those estimated in dairy cattle studies. In this species, repeatability across lactations for the RFI trait was estimated to be 0.20 by Connor et al. (2013) and from 0.10 to 0.35 by Tempelman et al. (2015) in Holstein cows. Over the same lactation period, efficiency traits showed moderate repeatability, from 0.30 to 0.36 for the ratio-type trait according to dairy cow breeds (Köck et al., 2018) and 0.47 for the RFI trait (Connor et al., 2013). The low repeatability values in the present study could be explained by the feed strategy that increased the proportion between products and resources over time. Milk production decreased while feed intake decreased more slowly during the indoor period, with a greater proportional difference for the less milk-productive ewes (De Boissieu et al., 2019). The partial data information to record feed values and the wide variety in feed diets may affect the repeatability of efficiency results.

The phenotypic and genetic correlations between LFCR and REI of −0.65 ± 0.004 and −0.63 ± 0.06, respectively (Table 5), showed a strong relationship between efficiency traits. This result was also reported by Vallimont et al. (2011) in Holstein dairy cows with a phenotypic correlation of −0.53 ± 0.03 and a genetic correlation of −0.69 ± 0.86 between net energy for lactation efficiency trait and RFI. Manafiazar et al. (2016) in Holstein cows reported genetic correlations of −0.57 ± 0.22 and 0.33 ± 0.23 between the lactation gross energy efficiency trait (lactation energy corrected milk/lactation actual energy intake) or LFCR-type trait (lactation DM intake/lactation fat corrected milk) and RFI, respectively.

In our study, feed efficiency traits were genetically dependent on milk production traits (Table 5). LFCR was more correlated with DMY than with milk components (0.74 ± 0.04 with DMY, 0.11 ± 0.07 with fat content and −0.18 ± 0.07 with protein content), whereas REI was highly correlated with these three dairy traits (−0.79 ± 0.04 with DMY, 0.46 ± 0.06 with fat content and 0.75 ± 0.04 with protein content). The high genetic correlation between LFCR and DMY was a consequence mainly led by the net energy of SMY and very few by DEI. REI and RFI must be independent by construction from the milk production traits considering the regression model used for their calculation, as shown in dairy cattle by Hurley et al. (2018) or Brito et al. (2020), who reviewed low genetic correlations between RFI and milk production traits. In our study, this dependence between REI and components from the regression model of REI could be explained by a lack of accuracy in DM intake and DEI measurements. On the other hand, it can also be hypothesised that in the specific context of feeding a flock of ewes, here at 110% of the energy requirements for an average ewe (Hassoun et al., 2018), the highest milk-producing ewes could also be the most efficient ones. This context would lead to the selection of the most productive ewes, which would also indirectly be the most efficient. However, an animal with low milk production cannot be shown to be efficient with the proposed traits studied on farms.

Additional analyses have been developed to better understand the relationship between DMY and REI according to environmental factors, which is illustrated in Fig. 2. A strong influence of flock, year and lactation month was shown on these traits. The interaction between flock and milk production year can be observed by discerning significantly different slopes. A stratification of the results between DMY and REI was also observed according to the stage of lactation. A second REI trait (REI2) was calculated, including additional independent variables, to consider the data stratification. REI2 was the residual of multiple linear regression of DEI on DMY, fat content, protein content, BSC_{Δ}, BW, and the interaction of flock-year-lactation month and was analysed by the same animal model as REI. Phenotypically and genetically, REI2 was less correlated with dairy traits. Phenotypic correlations between REI2 and DMY, fat content or protein content were −0.05 ± 0.01, −0.14 ± 0.01 and −0.05 ± 0.01, respectively. Genetic correlations between REI2 and dairy traits were lower, with −0.15 ± 0.11 for DMY, −0.34 ± 0.08 for fat content and −0.002 ± 0.08 for protein content. However, these estimates showed larger SEs than the original REI trait. The phenotypic correlation between REI and REI2 was 0.88 ± 0.002, and the genetic correlation was 0.36 ± 0.10. In the commercial farm context, environmental effects have a strong influence on the studied efficiency traits. The use of two genetically linked populations with a population phenotyped at the batch level trying to approach the feed consumed and not just the feed offered, combined with a population much more finely phenotyped at the individual level, would be interesting to improve data collection on farms.

Different applications could be considered depending on the efficiency traits. The ratio traits could be easier to understand, facilitate communication in the dairy sheep sector, and provide technical advice in flocks. However, several studies have raised the challenges of using this kind of trait, such as LFCR, in selection due to their construction as a ratio (Gunsett, 1984; Van der Werf, 2004; Fisher, 2017). The inability to predict the response of ratio traits makes their genetic selection inappropriate. In addition, the validation step showed a strong impact from non-individualised measures such as group intake data on ratio-type trait. Despite this, the heritabilities estimated from the two data sets (from commercial and experimental farms) were similar. However, the proposed LFCR trait was mainly guided by the net energy of SMY and only marginally influenced by traits in its denominator. The REI trait is a more complex indicator but is more efficient from a genetic selection perspective. In a collective feeding context, the variability of the trait being underestimated, most of the genetic variability was explained by milk production, which ultimately undermine the possibility to use this trait for selection.

Conclusion

The types of data needed to approach a reliable feed efficiency trait were targeted in this study. The results showed the limitations of studying feed efficiency at the individual level from collective feeding and in a diversified feeding and management context. Collective feeding remains the main challenge in evaluating feed-efficient traits and therefore limits the possibilities for the selection of efficient animals. The limitations of the on-farm dairy sheep measurements highlighted in these results indicate that high-throughput phenotyping will be a key point for the study of complex traits in future. This study demonstrated the interest of phenotyping feed intake as a tool to support breeders in the sheep sector, especially if measurements are taken during the sheepfold period to avoid sources of bias. The genetic variability of the proposed feed-efficient traits might suggest that these traits could be used in selection. However, validation and genetic analysis indicated that the construction of these traits still needs to be improved. The interpretation of the results was strongly linked to

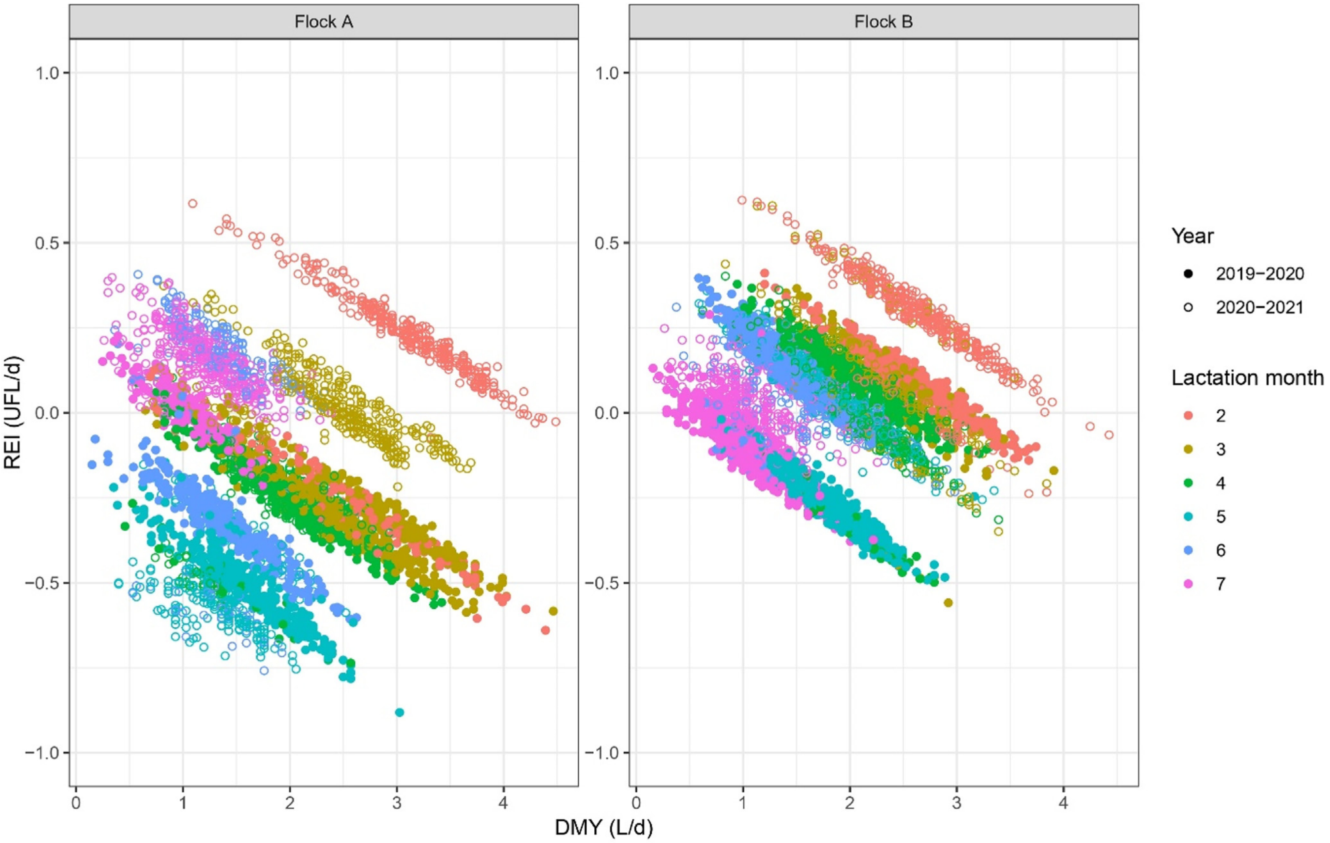

Fig. 2. Illustration of the phenotypic relationship between DMY and REI according to farm (two farms, for example), milk production year and lactation month from the commercial Lacaune dairy sheep farm dataset. Abbreviations: DMY = daily milk yield; REI = residual energy intake; UFL = unité fourragère lait.

the way the animals were bred. The results cannot be extended to systems very different from those practiced in the Lacaune breed. Therefore, this study should be continued in other breed systems, such as in Pyrenean breeds with a very different breeding context.

Supplementary material

Supplementary material to this article can be found online at https://doi.org/10.1016/j.animal.2023.100951.

Ethics approval

Formal ethical approval was not required for the commercial animal study because it was performed with data recorded from production animals. However, the measurement procedures were approved out of scope by the Regional Ethics Committee on Animal Experimentation - Animal Science and Health N°115- under the registration identification SSA_2020_013. For validation of feed efficiency traits, data came from the INRAE experimental farm of La Fage (user establishment: A312031), with breeding conditions similar to those of commercial sheep flocks. Individual measurements of feed intake followed a procedure approved by the Regional Ethics Committee on Animal Experimentation N°115 under the formal approval agreement APAFIS#5436-201605231517774.

Data and model availability statement

The datasets generated and/or analysed during the current study are not publicly available because they were partially produced by private professional partnerships. None of the data were deposited in an official repository.

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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Author contributions

PH, SP, CA and **DP** collected and provided data from the La Fage experimental unit. **GL and CM** assisted in the collection and editing of data from commercial farms. **JMA** transferred the data from official databases. **HL** and **CRH** designed the study. **CM** analysed the data and drafted the first version of the manuscript. **CM, CRG and HL** interpreted the results. **CRG, HL, PH** and **GL** revised and improved the manuscript. All authors read and approved the final manuscript.

Declaration of interest

The authors declare they have no competing interests.

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