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Relationship between feed efficiency and resilience in dairy ewes subjected to acute underfeeding

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ABSTRACT

Selection of dairy sheep based on production levels has caused a loss of rusticity, which might compromise their future resilience to nutritional challenges. Although refocusing breeding programs toward improved feed efficiency (FE) is expected, more-efficient ewes also seem to be more productive. As a first step to examine the relationship between FE and resilience in dairy sheep, in this study we explored the variation in the response to and the recovery from an acute nutritional challenge in high-yielding Assaf ewes phenotypically divergent for FE. First, feed intake, milk yield and composition, and body weight changes were recorded individually over a 3-wk period in a total of 40 sheep fed a total mixed ration (TMR) ad libitum. Data were used to calculate their FE index (FEI, defined as the difference between the actual and predicted intake estimated through net energy requirements for maintenance, production, and weight change). The highest and lowest FE ewes (H-FE and L-FE groups, respectively; 10 animals/group) were selected and then subjected to the nutritional challenge (i.e., withdrawing the TMR and limiting their diet only to the consumption of straw for 3 d). Afterward, sheep were fed again the TMR ad libitum. Temporal patterns of variation in performance traits, and ruminal fermentation and blood parameters were examined. A good consistency between FEI, residual feed intake, and feed conversion ratio was observed. Results supported that H-FE were more productive than L-FE sheep at similar intake level. Average time trends of milk yield generated by a piecewise model suggest that temporal patterns of variation in this trait would be related to prechallenge production level (i.e., H-FE presented quicker response and recovery than L-FE). Considering all studied traits, the overall response to and recovery from underfeeding was apparently similar or even better in H-FE than in L-FE. This would refute the initial hypothesis of a poorer resilience of more-efficient sheep to an acute underfeeding. However, the question remains whether a longer term feed restriction might impair the ability of H-FE ewes to maintain or revert to a high-production status, which would require further research.
Key words: nutrition, performance, residual feed intake, sheep

INTRODUCTION

Small ruminants have traditionally been reared in less-favored areas, including harsh environments in which other livestock systems would be hampered (Pardo and del Prado, 2020; Leite et al., 2021). They have developed high resistance and resilience, and their rearing has therefore been proposed as a promising option to ensure food security in a climate change scenario (Silanikove and Koluman, 2015; Pardo and del Prado, 2020).

In the last decades, however, selection of dairy sheep has focused on increasing their production levels. Thus, some of the most widespread breeds in leading dairy farms (e.g., Assaf ewes) have lost rusticity, which may be defined as a mixture of ancient character, roughness, and robustness (Sauvant and Martin, 2010). As a consequence, their productive lifespan has been affected by a greater incidence of metabolic disorders and mastitis (de Rancourt et al., 2006; Milán et al., 2011). The loss of rusticity might also compromise their future productivity due to nutritional challenges, which are expected to increase as a result of climate change and feed supply crises (Tedeschi et al., 2015; Joy et al., 2020).

Currently, breeding programs are being refocused toward improved feed efficiency (**FE**) instead of production level. However, the extent to which FE may be improved without affecting resilience is still largely unknown, not only in sheep, but in dairy ruminants in general (Zou et al., 2019; Bengtsson et al., 2022; Tarrah et al., 2022).

Resilience represents the ability of an animal to revert quickly to previous production level and health status in response to a perturbation (Tedeschi et al., 2015; Joy et al., 2020; Friggens et al., 2022). Thus, explor-

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ing the variation in the response to and the recovery from a nutritional challenge in animals of divergent FE may represent a first step in examining the relationship between FE and resilience in dairy sheep.

In a previous study in lactating sheep (Toral et al., 2021), we observed that more-efficient animals were also more productive. Thus, our initial hypothesis in the present trial was that more-efficient sheep would show a worse response (i.e., lower resilience) than less-efficient animals. In the best-case scenario, high- and low-FE sheep would have comparable resilience to the challenge and their initial performance would be recovered equally.

On this basis, we conducted this study to compare the temporal pattern of variation in animal performance, and ruminal fermentation and blood parameters in high-yielding dairy ewes phenotypically divergent for FE and subjected to an acute nutritional challenge (i.e., withdrawing the TMR and limiting their diet only to the consumption of straw for 3 d).

MATERIALS AND METHODS

Ethics Statements

All experimental procedures were approved by the Research Ethics Committees of the Instituto de Ganadería de Montaña, the Spanish National Research Council (CSIC), and the Junta de Castilla y León (Spain), following proceedings described in Spanish and European Union legislation (Royal Decree 53/2013 and Council Directive 2010/63/EU).

Animals, Experimental Diet, and Management

Forty Assaf ewes in their first lactation (BW = 64.8 ± 2.31 kg; DIM = 44.3 ± 2.58; milk yield (**MY**) = 2.52 ± 0.171 kg/d), and with similar genetic background, were housed in individual pens. Estrus had been synchronized and lambing was concentrated in few days to avoid potential variations due to lactation stage.

Sheep were milked twice daily at approximately 0830 and 1830 h in a 1 × 10 stall milking parlor (DeLaval). Ewes were fed a TMR from a commercial supplier and the offer was daily adjusted to ensure ad libitum intakes (10–15% orts). The TMR was formulated from alfalfa hay (particle size >4 cm) and concentrates (50:50 forage:concentrate ratio), including sugar beet molasses to hinder selection of dietary components (Table 1). Clean drinking water was always available.

The experiment was divided into 2 parts: a first part to estimate FE and select more and less-efficient ewes (preliminary phase), and a second part where selected animals were subjected to the nutritional challenge.

Table 1. Formulation and chemical composition of TMR and the wheat straw

Item	TMR[1]	Wheat straw[2]
Ingredients, % of fresh matter		
Dehydrated alfalfa hay, particle size > 4 cm	50	—
Whole corn grain	14	—
Whole barley grain	10	—
Soybean meal solvent 440 g CP/kg	15	—
Sugar beet pulp, pellets	5	—
Sugar beet molasses, liquid	4	—
Vitamin-mineral supplement[3]	2	—
Chemical composition, % DM		
OM	90.2 ± 0.22	95.2
CP	19.8 ± 0.27	2.9
NDF	30.9 ± 2.93	77.2
ADF	20.1 ± 1.70	43.4
ADL	4.1 ± 0.61	4.5
Starch	13.0 ± 1.72	1.3
Ether extract	2.4 ± 0.41	1.6

[1]The chemical composition is the mean ± SD of 2 representative samples.

[2]Chopped through a 3-cm screen. The composition represents the mean of one representative sample.

[3]MACROFAC Rumiantes (UP911755130; DSM Nutritional Products S.A.). Declared as containing: Ca (285 g/kg), Na (7.5 g/kg), Fe (3 g/kg), Mn (3 g/kg), Zn (2 g/kg), Mg (1 g/kg), P (910 mg/kg), Mo (100 mg/kg), Co (67 mg/kg), I (50 mg/kg), S (40 mg/kg), Se (7 mg/kg), vitamin A (200,000 IU/kg), vitamin D3 (40,000 IU/kg), vitamin E (667 mg/kg), ethoxyquin (12 mg/kg), and propyl gallate (2 mg/kg).

Feed Efficiency Estimation and Selection of Ewes (Preliminary Phase)

After adaptation of the ewes to the TMR (>3 wk), individual DMI and MY were daily measured over 3 wk to estimate the FE. Feed intake was calculated daily by weighing the amounts of DM offered and refused by each animal. Total milk produced by each animal at morning and evening milkings was collected and weighed to calculate daily MY. Composite samples of the milk produced by each ewe were prepared daily according to individual yields in both milkings. Aliquots of 40 mL of that composite milk were preserved with bronopol (D and F Control Systems Inc.) and stored at 4°C until analyzed for fat, protein, and lactose contents. Changes in BW were calculated for each sheep by recording BW on 2 consecutive days at the beginning and at the end of the period.

The FE index (**FEI**) was calculated as follows:

$$FEI = DMI_R - DMI_P,$$

where DMI_R is the mean value of recorded DMI over the 3-wk experimental period, and DMI_P is the mean value of predicted DMI for the same period.

The DMI_P was computed as:

$$DMI_P = NE_R / NE_{TMR},$$

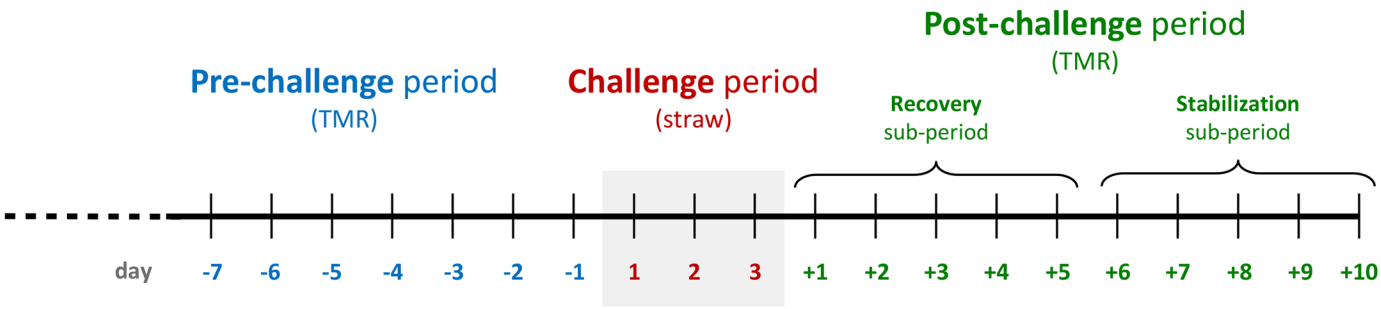

Figure 1. Diagram of the experimental schedule. High-feed efficiency and low-feed efficiency groups of ewes were subjected to an acute nutritional challenge (i.e., fed only straw for 3 d).

where NE_R are the net energy requirements [forage unit for lactation (**UFL**)/d] for maintenance, milk production, and BW change; and NE_{TMR} is the net energy of the TMR (UFL/kg DM), estimated on the basis of published net energy values of ingredients used in the TMR formulation, according to the INRA (2018) tables of nutritional value. The estimated NE_{TMR} was 0.930 UFL/kg DM. Net energy requirements for maintenance, production, and BW change were calculated using the equations proposed by the INRA (2018).

The 10 highest FE (**H-FE** group) and 10 lowest FE (**L-FE** group) animals were selected using this FEI.

In addition to this index, 2 more FE metrics were calculated: the residual feed intake (**RFI**) and the feed conversion ratio (**FCR**). The RFI values were estimated for the 40 ewes as residuals of the following regression model, using the GLM procedure of the SAS software package (version 9.4; SAS Institute Inc.):

$$\text{DMI} = \mu + a \times \text{ECM} + b \times \text{MBW} + c \times \text{BW} \times \text{BWC} + \text{RFI},$$

where DMI represents the mean dry matter intake during the experimental period (kg/d); μ is the intercept; ECM is the energy-corrected MY (kg/d); MBW is the mean metabolic BW ($BW^{0.75}$; kg); BW × BWC is the interaction between the BW (kg), and the BW change per day (kg/d); RFI is the residuals; and a, b, and c are the regression coefficients. The ECM was calculated using INRA (2018) equation for sheep [ECM = kg/d of MY × [(0.0071 × g/kg of milk fat) + (0.0043 × g/kg of milk protein) + 0.2224], which assumes a net energy concentration of 0.686 UFL/l (equivalent to approximately 4.88 MJ/kg).

The FCR was calculated as the ratio between DMI and ECM.

Nutritional Challenge

Selected ewes (H-FE and L-FE groups; 10 + 10) were then (i.e., after the period used to estimate FE) subjected to an acute nutritional challenge by withdrawing the TMR and feeding them only wheat straw (chopped through a 3-cm screen) for 3 d. As shown in Figure 1, measurements and sampling were conducted (i) before the challenge (prechallenge period), (ii) at the end of the challenge period, and (iii) after the challenge (postchallenge period). A posteriori, the postchallenge period was divided in 2 subperiods based on the dynamics of DMI and MY: recovery and stabilization periods.

During the prechallenged period, one ewe from each group was removed from the assay because of unexpected decreases in DMI (i.e., not associated with the challenge).

Feed Intake and Diet. Feed intake was measured daily by weighing the amount of DM offered and refused by each animal. Representative samples of the TMR and the wheat straw were collected in each period (i.e., in the pre- and postchallenge periods for the TMR, and in the challenge period for the straw), stored at –30°C, and then freeze-dried before chemical analysis.

Body Weight. Body weight was recorded on 2 consecutive days at the prechallenge (d −7 and −6) and postchallenge (d +9 and +10) periods.

Milk. Milk yield was recorded daily. Individual milk samples were collected on 2 consecutive days at the end of the prechallenge period (d −2 and −1), on the last day of the challenge (d 3), and on d +3, +8, and +9 of the postchallenge period. As mentioned before for the first part of the study, aliquots of 40 mL of milk were preserved with bronopol and stored at 4°C until analyzed for fat, protein, lactose, and TS concentrations, and for SCC.

Blood. At the end of each period, before the morning milking and the administration of the TMR, blood

samples were collected into clot activator tubes (BD Vacutainer), which were incubated at ambient temperature for 6 h, stored at 4°C overnight, and then centrifuged (1,811 *g*) at 4°C for 10 min. Aliquots of serum were stored at −80°C until analyzed for insulin, BHB, nonesterified fatty acids (**NEFA**), and urea concentrations. For plasma glucose determinations, additional blood samples were collected at the same time into lithium heparin tubes (BD Vacutainer), immediately centrifuged (1,811 *g*) at 4°C for 10 min, and then stored at −80°C until submitted for analysis.

Ruminal Fluid. On the last day of each period, animals were given free access to the TMR for 1 h after milking. Orts were then removed and, 3 h later, individual samples of ruminal fluid (ca. 150 mL) were obtained using an oral stomach probe (Ramos-Morales et al., 2014). The fluid was immediately strained through a nylon membrane (400 μm; Fisher Scientific S.L.). Then, 3 mL of ruminal fluid were acidified with 3 mL of 0.2 *M* HCl for ammonia analysis, and 0.8 mL was deproteinized with 0.5 mL of 20 g of metaphosphoric acid/L and 4 g of crotonic acid/L in 0.5 *M* HCl for VFA determinations. These samples were stored at −30°C until laboratory analyses.

Laboratory Analyses

Diets and Orts. Dry matter was determined in the TMR, wheat straw, and orts (ISO 6496:1999). The TMR and wheat straw were also analyzed for ash (ISO 5984:2002), and CP (ISO 5983–2:2009). The NDF and ADF were determined using an Ankom 2000 fiber analyzer (Methods 13 and 12, respectively; Ankom Technology Corp.); the former was assayed with sodium sulfite and α-amylase, and both were expressed with residual ash. Starch content was analyzed using a total starch assay kit (K-TSTA; Megazyme Intl. Ireland Ltd.).

Milk. Concentrations of fat, protein, lactose, and TS were determined by infrared spectrophotometry (ISO 9622:1999) using a MilkoScan FT6000 (Foss), combined with a fluoro-opto-electronic counter (Fossomatic 5000, Foss) for SCC (ISO 13366–2:2006).

Blood. Concentrations of BHB, glucose, NEFA, and urea were measured with a clinical chemistry analyzer (Biosystems BA400; Biosystems S.A.). Insulin was quantified using an immunoassay system (Immulite 2000 XPi; Siemens Diagnostics).

Ruminal Fluid. Ammonia concentration was measured spectrophotometrically, using the salicylate method (Reardon et al., 1966), and VFA were analyzed by gas chromatography, using crotonic acid as the internal standard (Ottenstein and Bartley, 1971).

Statistical Analyses

Piecewise Modeling. Challenge-response profiles of traits for which daily data were available (namely DMI and MY) were analyzed using 2 different piecewise mixed-effects models, one for DMI and another one for MY. Both models considered the fixed effect of group (i.e., H-FE and L-FE) and the random effect of individuals (adapted from Friggens et al., 2016). Each piecewise mixed-effects model was fitted with 4 parameters that describe the phases of the experimental challenge (V_1, V_3, and V_4 represent the same in both models; only V_2 varies for DMI or MY models):

- V_1, the model intercept that represents the prechallenge period.
- V_2. For DMI: the drop of DMI at the beginning of the challenge. For MY: the linear rate of response of MY to the 3-d challenge.
- V_3 and V_4, that represent, respectively, the linear rate of recovery from challenge and the quadratic rate of deceleration in the recovery period, which lasted until d 5 from refeeding (confirmed by visual inspection of data). The postchallenge stable level (V_5) can be calculated from V_1 to V_4 as follows:

$$V_5 = V_1 + (V_2 \times A) + (V_3 \times B) + (V_4 \times B^2),$$

where for the DMI model, A equals 1 because V_2 (kg) represents the drop of intake at the start of the challenge; and for the MY model, A equals 3 because V_2 (kg/d) corresponds to the linear response of production during the 3-d challenge.

For both models: B equals 5 because it corresponds to the 5 d of the recovery period.

The random effect of individuals was considered in all 4 parameters of the piecewise model and assumed to be $\sim$iidN(0, σ_B^2). The residual error of the piecewise model was assumed to be $\sim$N (0, R), with R as the heterogeneous autoregressive of order 1 error covariance structure, used to correct for lack of independence in the residual and heterogeneity of variances along predictions. The *lme* function of the *nlme* package (R Core Team, 2022) was used to fit the piecewise models using R software (v4.2.1). Contrasts on the model parameters, using general hypothesis testing, function *glht* of package *multcomp* (Hothorn et al., 2008), were used to test differences between prechallenge and postchallenge stabilization periods (V_1 vs. V_5).

All the graphics were performed using *ggplot2* package of software R. Statistical significance was set at $P \leq 0.05$.

Other Statistical Analyses. Statistical analyses of traits for which daily data were not available (i.e., all but DMI and MY) were conducted using the MIXED procedure of the SAS software package. First, data of FE predictors (preliminary phase of the experiment) and BW change (nutritional challenge assay) were subjected to ANOVA to test the fixed effects of the group (i.e., H-FE vs. L-FE). Second, data of milk composition, ruminal fermentation, and blood parameters (recorded at the end of each period) were subjected to repeated measurements analysis. The statistical model included the fixed effects of the group, the period (i.e., prechallenge, challenge, and postchallenge, which were included as repeated measurements) and their interaction, assuming a covariance structure fitted on the basis of Akaike information model fit criterion. Animals were nested within the group. Means were separated through the pairwise differences (pdiff) option of the least squares means (lsmeans) statement of the MIXED procedure and adjusted for multiple comparisons using a Bonferroni correction.

Differences were declared significant at $P < 0.05$ and considered a trend toward significance at $0.05 \leq P < 0.10$. Least squares means are reported.

RESULTS

Feed Efficiency Predictors

By design, FEI values differed significantly between H-FE and L-FE sheep ($P < 0.001$; Table 2). Similar differences were also observed for RFI and FCR ($P < 0.001$). Descriptive statistics of these predictors for selected groups of ewes are reported in Supplemental Table S1 (https://doi.org/10.20350/digitalCSIC/15094).

Animal Performance

Average time trends of DMI and MY generated by the piecewise model are shown in Figure 2, whereas the associated prediction model parameters are reported in Table 3 (see Supplemental Figure S1 and S2 for standardized residuals: https://doi.org/10.20350/digitalCSIC/15094). Starting with DMI, none of the parameters differed significantly between H-FE and L-FE groups ($P < 0.05$). Daily DMI during the 3-d challenge averaged 0.489 and 0.471 kg/d in H-FE and L-FE, respectively (SED, 0.0366: data not shown in tables). Only in L-FE ewes, V_5 was lower than V_1 ($P < 0.05$; data not shown in tables), which indicates that initial values of DMI were not fully recovered after the challenge.

Milk yield was higher in H-FE than in L-FE in the prechallenge period (V_1; $P < 0.05$), and the rate of response observed during the underfeeding challenge (V_2) was also more intense in H-FE ($P < 0.05$). Regarding the recovery period, the linear rate of recovery (V_3) tended to be greater in H-FE ewes ($P = 0.089$), but there was no significant difference in the rate of deceleration in recovery (V_4; $P > 0.10$). The value for the postchallenge stabilization period (V_5) was again clearly higher in the H-FE group ($P < 0.001$), but did not fully recover to the initial prechallenge levels (V_1) in either H-FE or L-FE ($0.05 < P < 0.10$ for the contrast V_1 vs. V_5; data not shown in tables).

Results of milk composition measures focusing on the interaction group × period are reported in Table 4. Supplemental Table S2 (https://doi.org/10.20350/digitalCSIC/15094) shows the main effects for group (H-FE vs. L-FE) and period for those parameters for which there was no significant group × period interaction.

Overall, the concentrations of milk fat, protein, lactose, and TS did not significantly differ between groups before the challenge ($P > 0.10$; Table 4). However, H-FE ewes were characterized by greater yields of all these milk components ($P < 0.01$) and lower milk SCC than L-FE ($P = 0.037$). In contrast, the period significantly affected most traits ($P < 0.001$). Lactose concentration was transiently reduced due to underfeeding ($P < 0.001$), but no statistical difference between FE groups was observed in this trait and in protein content in the challenge and postchallenge periods ($P > 0.10$). An interaction between the effects of group and period was detected for milk fat and TS concentrations ($P < 0.05$), but no differences in fat content between H-FE and L-FE were found after adjustment for multiple comparisons using a Bonferroni correction. Conversely, the increase in TS due to the underfeeding was greater in H-FE sheep ($P = 0.003$).

The negative effect of underfeeding on the yields of protein, lactose, and TS removed the between-group differences during the challenge, and both H-FE and L-FE fully recovered their initial production levels (and differences) in the postchallenge ($P < 0.05$ for the

Table 2. Feed efficiency index (FEI), residual feed intake (RFI), and feed conversion ratio (FCR) in the high-feed efficiency (H-FE) and low-feed efficiency (L-FE) groups of ewes

Item	H-FE	L-FE	SED[1]	*P*-value
FEI	0.131	0.546	0.0348	<0.001
RFI	−0.120	0.122	0.0392	<0.001
FCR	1.16	1.59	0.084	<0.001

[1]SED = standard error of the difference.

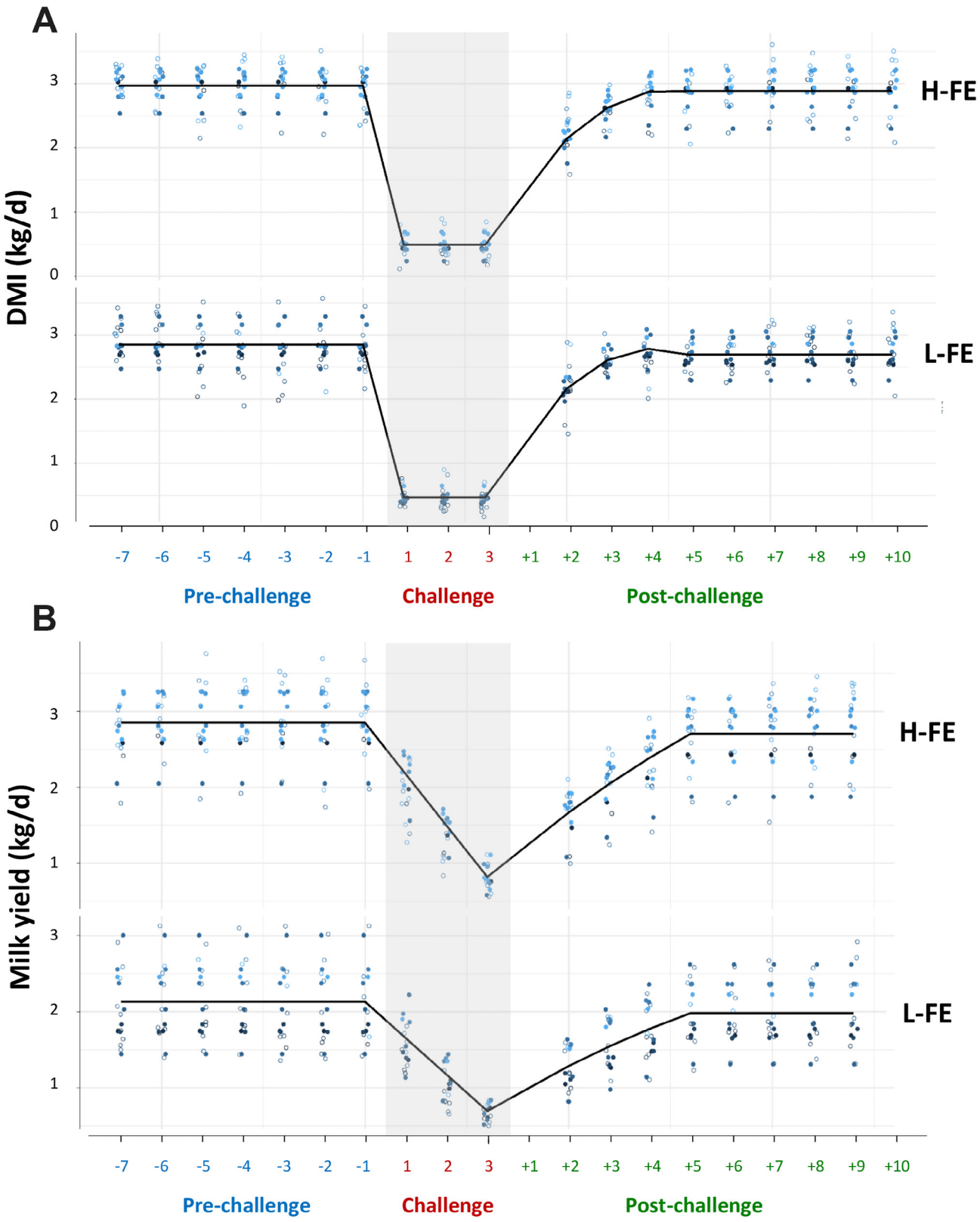

Figure 2. Average time trends of (A) DMI (kg/d) and (B) milk yield (kg/d) through the prechallenge, challenge, and postchallenge periods for the high-feed efficiency (H-FE) and low-feed efficiency (L-FE) groups of ewes, generated by a piecewise model. Filled and empty circles represent predicted and observed values, respectively, for each ewe.

Table 3. Prediction model parameters in the high-feed efficiency (H-FE) and low-feed efficiency (L-FE) groups of ewes subjected to an acute nutritional challenge (i.e., fed only straw for 3 d)[1]

Trait	Parameter	H-FE	L-FE	SED[2]	*P*-value
DMI	V_1: Prechallenge constant (kg)	2.967	2.849	0.1089	0.385
	V_2: Drop on d 1 of the challenge (kg)	−2.477	−2.378	0.0931	0.447
	V_3: Rate of recovery from challenge (kg/d)	1.058	1.115	0.0185	0.487
	V_4: Rate of deceleration in recovery (kg/d^2)	−0.116*	−0.134	<0.001	0.241
	V_5: Postchallenge constant, stabilization (kg)	2.887	2.690	0.1234	0.155
Milk yield	V_1: Prechallenge constant (kg)	2.847	2.133	0.2140	0.005
	V_2: Rate of response to the challenge (kg/d)	−0.676	−0.480	0.0673	0.006
	V_3: Rate of recovery from challenge (kg/d)	0.457	0.323	0.0579	0.089
	V_4: Rate of deceleration in recovery (kg/d^2)	−0.016*	−0.013	0.0053	0.816
	V_5: Postchallenge constant, stabilization (kg)	2.706	1.984	0.1986	<0.001

[1]Values were estimated using a piecewise mixed model.

[2]SED = standard error of the difference.

*Indicates that the corresponding value is not significantly different from 0 ($P > 0.10$).

interaction group × period). In contrast, similar differences in milk fat yield due to FE level were observed throughout the trial ($P < 0.001$), and reductions due to the challenge were not fully reversed 10 d afterward ($P < 0.001$).

Milk SCC was greater in the L-FE group in both pre- and postchallenge periods. However, its increase during the challenge was significant for H-FE but not for L-FE ($P = 0.008$ for the interaction group × period). Initial SCC were recovered in the postchallenge in H-FE (approx. 101 × 10^3 cells/mL).

More-efficient sheep had lower initial BW than L-FE (63.7 vs. 70.3 kg, respectively; $P < 0.001$; results not reported in tables). In addition, H-FE tended to lose more weight throughout the trial than L-FE (on average, −2.50 vs. 0.77 kg, respectively; $P = 0.080$).

Blood Parameters

As reported in Table 5 and Supplemental Table S2 (https://doi.org/10.20350/digitalCSIC/15094), no difference due to FE was found for glucose, insulin, and NEFA levels ($P \geq 0.22$), whereas urea was higher in more-efficient sheep ($P = 0.009$). Initial BHB values were similar in H-FE and L-FE ewes, but underfeeding increased its concentration in H-FE, an effect that was reversed in the postchallenge period ($P = 0.022$ for the interaction group × period). An increase in NEFA was also found during the challenge ($P < 0.001$), with a comparable magnitude in L-FE and H-FE ($P = 0.47$ for the interaction group × period). In addition, the lowest NEFA concentrations in both groups were observed at the end of the trial ($P < 0.001$). In contrast, glucose, insulin, and urea were negatively affected by underfeeding ($P < 0.01$) and, in the postchallenge period, initial values were recovered for insulin and urea, but not for glucose ($P < 0.01$).

Ruminal Fermentation

Differences in ruminal fermentation parameters between H-FE and L-FE were only minor (Table 6 and Supplemental Table S2; https://doi.org/10.20350/digitalCSIC/15094). Total VFA was the only parameter showing significant variation, with a lower concentration in H-FE than L-FE ($P = 0.012$), whereas pH, ammonia content, and molar proportions of VFA showed similar values in the 2 groups ($P > 0.10$).

Propionate proportion was unaffected by the challenge ($P = 0.23$), but underfeeding caused increments in pH, molar proportions of acetate and minor VFA, and acetate:propionate ratio ($P < 0.01$), and reductions in the concentrations of ammonia and total VFA, and in the proportion of butyrate ($P < 0.001$). Prechallenge values were re-established at the end of the trial for pH, ammonia, and total VFA, but not for the molar proportions of acetate and butyrate, and for the acetate:propionate ratio. The effect of the interaction group × period was never significant (i.e., ruminal fermentation parameters showed similar patterns of variation over time for H-FE and L-FE sheep; $P > 0.39$).

DISCUSSION

Increasing FE of dairy flocks will likely improve farm sustainability through reduced feeding costs per unit of milk produced (Connor et al., 2012; Løvendahl et al., 2018). However, there is uncertainty about the possibility of enhancing FE without impairing animal resilience (Tempelman and Lu, 2020; Bengtsson et al., 2022). This study aimed at increasing our knowledge on the relationship between FE and resilience in dairy sheep by examining how ewes divergent for FE respond to an acute nutritional challenge. Results on the link between short-term efficiency and resilience would be

Table 4. Animal performance and milk SCC in the high-feed efficiency (H-FE) and low-feed efficiency (L-FE) groups of ewes subjected to an acute nutritional challenge (i.e., fed only straw for 3 d)[1]

	H-FE			L-FE				*P*-value		
Item	Prechallenge	Challenge	Postchallenge	Prechallenge	Challenge	Postchallenge	SED[2]	Group	Period	Group × period
Concentration, %										
Fat	5.52^{bc}	10.15^{a}	5.17^{bc}	5.61^{b}	8.41^{a}	4.82^{c}	0.735	0.071	<0.001	0.026
Protein	4.61	4.85	4.89	4.54	4.65	4.77	0.190	0.385	0.054	0.800
Lactose	4.93	3.86	4.89	4.91	3.90	4.94	0.121	0.721	<0.001	0.873
TS	16.1^{c}	20.0^{a}	16.0^{c}	16.1^{c}	18.0^{b}	15.6^{c}	0.49	0.054	<0.001	0.003
Yield, g/d										
Fat	154.9	81.4	143.9	111.6	57.0	99.1	12.47	<0.001	<0.001	0.402
Protein	130.1^{a}	38.4^{c}	138.1^{a}	90.8^{b}	31.5^{c}	97.7^{b}	9.48	0.002	<0.001	0.002
Lactose	139.7^{a}	31.5^{c}	137.9^{a}	98.5^{b}	26.6^{c}	101.5^{b}	10.30	0.004	<0.001	0.004
TS	454^{a}	160^{c}	450^{a}	321^{b}	123^{c}	320^{b}	31.5	0.001	<0.001	0.009
SCC, $\log_{10} \times 10^3$/mL	1.88^{c}	3.25^{a}	2.01^{bc}	2.66^{ab}	3.15^{a}	2.62^{abc}	0.250	0.037	<0.001	0.008

[a–c]Within a row, different superscripts indicate significant differences ($P < 0.05$) due to the effect of group × period.

[1]Measurements and samplings were conducted before the challenge (prechallenge), at the end of the challenge (challenge), and 9–10 d after the challenge (postchallenge).

[2]SED = standard error of the difference.

Table 5. Blood parameters in the high-feed efficiency (H-FE) and low-feed efficiency (L-FE) groups of ewes subjected to an acute nutritional challenge (i.e., fed only straw for 3 d)[1]

	H-FE			L-FE				*P*-value		
Item	Prechallenge	Challenge	Postchallenge	Prechallenge	Challenge	Postchallenge	SED[2]	Group	Period	Group × period
Glucose, mg/dL	72.44	61.87	65.12	71.80	59.77	65.88	3.918	0.741	<0.001	0.795
Insulin, μIU/mL	14.32	4.16	13.56	18.93	4.58	17.35	6.011	0.506	0.003	0.769
Nonesterified fatty acids, mmol/L	0.18	1.75	0.10	0.14	1.54	0.09	0.194	0.226	<0.001	0.474
Urea, mg/dL	69.14	51.76	67.29	64.52	41.39	60.31	4.768	0.009	<0.001	0.515
BHB, mg/dL	9.26^{b}	12.30^{a}	8.63^{b}	8.18^{b}	8.05^{b}	7.83^{b}	1.034	0.021	0.014	0.022

[a,b]Within a row, different superscripts indicate significant differences ($P < 0.05$) due to the effect of group × period.

[1]Measurements and samplings were conducted before the challenge (prechallenge), at the end of the challenge (challenge), and 9–10 d after the challenge (postchallenge).

[2]SED = standard error of the difference.

Table 6. Ruminal fermentation parameters in high-feed efficiency (H-FE) and low-feed efficiency (L-FE) groups of ewes subjected to an acute nutritional challenge (i.e., fed only straw for 3 d[1]

	H-FE			L-FE				*P*-value		
Item	Prechallenge	Challenge	Postchallenge	Prechallenge	Challenge	Postchallenge	SED[2]	Group	Period	Group × period
pH	6.72	7.24	6.77	6.64	7.16	6.70	0.083	0.197	<0.001	0.994
Ammonia, mg/L	135.1	59.0	133.7	133.0	47.6	129.3	14.07	0.600	<0.001	0.810
Total VFA, mmol/L	102.0	22.6	117.2	118.1	24.5	136.4	11.33	0.015	<0.001	0.342
VFA, mol/100 mol										
Acetate	63.0	72.0	69.4	63.1	72.0	69.0	1.57	0.866	<0.001	0.985
Propionate	17.4	15.8	15.9	17.5	16.8	16.2	1.18	0.552	0.226	0.844
Butyrate	16.1	6.8	12.0	15.6	6.9	12.3	1.02	0.991	<0.001	0.823
Other VFA	3.45	5.33	2.70	3.82	4.27	2.43	1.234	0.510	<0.001	0.392
Acetate:propionate ratio	3.65	4.81	4.47	3.64	4.47	4.31	0.411	0.467	0.005	0.853

[1]Measurements and samplings were conducted before the challenge (prechallenge), at the end of the challenge (challenge), and 9–10 d after the challenge (postchallenge).
[2]SED = standard error of the difference.

an important evidence as we start to consider how to move toward selecting animals for sustainable (long-term) efficiency.

Prechallenge (Underlying Differences in Feed Efficiency)

A major aspect in determining the relationship between FE and resilience might lie in the definition of FE itself. According to the literature in dairy ruminants (e.g., Connor et al., 2013; Kidane et al., 2018; González-García et al., 2021), the most efficient animals could be those showing a lower feed intake for the same production level or those showing a higher production level for the same feed intake, although other phenotypes may also exist. Several studies have revealed that high-performance dairy ruminants have a shorter lifespan (De Vries and Marcondes, 2020), and seem more prone to certain alterations (e.g., in ruminal digestion; Baldin et al., 2018). Therefore, when more-efficient animals are those with higher production levels, we would expect them to have a worse response in terms of resilience.

In general, there is consensus in beef cattle that more and less-efficient animals have a comparable performance level, but different feed intake (Arthur et al., 2014; Cantalapiedra-Hijar et al., 2018), and similar results have been observed in Holstein cows (Connor et al., 2013; Xi et al., 2016; Elolimy et al., 2022). However, the scarcer literature on minor breeds and other species is less consistent. For example, a report in Norwegian Red cows associated RFI with divergences in MY at similar DMI (Kidane et al., 2018). This phenotype is similar to that found in our previous study in dairy Assaf ewes (Toral et al., 2021) and in the present trial. Relevant differences in MY with the same or very close DMI were also related to greater FE in the comparisons between Lacaune of high and low genetic merit, and between Lacaune and Manchega ewes (Marie et al., 2002). In contrast, González-García et al. (2021) reported that FE was independent of the individual milk production in Lacaune. Without direct comparisons, it is difficult to discern whether these variations are due to breed, species, production potential, or other reasons. Actually, the index used as a proxy of FE might be another putative confounding variable (Hurley et al., 2016, 2017; Tempelman and Lu, 2020). Nevertheless, we observed a good consistency between RFI, FEI, and FCR in the present study, with no overlapping between H-FE and L-FE groups, except for the interchange of 2 ewes when FCR was employed.

It is noteworthy that the higher MY in H-FE ewes was not associated with a dilution effect on milk fat and protein concentrations, which is in agreement with our previous results (Toral et al., 2021) and those of

Marie et al. (2002) in Lacaune ewes, and of Kidane et al. (2018) in Norwegian Red cows. Regarding SCC, the few existing data in the literature suggest that a high SCC is associated with a loss in MY and a subsequent reduced FE (namely FCR) in lactating dairy cows (Potter et al., 2018), which would be in line with our data in sheep. Ranges of SCC considered as healthy are not clear in dairy sheep: studies in Assaf sheep suggested that individual SCC $> 400 \times 10^3$ cells/mL ($2.60 \log_{10} \times 10^3$ cells/mL) would be more likely to be microbiologically positive for mastitis pathogens (González-Rodríguez et al., 1995). However, in general, SCC up to 750×10^3 cells/mL ($2.88 \log_{10} \times 10^3$ cells/mL) would be indicative of acceptable mammary health (Gonzalo, 2018).

A relationship between the observed difference in serum urea contents and FE is not clear. In fact, no variations were found in rumen ammonia concentration. Thus, as milk protein yield was significantly higher in H-FE than in L-FE, despite both groups consumed the same diet at a similar DMI, it is tempting to propose differences in protein utilization between more and less-efficient ewes. However, it would be too speculative without data on some determinant factors, such as diet selection or nitrogen recycling.

Concerning rumen fermentation, although it may seem surprising that total VFA concentration was higher in L-FE than in H-FE, the literature does not show a consistent relationship between FE and ruminal fermentation parameters (Lam et al., 2018; McGovern et al., 2018; Durunna et al., 2019). Accordingly, our results do not allow to confirm the lower acetate: propionate ratio and ammonia concentration in more-efficient ewes reported by Toral et al. (2021). However, it must be mentioned that spot sampling could affect the representativeness of dynamic fermentation parameters subject to differences in production and absorption rates. Indeed, it cannot be ruled out that variations in total VFA derive from a higher or faster ruminal VFA absorption in H-FE. In this regard, individual differences in eating behavior (including diet selection) and digestion kinetics would require further research in FE studies. We must acknowledge a limitation of this study: we did not analyze diet selection. Therefore, we cannot be sure that part of the variation in FE was not due to variation in feed selection, as it remains unclear how feed efficiency may be influenced by different diets. In our experiment, all animals were fed a TMR (i.e., a mixture of all dietary ingredients, blended thoroughly) with molasses to help to reduce separation or sorting, but some kind of diet selection cannot be excluded. Thus, further research on this issue is still necessary.

Finally, the lack of differences in plasma glucose between H-FE and L-FE is consistent with the tight regulation of its blood levels in ruminants (Herbein et al., 1985), and with the lack of apparent relationship between FE and glucose levels observed in other studies in bovine (Clemmons et al., 2017; Cônsolo et al., 2018). Although a higher glucose concentration has recently been reported in the plasma of less-efficient dairy cows (Elolimy et al., 2022), those data were recorded during the transition period and associated with a 31% difference in DMI.

Challenge (Effects of Underfeeding)

In general, results were consistent with the known effects of underfeeding in ruminants (Chilliard et al., 2000; Friggens et al., 2016; Leduc et al., 2021). Starting with ruminal fermentation, where most of the studies in ruminants have focused, the increase in pH, together with the shift toward more acetic fermentation and decreased ammonia concentration would be due to the well-known effects of lower DMI and replacement of a high-concentrate diet by a forage (Ramos-Morales et al., 2014; Zou et al., 2019; Ahmad et al., 2020). Associated effects on blood parameters (i.e., decreases in glucose, insulin and urea levels, and increases in BHB and NEFA) and on milk production match with expectations of acute nutritional deprivation (Friggens et al., 2016; Zou et al., 2019; Leduc et al., 2021). Similarly, increased milk fat concentrations would result from the well-documented effect of a quick drop in MY, whereas effects on protein concentration appear to be highly variable, with reports of decreases, no change or increases in the literature (Pulina et al., 2012; Tsiplakou et al., 2012; Leduc et al., 2021). Furthermore, the higher milk SCC found in the challenge would also be consistent with the drop in MY, which would mimic the drying-off and its known effect as a noninfectious cause of increase in SCC in dairy sheep (Gonzalo et al., 1993).

Focusing on the comparison between H-FE and L-FE groups, the lack of differences in DMI observed in the prechallenge were maintained in the challenge, with no significant variation in the drop of intake at the beginning of the challenge (V_2). Nonetheless, for MY, this parameter indicated a sharper drop in more-efficient sheep.

Our results agree with those of Friggens et al. (2016) in dairy goats, and Orquera-Arguero et al. (2022) in dairy cows, showing that underfeeding caused a faster decrease in MY in animals with higher production level. Nevertheless, in our trial, some traits (namely TS concentration and fat yield) would suggest that H-FE sheep were still able to maintain a slightly greater performance. In this regard, changes in blood BHB might support that the metabolic adaptation during the underfeeding period was higher (or faster) in H-FE than

in L-FE, suggesting a greater tissue mobilization in the most efficient ewes. In any case, it is possible that this apparently better adaptation of H-FE to underfeeding was only successful in the short-term. The question remains whether these more-efficient sheep would be able to maintain energy mobilization in the longer term (Tsiplakou et al., 2012; Leduc et al., 2021), as they tended to lose more BW throughout the trial.

Finally, according to literature, feed restriction invariably increases NEFA levels in blood, whereas increments in BHB are less consistent (Pulina et al., 2012; Friggens et al., 2016; Leduc et al., 2021). In line with this, NEFA was significantly higher during the challenge in both groups of ewes (L-FE and H-FE). However, BHB was only greater in H-FE, which may suggest that inconsistencies between BHB and NEFA might derive, at least to some extent, from individual variations in FE.

Postchallenge (Resilience)

Results from the postchallenge period can provide an insight into the resilience of sheep to acute underfeeding in terms of their rates of response and recovery, in addition to their ability to revert to initial status (Tedeschi et al., 2015; Joy et al., 2020). Values of DMI and MY reached a steady level 5 d after the end of the challenge in both H-FE and L-FE. However, prechallenge levels of DMI were only recovered in H-FE (and they remained 6% lower during the stabilization period in L-FE), suggesting a higher resilience in more-efficient ewes. In contrast, initial MY values were not fully recovered (V_1 vs. V_5) in either group, which does not seem to be explained by advancing stage of lactation because there was only an 8-d difference between periods. Thus, a persistent detrimental effect of the challenge, at least in the short-term, cannot be ruled out.

Focusing on MY, differences in the rate of recovery from the challenge (V_3) would reflect a faster adaptation of H-FE ewes to refeeding. Furthermore, milk fat content dropped below prechallenge levels in L-FE, but not in H-FE. Overall, the higher production level in more-efficient sheep did not detrimentally affect their ability to recover from the challenge, which agrees with a recent study in lactating beef cows (Orquera-Arguero et al., 2022).

Several reports have shown than NEFA concentrations revert to low values before 10 d of refeeding (DiMarco et al., 1981; Keogh et al., 2015). In our study, decreases in NEFA levels during the postchallenge would even suggest a lower fat mobilization relative to the prechallenge period. These results seem to be in agreement with findings in yaks by Zou et al. (2019), who observed a higher energy and protein utilization efficiency during the refeeding period after starvation. Some other blood metabolites were also expected to quickly respond to re-alimentation after acute underfeeding (Delavaud et al., 2007; Kalyesubula et al., 2020), but no significant increase in glucose concentration was detected on d 10 of the postchallenge. Even when it is possible that longer refeeding periods are needed to recover initial glycaemia, the literature reflects discrepancies on this issue (Delavaud et al., 2007; Friggens et al., 2016; Song et al., 2018).

In general, compared with the quick recovery in production traits, postchallenge data on ruminal fermentation points to a slower recovery. Results support the persistency of a more acetic type of fermentation, probably because rumen microbiota need a longer time to recover from underfeeding. Yet, it is unclear whether this is due to effects of feed deprivation and re-alimentation on microbial composition or function (Potter and Dehority, 1973; Zou et al., 2019). In any event, no differences, beyond those described for the prechallenge period, were observed between more and less feed efficiency groups, which would also support that H-FE ewes would not be less resilient to acute underfeeding than their counterparts in L-FE.

CONCLUSIONS

Comparison of dairy ewes phenotypically divergent for FE (H-FE and L-FE groups) shows that more-efficient animals are more productive at similar DMI. Nevertheless, despite the higher performance of the H-FE group, their overall response to and recovery from an acute nutritional challenge (i.e., underfeeding) appears to be comparable or even better than that of L-FE sheep. This is supported by temporal patterns of variation in production traits, ruminal fermentation and blood parameters, and would refute the initial hypothesis of a poorer resilience of more-efficient sheep to an acute underfeeding. However, the question remains whether a longer term feed restriction would impair the ability of more-efficient ewes to maintain or revert to a high-production status, which would require further research.

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