



# The effect of tissue mobilization and stage of lactation on energy partitioning in lactating sows: an analysis of commercial data

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## Animal Research Paper

**Cite this article:** Gasa J, Capalbo S, Ellis J, Sola D, France J (2023). The effect of tissue mobilization and stage of lactation on energy partitioning in lactating sows: an analysis of commercial data. *The Journal of Agricultural Science* **161**, 847–856. <https://doi.org/10.1017/S0021859623000564>

Received: 6 March 2023  
Revised: 30 August 2023  
Accepted: 23 October 2023  
First published online: 24 November 2023

**Keywords:**  
commercial data; energy mobilization; energy partitioning; lactation; sows

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### Abstract

The objective of this paper was to investigate how the predicted level of body energy mobilized and the stage of lactation affects performance and energy partitioning in lactating sows kept under commercial conditions. Seventy-seven lactating sows from three consecutive batches were weaned at 28 d and all measures were taken over the first 20 d. Total feed consumption was measured and sows' live weight was registered when entering the lactation facilities and at 21 d of lactation. Blood samples were collected at farrowing and once a week thereafter. Net energy (NE) mobilization or loss was calculated by difference using the general NRC equation for ME partitioning. Compared to low mobilizers (low NE loss values), high mobilizing sows had lower feed intake and higher loss of live weight, body fat and body protein. High mobilizers also weaned more piglets and had heavier litters than low mobilizers. Energy mobilization (NE loss) was higher from day 1 to 10 of lactation compared to day 11 to 20, and the difference in mobilized energy between high and low mobilizing sows was also higher in the first than in the second half of lactation. Body weight and back fat thickness losses were significantly correlated with NE loss. A more accurate prediction of the changes in live weight or back fat thickness over lactation should help better predict total amount of energy mobilized, and more research is needed to assess the relative contribution of lean and fat to mobilized tissue.

### Introduction

Lactation is the most demanding period of a sow's reproductive cycle and optimizing nutrition appears an excellent tool to ensure health, wellbeing and long-term productivity (Trottier *et al.*, 2015; Tokach *et al.*, 2019). Milk production depends on the sow's genetic potential and feed intake, but it is strongly related to litter size and piglet suckling capacity (Hartmann *et al.*, 1997; Eissen *et al.*, 2000; King, 2000). During lactation ( $\geq 3$  wk), many sows undergo negative net energy balance (losing up to 40 kg of body weight (BW) and 5–10 mm of back fat thickness (BT)) to produce milk (Rojkittikhun *et al.*, 1993; Dourmad *et al.*, 1996; Thaker and Bilkei, 2005; Cerisuelo *et al.*, 2008; Gourley *et al.*, 2020) affecting subsequent reproductive performance (Johnston *et al.*, 1989; Zak *et al.*, 1997; Yoder *et al.*, 2013). However, other authors (Willis *et al.*, 2003) have also pointed out that those lactation effects on reproductive performance are marginal. Studies on sows show contradicting results regarding the link between body mobilization and milk production, and whether high feed intake (5.0 to 7.6 kg/day) can prevent excessive BW loss (Eissen *et al.*, 2003; Mosnier *et al.*, 2010; Strathe *et al.*, 2017).

More than thirty years ago, Noblet and coworkers did foundational work studying energy and protein metabolism of lactating sows (Noblet and Etienne, 1987; Noblet *et al.*, 1990; Quiniou and Noblet, 1999) and established the principles of sow's energy and tissue mobilization. However, direct measurement of energy and tissue mobilized in lactating sows is difficult and expensive (Everts and Dekker, 1994b; Dourmad *et al.*, 1997) and they are often predicted using the variation of maternal body fat and protein pools, calculated from changes in maternal empty body weight and in P2 back fat thickness (Dourmad *et al.*, 2008; NRC, 2012). The first equations were mainly obtained from original slaughtering data published by Dourmad *et al.* (1997). In any case, quantifying the variability in composition of BW loss during lactation has received limited attention and NRC (2012) assumed it constant. However, the rate and composition of tissue mobilized may change substantially with genetic line, age and stage of lactation, body composition at farrowing and even individually between sows (Mullan *et al.*, 1989; Noblet *et al.*, 1990; Sauber *et al.*, 1998; Kim and Easter, 2001; Gauthier *et al.*, 2019; Pedersen *et al.*, 2019). Furthermore, other factors, such as litter size and vigorosity of the suckling piglets, pattern and management of feed intake, environmental conditions and sow genetic potential (Eissen *et al.*, 2000; Kim and Easter, 2001) may also have an effect.

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The aim of the present study was to investigate how the predicted level of body energy mobilized and the stage of lactation (first and second half) affects performance and energy partitioning of lactating sows kept under commercial conditions.

## Material and methods

### *Animals, management, experimental design and measurements*

The data were collected from a commercial farm located in Osona (Barcelona, Spain) in 2014, with a breeding stock of 350 Landrace × Large White (LD × LW) sows. The general management of the farm was a three week batch system line.

Sows from three consecutive batches were used. After weaning, sows were monitored daily for signs of oestrus. At oestrus, each sow was subjected to insemination with refrigerated semen following the detection of heat by a teaser boar. The sows remained in individual stalls for approximately 30 d until pregnancy testing, after which pregnant sows were group housed in gestation pens holding 8–10 sows each. Approximately 3–4 d before farrowing, all sows in the gestation pens were moved to the farrowing building and were allocated to individual farrowing crates. Each farrowing crate was previously thoroughly washed and disinfected. The introduction of late gestation sows to the rooms was never earlier than 1–2 d after disinfection. All farrowing rooms were naturally ventilated and were equipped with commercial crates for each sow including a creep area for her piglets. The sow area had a metal slatted floor whilst that of the creep area was partially slatted and concrete. All farrowing crates were equipped with two nipple drinkers for sow and piglets, and a feeder for sows. Twice a day extra water was dispensed via the feeder to all sows. Every three weeks a new batch of pre-partum sows filled the crates and remained there until the weaning of their litters approximately 28 d post farrowing. All batch piglets were then moved to the nursery building, whereas their dams were moved to the breeding–gestation building and placed separately in individual stalls, each with an automatic feed dispenser and water permanently available.

The experiment included 77 sows (28, 20 and 29 sows from each batch) distributed by parity from gilts up to seventh parity sows (22 gilts; 35 from 2<sup>rd</sup> to 4<sup>th</sup> parity, and 20 >4<sup>th</sup> parity). Farrowing was performed with minimal use of pharmacological products and low human intervention. Cross-fostering was permitted only within 24 h post farrowing and was carried out following the protocol of the commercial farm. Litters of between 9 and 14 piglets born alive were started, the litters were equalized to 12, trying to leave most piglets with their mothers and make as few changes as possible. Some gilts were allocated 13 piglets. Piglets were treated using routine management practices (ear notching, iron injection and deworming) in the first 48 h post farrowing. Extra heat was provided for piglets from a proper heated area plus using infrared electric lamps placed in the creep area for the first 2 d of life. Each farrowing crate was cleaned daily. No creep feed was provided before day 20 of lactation.

As farrowing in each batch spread from Tuesday to Saturday, sows were offered a predetermined amount of gestation feed [12.43 MJ metabolizable energy (ME)/kg, 13.5% crude protein (CP) and 0.64% total lysine] until the following Monday, at a rate of 1.5, 3.0; 4.0; 4.5 and 5.0 kg/sow, starting the day after farrowing. On Monday, lactation feed was offered twice a day by hand, to reach maximum daily intake as soon as possible whilst

trying to avoid refusals. Table 1 shows the composition of the lactation feed.

Total cumulative feed intake at day 20 of lactation, gestation plus lactation feed, was measured individually. Furthermore, feed consumption was registered by weighing the feed on offer and the refusals every Monday, Wednesday and Friday of the lactation weeks starting the first Monday post farrowing. By the end of the 20 d lactation period, a total of 9–10 cumulative feed intake observations had been made for each sow. All piglets were individually weighed on day 20 post farrowing and litter weight was measured four or five times, i.e. during the 24 h after farrowing and every Wednesday throughout lactation. Mean, maximum and minimum ambient temperatures were also monitored (HOBO UX100-003 Temperature/Relative Humidity data logger; Onset Computer Corporation, Bourne, MA) daily in each farrowing room.

All sows were weighed when entering the farrowing room and again on day 21 of lactation. Back fat thickness was measured by ultrasound at the P2 position (65 mm from the midline over the last rib) when sows entered the farrowing room and on each Monday throughout lactation (five recordings for each sow). Sow BW at farrowing was estimated using the equation published

**Table 1.** Ingredients and nutrient composition of lactation diet

Ingredients, g/kg	
Corn	200.0
Barley	250.0
Wheat	184.5
Extruded soybeans	125.3
Corn gluten feed	80.0
Soybean meal 44% CP	68.5
Rapeseed meal	50.0
Calcium carbonate	16.9
Di calcium phosphate	11.42
Salt	4.86
L-Lysine-HCl	3.40
DL-Methionine	0.51
L-Threonine	1.11
Vitamin and mineral complex	3.50
Chemical composition, % as feed	
Dry matter	88.89
Organic matter	83.50
Crude protein	17.50
Crude fibre	3.90
Ether extract	4.16
Total lysine	1.02
Metabolizable energy, MJ/kg	12.93

Vitamin and mineral complex provided the following per kg of feed: 12 500 IU of vitamin A, 2000 IU of vitamin D3, 20 mg of vitamin E, 2 mg of vitamin K3, 4 mg of vitamin B1, 5 mg of vitamin B2, 25 mg of vitamin B3, 2.6 mg of vitamin B6, 0.02 mg of vitamin B12, 12 mg of calcium pantothenate, 25 mg of nicotinic acid, 0.100 mg of biotin, 300 mg of choline-Cl, 100 mg of Fe, 10 mg of Cu, 0.5 mg of Co, 100 mg of Zn, 80 mg of Mn, 0.5 mg of I and 0.22 mg of Se.

by Mallmann *et al.* (2018); post-farrowing sow body weight (kg) = 13.03 + (0.93 × pre-farrowing body weight, kg) + (-1.23 × total piglets born). The individual sow's lipid and protein body mass were estimated using sow BW and BT and following Dourmad *et al.* (2008). Thereafter, total loss of lipid and protein through 20 d of lactation (kg) were also calculated individually, subtracting the total predicted protein and lipid amount obtained at weaning from that obtained at farrowing.

Blood samples (of approximately 10 ml) were collected from the external jugular vein at farrowing and each Wednesday until day 20 of lactation (four samples for each sow). Blood collections were done, on average, between 3 and 4 h after the morning meal. All blood samples were centrifuged at 800 g for 10 min for serum recovery, which was frozen and stored at -80°C for further analyses. Serum samples were analysed for NEFA, glycerol, urea and creatinine. Briefly, the following methods were used for metabolite determination: reagent NEFA C (Wako Chemicals GmbH, Germany) for non-esterified fatty acid (NEFA); glycerol phosphate oxidase enzymatic method (Beckman Coulter Reagent) for triglycerides; glucose-dehydrogenase (GLDH) for urea; and colorimetric Jaffé method reaction for creatinine. All the assays were performed with an Olympus AU400 analyser following the manufacturer's recommendations for the different metabolites.

**Energy partitioning: assessing stage of lactation and individual energy balance**

Under commercial conditions a well-managed and not pharmacologically induced farrowing batch lasts several days (3 d minimum) and, as weaning is completed at a fixed day, lactation length differs between litters. In such circumstances, to follow individual sows day by day from farrowing to weaning slows down regular management at the farrowing house, and collecting feed intake and litter growth data on fixed days and adjusting the individual curves later provides an alternative approach to measuring energy balance.

The individual feed intake data collected from farrowing to weaning (kg fresh feed/sow and day) were fitted using a rectangular hyperbola, a simplification of the modified generalized Michaelis-Menten proposed by Schinckel *et al.* (2010) and adopted by the NRC (2012):

$$DMI \text{ (kg/d)} = a / (1 + (b/t)) \tag{1}$$

where DMI is dry matter intake, *t* is day of lactation, *a* is the asymptote of the curve, and *b* is a parameter representing *t* at the half-maximal value of *a*.

Likewise, the litter weight (LW, kg) recorded over lactation was fitted using a simple polynomial, i.e. the quadratic equation:

$$LW \text{ (kg)} = a + bt - ct^2 \tag{2}$$

where *t* is day of lactation and *a*, *b* and *c* are equation parameters. For about 12% of litters, the weight at cross fostering was not available when fitting the curve.

Provided with Equations (1) and (2), total, partial and daily ME partitioning in the body of the sow (Mcal/sow/d) was expressed as:

$$ME_{\text{intake}} = ME_{\text{maintenance}} + ME_{\text{for milk}} \pm ME_{\text{from body tissues}} \tag{3}$$

and consequently, the contribution of tissue mobilization to the overall ME pool (ME equivalent from tissues; Mcal) was calculated by difference, using the equation:

$$ME \text{ from body tissues} = ME \text{ intake} - (ME \text{ maintenance} + ME \text{ excreted in milk}) \tag{4}$$

where ME intake was determined by multiplying total feed intake (kg DM) by ME concentration of the feed (MJ/kg DM), ME maintenance was calculated assuming 460 kJ ME/kg of the mean metabolic body weight (Dourmad *et al.*, 2008), and ME for milk (ME dedicated to milk production) was determined using the NRC (2012) equation to estimate mean milk energy output, knowing mean litter growth (g/d), and assuming an efficiency of utilization of ME for milk production (*K<sub>m</sub>*) of 0.72 (Dourmad *et al.*, 2008). Calculations for the 20 d lactation were carried out using individual measured feed intake and litter growth, with calculations for the remaining days (of the 4-week period) based on the fitted curves.

Knowing the ME contribution from tissues, total NE loss or mobilized (MJ/d) was calculated. Values of 0.72 for *K<sub>m</sub>*, 0.87 for the efficiency of energy utilization from body reserves for milk production and 0.75 for the efficiency of energy utilization for the sow growth during lactation were assumed (Dourmad *et al.*, 2008).

Although calculation of NE loss is obtained by difference and is affected by errors in quantifying the other components of Equation (4), we propose a simple factorial approach to categorize sows according to their NE mobilization. Table 2 classifies the sows as High, Medium or Low mobilizers (including sows in positive energy balance), the theoretical amount of BW lost (kg/d), and theoretical composition of the tissue mobilized. The latter is considered in two extreme scenarios (850 g/kg fat and 150 g/

**Table 2.** Proposed range of energy mobilization (MJ NE/d) of lactating sows depending on theoretical total body weight (BW) loss and composition of that loss (fat or lean tissue)

Item	High mobilizers	Medium mobilizers	Low mobilizers
Total BW loss in 20 d, kg	>30	30–15	<15
Average BW loss, kg/d 20 d lactation	>1.5	1.5–0.75	<0.75
NE loss, MJ/d			
850/150 g/kg, Fat/lean 20 d lactation	>50.0	50.0–25.0	<25.0
550/450 g/kg, Fat/lean 20 d lactation	>33.3	33.3–16.7	<16.7

NE loss was calculated assuming that each kg of BW loss contained either 850 or 550 g/kg of fat tissue (97% lipid and 38.1 kJ/g) and either 150 or 450 g/kg of lean tissue (23% of protein and 5.4 kJ/g), following Kim and Easter (2001), Whittemore *et al.* (2003) and NRC (1998). Both scenarios represent two extreme options, high fat sows or high lean sows.

kg lean or 550 g/kg fat and 450 g/kg lean), following the results of Kim and Easter (2001). It is assumed that body fat and protein contain 39.3 and 23.4 kJ/g, respectively (Whittemore *et al.*, 2003), and that fat tissue is 970 g/kg lipids and lean tissue is 230 g/kg protein (NRC, 1998).

### Statistical analysis

All statistical procedures employed were part of the SAS V.9.3 statistical package (SAS Inst. Inc., Cary, NC) and R. The data were analysed for normality and homoscedasticity using the Shapiro-Wilk test of the Univariate procedure and the GLM procedure, respectively. Energy partitioning and performance were analysed as a 2 × 3 factorial arrangement of treatments for main effects of parity (primiparous or multiparous) and degree of mobilization (high (H); medium (M) or low (L), as categorized earlier) and degree of interaction of parity × mobilization, using the maximum likelihood method and considering the individual sow as a random effect. No effect of batch was observed and therefore it was not considered for further analysis. Serum metabolite concentrations were analysed using first and second order polynomial models, adjusted by means of the `gls:nmle` function in R (Pinheiro and Bates, 2023), in order to perform a repeated measures analysis with an unstructured covariance matrix (Pinheiro and Bates, 2000; Piepho and Edmondson, 2018). In the second order models, orthogonal polynomials were selected due to their computational benefits and the stability of the estimates. Indeed, removing higher order terms did not affect estimates of the coefficients of the lower order terms when orthogonal polynomials were used. Furthermore, piglet number at cross-fostering and at weaning as count variables did not satisfy normality and homoscedasticity of the variances. Therefore, they were analysed by logistic regression with generalized linear models following the same factorial arrangement previously described, with the GENMOD procedure fitting a Poisson distribution. The individual sow or litter was the experimental unit for all parameters. When significant *P* values (*P* < 0.05) were observed, least square-mean (LS-mean) comparisons were performed with a Tukey adjustment test for the ANOVA and 0.95 confidence limits for each of the LS-means for the non-normal data. Means were considered significantly different when *P* < 0.05 in both cases.

### Results

Mean daily temperature in the farrowing barn was always below 24.5°C, with maximum daily variations between 3 and 6°C; humidity was permanently registered below 70%.

Table 3 shows the mean, standard deviation, and minimum and maximum values of the main recorded or calculated performance parameters. Mean daily feed intake was 5.03 kg/d, total average litter gain 46.6 kg and sows lost an average of 21.1 kg BW and 2.68 mm of BT. Weaning to oestrus interval averaged 5.5 d though in some sows it extended up to 15 d. As far as some calculated parameters were concerned, total lipid and protein predicted losses accounted for 6.9 and 2.7 kg/sow, respectively, and the mean calculated NE loss was 601.7 MJ in 20 d.

Net energy loss was negatively and positively related to ME intake and ME for milk, respectively. The *r* value was higher for ME for milk (0.790; *P* < 0.001) than for ME intake (0.541; *P* < 0.001) and this relationship was higher for the first than for the second part of lactation (*r* values of 0.809 and 0.720 and of 0.566 and 0.484 for ME for milk and ME intake, respectively).

**Table 3.** Sow performance parameters for the lactating period (20 d)

Item	Mean	SD	Min.	Max.
n = 77	77	–	–	–
ME intake, MJ/sow	1323	205.6	721	1740
ADFI, kg/sow per d	5.0	0.79	2.75	6.88
ME for maint., MJ/sow	559	68.5	414	695
ME in milk, MJ/sow	1158	257.4	539	1549
N° Piglets cross fostering	12	1.2	10	14
N° Piglets 20 d	11.1	0.92	9	13
Litter weight cross CF, kg	20	3.8	11.7	29.6
Litter weight 20 d, kg	66	10.3	46.3	81.7
BW at farrowing, kg	255	36.7	178.0	322.5
BW loss 20 d, kg	21	11.4	–6.5	40.7
BT at farrowing, mm	17	3.6	11.0	25.0
BT loss 20 d, mm	3	1.9	0.0	9.00
Lipid loss 20 d, kg	7	3.4	–0.9	16.6
Protein loss 20 d, kg	3	1.7	–1.5	5.7
% lipid in total losses	72	9.0	55.4	95.4
NE loss MJ/sow	602	503.0	–479	1782
Weaning oestrus interval, d	6	3.5	4	15

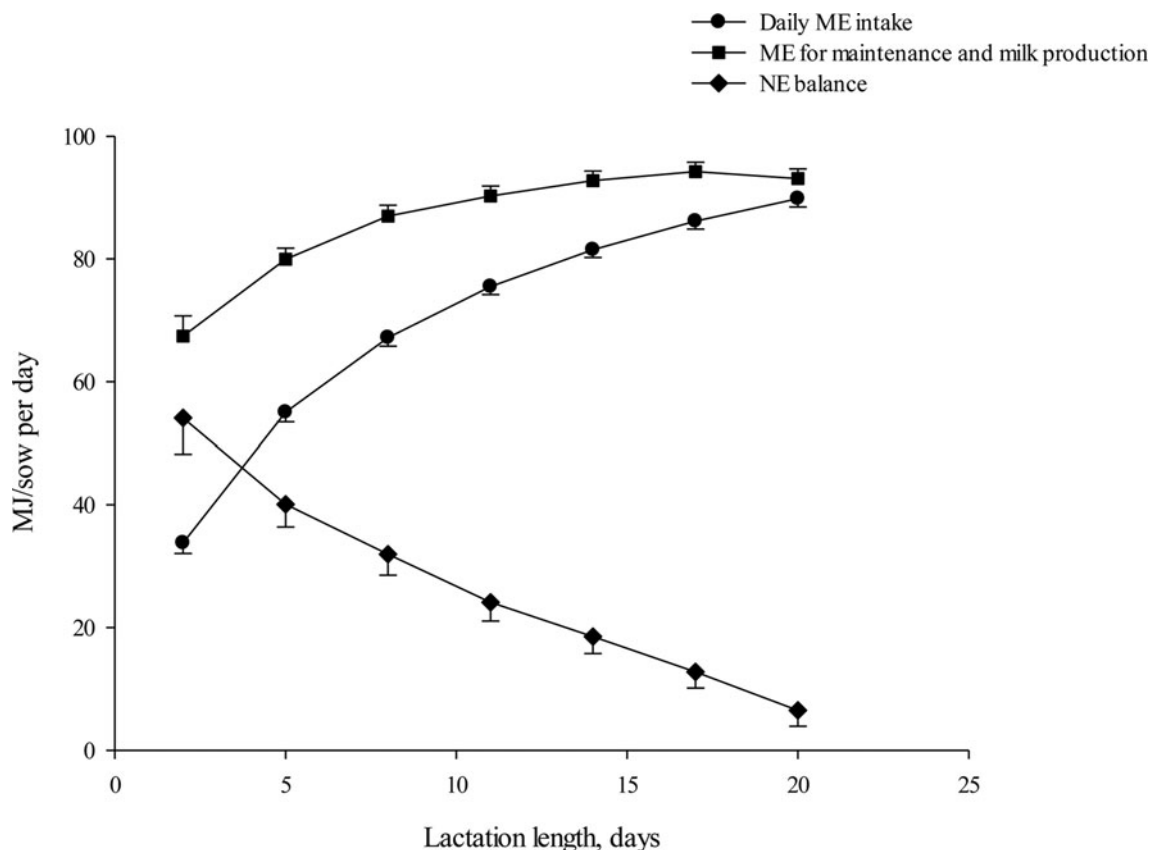
ADFI, average daily feed intake; CF, cross fostering; BW, body weight; BT, back fat thickness. BW at farrowing corrected according to NRC (2012). Lipid and protein losses calculated according to the equations given by Dourmad *et al.* (2008). NE loss obtained by difference and assuming a constant value of 0.72 ( $K_{m}$ ) and 0.87 ( $K_{b,m}$ , efficiency of utilization of body reserves for milk production; Dourmad *et al.*, 2008). The efficiency of utilization for growth during lactation ( $K_{mb}$ ) was assumed to be 0.75.

Net energy loss only had a moderate relationship with sow body weight loss (*r* = 0.517; *P* < 0.001), BT total loss (*r* = 0.464; *P* < 0.001) and BT loss as a percentage of BT at farrowing (*r* = 0.474; *P* < 0.001).

### Effect of stage of lactation

Figure 1 shows daily means (MJ/sow) and standard error of ME intake, ME used for maintenance and milk production, and NE mobilized. As expected, at the beginning of lactation ME used increased faster than ME intake, although the average sow continued mobilizing throughout the 20 d of lactation. The standard errors were high at the beginning of lactation and reduced thereafter. Overall, NE losses had the highest standard error, followed by ME used for maintenance and milk production, and ME intake. Differences among the latter two were mainly found during the first days of lactation.

Effect of week of lactation and age on blood parameters comparing gilts and multiparous sows is shown in Fig. 2 and Table 4 and include the statistical analysis. A quadratic model was preferred for all the metabolites studied (Table 4). The models, significantly differ from the constant model (see the *P*-value (Trend) column; Table 4). All values increased throughout lactation and were significantly higher than on the day of farrowing (Fig. 2). NEFA, glycerol and urea levels increased faster for multiparous sows than for gilts, even though gilts reached higher serum concentrations in week three (Fig. 2). Also in Fig. 2, gilts show lower creatinine concentration and a higher urea:creatinine



**Figure 1.** Daily ME intake (MJ/sow/d; circle), ME needed for maintenance and milk production (square) and NE loss (MJ/sow/d; diamond). Mean values (symbols) and standard error of the mean (error bars) are illustrated.

ratio than multiparous sows over the whole lactation; the differences in urea:creatinine ratio increased through lactation.

#### Effect of sow's age and level of energy mobilization

Results presented in Tables 5 and 6 refer to 20 d of lactation and presupposes an average constant composition of mobilized tissue of 720 g/kg fat and 280 g/kg protein, coincident with the mean individual values of total predicted lipid and protein losses (see Table 3). Table 5 shows the effects of level of energy mobilization and age for gilts *vs.* multiparous sows on the main performance parameters, and Table 6 on energy partitioning in the body of the sow and losses of body weight, BT, lipid and protein.

Gilts weaned more piglets ( $P < 0.006$ ) and had a lower piglet mortality ( $P = 0.004$ ) compared to multiparous sows, but multiparous sows produced higher piglet gain ( $P < 0.001$ ). As a result, litter gain (kg) in the 20 d period did not differ between gilts and multiparous sows (45.1 *vs.* 46.7,  $P = 0.344$ , respectively). Accordingly, gilts used a similar amount of ME for milk production ( $P = 0.416$ ) but had a lower ME intake ( $P = 0.015$ ), a higher body weight loss ( $P = 0.004$ ) and a higher body lipids loss ( $P = 0.020$ ). Gilts also apparently ( $P > 0.05$ ) lost more BT and body protein than multiparous sows, although NE losses do not reflect body composition changes. Gilts had a higher weaning to oestrus interval ( $P = 0.006$ ). The interaction found with BT loss ( $P = 0.030$ ) indicates that BT loss increases with energy mobilization only with multiparous sows while medium mobilizing gilts registered the highest BT loss.

As expected (Tables 5 and 6), high mobilizing sows had lower ME intakes than low mobilizers ( $P = 0.006$ ) and, consequently, they lost more body weight ( $P = 0.003$ ), body lipids ( $P = 0.002$ ) and body protein ( $P < 0.001$ ). High mobilizing sows used more ME to produce milk ( $P < 0.001$ ), and compared to low mobilizers, promoted higher litter gains ( $P < 0.001$ ) as they weaned more piglets ( $P = 0.010$ ), with those piglets being heavier ( $P < 0.001$ ) and having lower lactation mortality ( $P = 0.013$ ). Medium mobilizers were found as well as high and low mobilizing sows for all parameters studied (Tables 5 and 6).

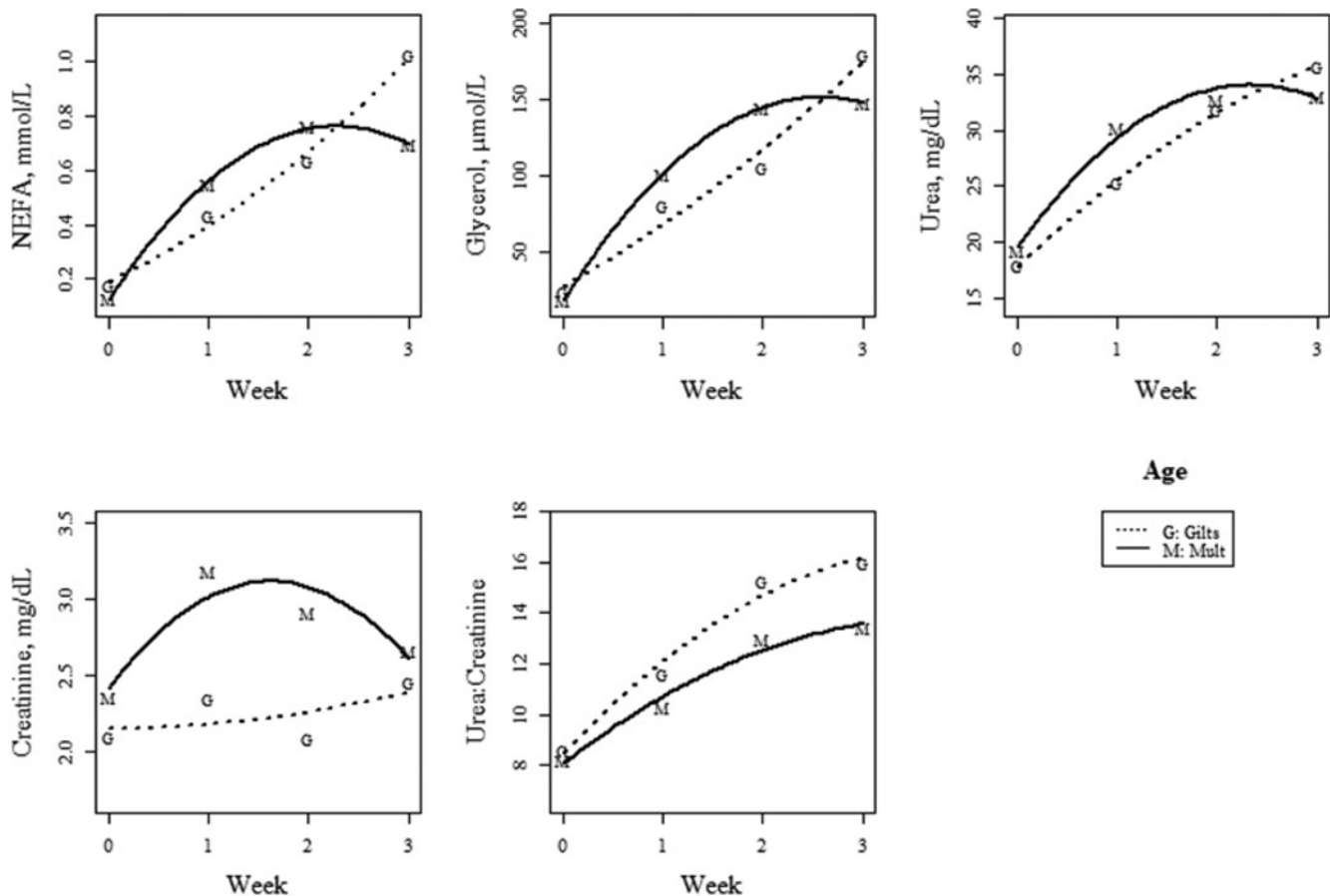
Table 7 shows the effect of the sow's level of mobilization and stage of lactation (day 0 to 10 *vs.* day 11 to 20) on ME intake, ME for milk and NE balance (MJ/sow/d). As expected, ME intake and ME for milk was higher in the second half of lactation than in the first ( $P < 0.001$ ), while NE balance (NE loss) trended in the opposite direction ( $P < 0.001$ ).

The interactions found between level of mobilization and stage of lactation for ME for milk ( $P < 0.022$ ) and NE losses ( $P < 0.010$ ) show that the difference in ME for milk among high and low mobilizing sows (MJ/d) was greater in the first (68.2 *vs.* 41.8) than in the second half of lactation (76.0 *vs.* 59.4), in accordance with a higher NE loss difference (59.1 *vs.* 39.7 MJ/d, respectively).

## Discussion

### Prediction of lactation energy balance

Sow and litter performance are in line with those reported in recent publications with similar lactation length (Stewart *et al.*,



**Figure 2.** Adjusted first (linear) and second (quadratic) order polynomials for the serum metabolite concentrations (NEFA, mmol/L, glycerol,  $\mu\text{mol/L}$ , urea, mg/dL, creatinine, mg/dL and urea:creatinine ratio) over the lactation period according to the age of the sow (gilts, G vs multiparous, M).

2021, Williams *et al.*, 2021; Ye *et al.*, 2022). Milk production has the highest priority for the sow during lactation, which means that energy and most dietary nutrients are directed toward the mammary glands (Strathe *et al.*, 2017). In fact, almost 100% of maternal dietary energy intake (or even more) may be required for milk synthesis (Pluske *et al.*, 1995; Pedersen *et al.*, 2019; also Table 3) and among sows within farms, milk production costs explain 95% of variability in the daily ME requirement (Gauthier *et al.*, 2019). The fact that in this study ME intake and ME used for milk production were poorly correlated suggests that, probably, daily feed intake did not reach full *ad libitum* and illustrates the importance

of energy mobilization. Adiposities reduce in size and lipoprotein lipase activity in fat tissue decreases considerably during lactation (Steingrimsdottir *et al.*, 1980), and a considerable amount of protein can be depleted from lean tissue stores (Kim and Easter, 2001). In fact, the sow compensates for inadequate feed intake to maintain a high milk production, even though it is expensive as the body reserves lost must be reconstituted during the following gestation, resulting in an increased feed cost (Strathe *et al.*, 2017).

Energy mobilization (NE loss) is mainly a consequence of a limitation on feed intake (Eissen *et al.*, 2000; Gauthier *et al.*,

**Table 4.** Akaike information criterion (AIC) for the linear and quadratic tendency and the effect of the age of the sow (gilts vs multiparous), the tendency and their interaction on serum concentration of non-esterified fatty acids (NEFA), glycerol, urea and creatinine plus the urea:creatinine ratio

Item	AIC		P-value ANOVA	P-value			RSE
	Lin	Quad		Age	Trend	Age $\times$ Trend	
NEFA, mmol/L	435	418	<0.001 (Q)	0.677	<0.001	0.012	0.270
Glycerol, $\mu\text{mol/L}$	3438	3430	0.003 (Q)	0.667	<0.001	0.076	25.3
Urea, mg/dL	2111	2094	<0.001 (Q)	0.236	<0.001	0.071	6.15
Creatinine, mg/dL	871	863	0.002 (Q)	0.000	<0.001	0.148	0.300
U:C	1509	1505	0.022 (Q)	0.0480	<0.001	0.047	2.39

U:C: urea:creatinine ratio, RSE: residual standard error. ANOVA comparing quadratic (Q) against linear model.

**Table 5.** Effect of level of NE mobilized (high, medium, low) and age of the sow (gilts, G vs. multiparous, M) on litter and piglet performance and the sow's weaning to oestrus interval (WEI)

Item	NE mobilized (Mob.)			Age		SD	P-value		
	High	Med.	Low	G	M		Mob.	Age	Inter.
n sows	26	25	26	22	55				
Weaned	11.5	11.4	10.8	11.5	10.9	0.87	0.010	0.006	0.515
Mortality, %	5.0	5.7	12.2	5	11	7.8	0.013	0.004	0.840
Litter gain 20 d, kg	54	47	39	45	47	6.3	<0.001	0.344	0.458
BW at CF, kg	1.7	1.7	1.6	1.6	1.6	0.31	0.636	0.742	0.629
Piglet gain, kg	4.8	4.2	3.7	4.0	4.5	0.52	<0.001	<0.001	0.140
WEI, d	6	6	6	7	5	2.1	0.925	0.006	0.948

SD: standard deviation, CF: cross-fostering. Eight sows included as low mobilizers, two gilts plus six multiparous, showed positive NE balance over the entire lactation.

**Table 6.** Effect of level of NE mobilized (high, medium, low) and age of the sow (gilts, G vs. multiparous, M) on metabolizable energy partitioning, body weight (BW) and back fat thickness (BT) measured pre-farrow and BW estimated just post-farrow and BT, BW and body lipid and protein (kg) losses, and the NE balance over the 20 d lactation period

Item	NE mobilized (Mob.)			Age		SD	P-value		
	High	Med.	Low	G	M		Mob.	Age	Inter.
n sows	26	25	26	22	55				
ME intake, MJ	1187	1307	1389	1237	1352	176.7	0.006	0.015	0.625
ME in milk, MJ	1368	1183	887	1127	1164	172.0	<0.001	0.416	0.230
BW pre-farrow, kg	263	259	264	225	299	22.4	0.738	<0.001	0.803
BW post-farrow, kg	242	239	244	207	276	20.1	0.732	<0.001	0.883
BW loss, kg	31	30	18	31	22	10.5	0.003	0.004	0.931
BT pre-farrow, mm	17	17	17	16	18	3.7	0.802	0.283	0.996
BT loss, mm	3	3	2	3	2	1.6	0.069	0.107	0.030
Lipid loss, kg	9	8	5	8	6	2.9	0.002	0.020	0.447
Protein loss, kg	4	3	2	3	3	1.4	<0.001	0.112	0.914
NE loss, MJ	1100	607	57	557	618	226.4	<0.001	0.299	0.402

SD: standard deviation. Eight sows included as low mobilizers, two gilts plus six multiparous, showed positive NE balance over the entire lactation. ME in milk calculated using a constant value of 0.72 for  $K_m$  (efficiency of utilization of ME for milk synthesis) according to Dourmad *et al.* (2008). Lipid and protein losses were estimated using the NRC (2012) equations. NE loss obtained by difference assuming constant values of 0.72 ( $K_m$ ) and 0.87 ( $K_{bm}$ , efficiency of utilization of body reserves for milk production; Dourmad *et al.*, 2008). The efficiency of utilization for growth during lactation ( $K_{mb}$ ) was assumed to be 0.75.

2019). However, a better relationship with ME for milk ( $r = 0.790$ ) than with ME intake ( $r = 0.541$ ) was found, suggesting litter size and vitality of the piglets, which are the main determinants of milk production (Hartmann *et al.*, 1997), are also responsible.

In any case, the mean value for lactation efficiency, defined by Bergsma *et al.* (2009) as ME for milk divided by the sum of ME intake and ME equivalent from body reserves, was 0.678 (SD = 0.055). This mean value is similar to the found by Everts and Dekker (1994a) using respiratory chambers, but lower than that found by Pedersen *et al.* (2019) using D<sub>2</sub>O space to assess energy mobilization (0.87). Cabezón *et al.* (2017) also found substantial variation in daily heat production between sows within the same parity. In any case, the correlations observed between changes in BT or BW and NE loss ( $r \leq 0.55$ ) may suggest that both changes in BT and BW are useful predictors of energy mobilization but the way to utilize them may need to be re-evaluated.

Higher body NE loss was found during the first half of lactation compared to the second half. This is because of the higher difference between ME intake and ME used for maintenance and milk production (Fig. 1, Table 7), and is in agreement with other published results (Rojkittikhun *et al.*, 1993; Gauthier *et al.*, 2019; Tokach *et al.*, 2019). The origin of the tissue mobilized is also different. First, protein accumulated during gestation in the reproductive tract and other internal viscera is quickly mobilized at the beginning of lactation (Kim and Easter, 2001; Theil, 2015; Gauthier *et al.*, 2019). It has been estimated that the regressing uterus released about 14 MJ ME into the endogenous plasma pool during lactation (Feyera and Theil, 2017), contributing to total energy supply with the same efficiency as that from body reserves; the half-life of post-partum uterine involution is 6.2 d (Gauthier *et al.*, 2019). Second, since deposition of adipose tissue in mammals occurs in at least two different anatomic depots, namely around abdominal viscera in the mesentery and

**Table 7.** Effect of amount of energy mobilized (High, Medium, Low) and stage of lactation (SL: first vs. second half) on metabolizable energy intake, metabolizable energy for milk and net energy loss (MJ/sow/d)

Item	First half (1–10 d)			Second half (11–20 d)			SD	Significance		
	High	Med.	Low	High	Med.	Low		Mob.	SL	Inter.
ME intake, MJ/sow/d	44	50	53	77	84	85	3.4	0.003	0.001	0.730
ME in milk <sup>1</sup> , MJ/sow/d	68	57	42	76	68	59	3.4	<0.001	<0.001	0.022
NE loss <sup>2</sup> , MJ/sow/d	81	53	22	43	19	4	5.7	<0.001	<0.001	0.010

SD: standard deviation. ME in milk calculated using a constant value of 0.72 for  $K_m$  (efficiency of utilization of ME for milk synthesis) according to Dourmad *et al.* (2008). NE loss obtained by difference assuming constant values of 0.72 ( $K_m$ ) and 0.87 ( $K_{bm}$  efficiency of utilization of body reserves for milk production; Dourmad *et al.*, 2008). The efficiency of utilization for growth during lactation ( $K_{mb}$ ) was assumed to be 0.75.

omentum, and in a subcutaneous location (Pond, 1992), the way fat is mobilized may be different. Straughen *et al.* (2013) indicated that both fat depots in humans differ in endocrine function and lipolytic activity. Furthermore, Frayn *et al.* (2003) indicated, also in humans, that visceral fat, mainly accumulated during gestation, is mobilized faster than subcutaneous fat because intra-abdominal adipocytes have a higher rate of lipolysis when stimulated with a beta-adrenoreceptor agonist. However, Pond (1992) pointed out that the distribution of adipose tissue differs greatly between species and is physiologically adaptive. This author indicated that the relative volume of adiposities in different depots is constant but the relative numbers of such adiposities, and hence the relative mass of the depots, varies greatly between species, and to a lesser extent between individuals of the same species. Compared to humans, pigs probably have proportionately less intra-abdominal adipose tissue, and more subcutaneous depots, but since the larger depots are less metabolically active and less responsive than the smaller ones (Pond, 1992), intra-abdominal fat still may make a key contribution to energy balance in early lactation.

As lactation progresses, serum NEFA and glycerol concentrations increase (Fig. 2) while energy mobilization decreases (Fig. 1) and, although blood levels of glycerol and NEFA are respective indicators of body fatness and fat mobilization (Revell *et al.*, 1998), they were not correlated ( $r < 0.17$ ) with either calculated body energy or lipid loss during lactation. Frayn *et al.* (2003) indicate that visceral adipose tissue provides little NEFA and no glycerol to the systemic circulation and that the specific contribution to NEFA delivery to the liver from visceral depots is small relative to the contribution of subcutaneous fat. In fact, Despres and Lemieux (2006) indicate that, in humans, visceral fat goes directly to the liver via the portal vein and, consequently, does not necessarily contribute to increase plasma NEFA concentration. As those visceral fat depots are mobilized quickly, this would justify part of the discrepancy found between NEFA and glycerol serum concentrations and energy mobilization at early lactation. The increase in urea serum concentration and in the ratio urea:creatinine (Fig. 2) would be a direct consequence of the increase of feed intake through lactation.

### Effect of level of energy mobilization

The range of NE loss is broad and has a high standard deviation (Table 3). This large variability may be partially attributed to calculation errors but must be mainly due to other factors related to the sow or the environmental conditions. Grandinson *et al.* (2005) reported heritability coefficients ( $h^2$ ) for body weight loss and back fat loss in lactating cows of 0.20 and 0.10, respectively. Dairy cows with high genetic merit for milk production

mobilize more body reserves than cows of low genetic merit (Pryce *et al.*, 2001) and there appears considerable variation between selected dairy cows for releasing energy fuels from adipose tissue stores (Hammon *et al.*, 2009). These results for cows suggest some genetic capacity or animal predisposition for tissue and energy mobilization in lactation, and perhaps this could be extended to sows. Bergsma *et al.* (2008) found a high  $h^2$  in sows for body weight and body composition at the beginning of lactation (0.4 to 0.5), but mobilization of body tissue during lactation was less heritable (<0.1).

The way of distributing sows between their levels of energy mobilization (Table 2) may be criticized. The method employed is empirical and factorial. The main concerns are the assumption of constant values and the means of deciding the composition of mobilized tissue and consequently the origin of body energy losses. Whilst acknowledging that the composition of mobilized tissues varies with several factors during the sow's lactation, NRC (2012) assume constant values and even more recent models fail to take this into account (Gauthier *et al.*, 2019). The proportions of fat and protein chosen (720 and 280 g/kg, respectively) are the mean of results presented here (Table 3) and agree well with data reported in several studies (e.g. Everts and Dekker, 1994b; Revell *et al.*, 1998; Sauber *et al.*, 1998; Kim and Easter, 2001; Bergsma *et al.*, 2009; Strathe *et al.*, 2017). However, there are other approaches to distributing sows according to their energy or tissue mobilization. Weber *et al.* (2013), studying fat mobilization in cows around calving, distributed the animals between high and low mobilizers depending on their liver fat concentrations post-partum measured by liver biopsy. Mitchell *et al.* (2001) used magnetic resonance imaging and Arthur *et al.* (2011) X-ray-computer tomography to estimate the body composition of growing pigs. Recently, Pedersen *et al.* (2019 and 2020) used deuterated water ( $D_2O$ ) to estimate sow's body composition around farrowing and Johnson *et al.* (2022) used indirect calorimetry to determine total metabolic heat production in lactating sows. A sequential slaughtering experiment would also give an accurate picture (Everts and Dekker, 1994a). However, these methodologies are expensive, all have their own limitations, and most of them would be difficult to perform under commercial conditions.

The results appear generally sound and in agreement with Strathe *et al.*, (2017) when comparing gilts and multiparous sows (Tables 5 and 6), and as gilts consume less ME than multiparous sows, they made greater metabolic effort to achieve similar total litter gains. Consequently gilts lost more body weight during lactation, i.e. more lipid and protein. However, mean NE loss for the gilts did not differ from that for multiparous sows. The composition of the tissue loss may be different. Mullan *et al.* (1989) suggest that the composition of mobilized tissue during lactation



changes with age of the sow, and it appears that the composition of tissue losses may play a central role. The different evolution of the serum NEFA and glycerol concentrations through lactation between gilts and multiparous sows (Fig. 2) may support this idea. Furthermore, Pluske *et al.* (1995) demonstrate that increasing the energy intake of gilts above *ad libitum* feeding via a gastric cannula did not stimulate milk production and suggest that, unlike the sows, gilts are likely to partition extra energy into body growth rather than milk production. The lower creatinine level and the higher urea:creatinine ratio found in the serum of gilts compared to multiparous sows (Fig. 2) may indicate a lower rate of protein and lean tissue mobilization.

In agreement with some authors (e.g. Rojkittikhun *et al.*, 1993; Everts and Dekker, 1994b; Revell *et al.*, 1998; Kim and Easter, 2001; Bergsma *et al.*, 2009), high mobilizing sows had a lower ME intake (Table 6) than low mobilizers. As a consequence, the high mobilizers lost more body weight, BT, lipid and protein. In cows, Weber *et al.* (2013) also found that the decrease in body weight post-partum was greatest in high fat-mobilizers, but the decrease in back fat thickness was greatest in medium fat-mobilizers.

Finally, since high mobilizing sows, compared to low mobilizers, used a greater amount of ME for milk production (Table 6), which is in agreement with a higher litter gain (Table 5), the results suggest that mobilizing up to a certain amount of body energy improves litter gain without seriously damaging the mother. Besides, it may also be of interest to identify the sows with positive energy balance, which might result from low milk production or a large appetite (Gauthier *et al.*, 2019). However, such results may be different depending on litter size and body composition of the sow.

## Conclusion

Reliable values of NE loss during lactation may be obtained by difference after curvilinear fitting daily feed intake and litter growth data. The results showed that in controlled commercial conditions, sows that mobilize more tissue and energy up to a certain level have a lower feed intake, but weaned more piglets and heavier litters than the other sows. Net energy loss was higher over the first half of lactation than thereafter. More research is required to assess the total amount and a safe threshold of energy mobilized by the lactating sow and the relative contribution of lean and fat tissue mobilized. A better understanding of the changes in live weight or back fat thickness would be helpful.

**Acknowledgement.** We are indebted to the late Dr Kees de Lange for his insight and encouragement during the genesis of this manuscript. We also thank Dr Merce Farré for expert statistical advice.

**Author's contributions.** Conceptualization J. G. and J. F.; methodology J. G., S. C., J. L. E., D. S.-O. and J. F.; formal analysis J. G., S. C., J. L. E., and D. S.-O.; writing—original draft preparation J. G. and J. F.; writing—review and editing J. G., S. C., J. L. E., D. S.-O. and J. F. All authors have read and agreed to the published version of the manuscript.

**Funding statement.** This research did not receive any specific grant from funding agencies in the public, commercial or not-for-profit sectors.

**Competing interests.** None.

**Ethical standards.** The Ethical Committee on Animal Experimentation at the Universitat Autònoma de Barcelona reviewed and approved the protocols for the experiments (reference number 2788M2). LW × LD females were used for the present procedure.

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