

Journal of Animal Science, 2020, 1–14

doi:10.1093/jas/skz379

Advance Access publication December 25, 2019 Received: 14 October 2019 and Accepted: 24 December 2019 Non Ruminant Nutrition

NON RUMINANT NUTRITION

Effect of increasing dietary energy density during late gestation and lactation on sow performance, piglet vitality, and lifetime growth of offspring

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Abstract

Genetic selection for hyperprolificacy in sows has resulted in a significant increase in the number of piglets born alive per litter but subsequently, decreased piglet vitality and growth. As a consequence, increasing sows' energy intake during lactation to help increase piglet vitality and growth is increasingly important. The objective of this study was to investigate the effect of increasing dietary energy density for lactating sows on weight and back-fat changes in sows, milk composition, and vitality and growth of progeny. Gestating sows (N = 100; Large White × Landrace) were randomly assigned to one of four energy dense diets at day 108 of gestation until subsequent service; 13.8 (LL), 14.5 (L), 15.2 (H), and 15.9 MJ DE/kg (HH). All diets contained 1.2% total lysine. Blood samples from sows were taken on day 108 of gestation and at weaning (day 26 of lactation) and colostrum (day 0) and milk samples (day 14) were collected during lactation. Sow lactation feed intakes were recorded daily. The number of piglets born per litter (total and live), piglet birth weight (total and live), intrauterine growth restriction (IUGR) traits and muscle tone were recorded in piglets at birth. Piglet tympanic ear temperature (TEMP) was recorded at birth and at 24 h. Pigs were weighed on days 1, 6, 14, 26, 33, 40, 54, 75, and 141 of life. Postweaning (PW) pigs were fed standard cereal-based diets. Pig carcass data were collected at slaughter (day 141). Lactation energy intake was higher for HH sows than for all other treatments (P < 0.01). Colostrum and milk composition and lactation feed intake were not affected by treatment. The number of piglets born per litter (total and live) and piglet birthweight (total and live) was similar between treatments. Piglets from LL sows had more IUGR traits (P < 0.01), while those from HH sows had better muscle tone (P < 0.01) than all other treatments. Piglets from LL sows (P < 0.01) and piglets from H sows (P < 0.01) had a higher 24 h TEMP than piglets from HH sows. H sows weaned a greater number of piglets than L sows (P < 0.05) and HH sows (P < 0.01), while L sows weaned lighter litters than H (P < 0.05) and LL sows (P < 0.05). Pig growth PW was unaffected by treatment. High energy dense diets increased energy intake in sows, without depressing appetite. Feeding an HH diet improved piglet muscle tone at birth, whereas feeding an H diet increased litter size at weaning. Inconsistent results were observed for other traits of piglet vitality and for preweaning litter growth performance.

Key words: energy density, growth, lactation feeding, milk, piglet, vitality

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Introduction

Large litter size in sows is associated with a decrease in mean piglet birth weight and consequently, piglet vitality (defined here as piglet strength and vigor), and growth (Vanden Hole et al., 2018). Much of the research on feeding strategies to increase piglet vitality has focused on nutritional strategies that are directly applied to the piglet in the form of supplementary milk, or substances rich in energy (Casellas et al., 2005; Declerck et al., 2016; Schmitt et al., 2019), with only a small number of sow feeding studies conducted. Feeding supplemental soya bean oil to sows in late gestation increased piglet vitality at birth (Rooke et al., 1998), while the addition of *n*-3 polyunsaturated fatty acids to sow diets in mid-gestation had no effect on piglet vitality (Tanghe et al., 2014). However, we are unaware of any study that has looked at the effect of incremental increases in dietary soya oil levels in late gestation and lactation on indicators of piglet vitality at birth.

As sow productivity has dramatically increased over the last two decades, sow energy requirements during lactation need to be re-evaluated to ensure optimum sow productivity and litter growth. Increasing the energy density of the lactation diet may increase lactation energy intake in sows and the growth rate of nursing piglets (Craig et al., 2016; Choi et al., 2017). Sow milk yield is relatively unresponsive to altered dietary energy supply (Pedersen et al., 2016) and therefore, increased offspring growth is likely mediated through changes in the fat and lactose concentration of colostrum and milk (Kim et al., 2018; Che et al., 2019). Large litter sizes are also associated with a high maternal requirement for energy, due to greater demands for milk by the suckling piglets. Sows are often unable to sustain the high volume of milk output required by the litter through dietary intake alone, and as a result, mobilization of maternal reserves and often excessive BW loss occurs during lactation (Rutherford et al., 2013; Theil, 2015). Previously, sow lactation BW losses were reduced when sows were fed a 13.5 MJ DE/kg diet compared with a 13.1 MJ DE/kg diet from day 109 of gestation to weaning (Kim et al., 2018). The present study was conducted to investigate the effect of incremental increases in dietary energy density from 13.8 to 15.9 MJ DE/kg during late gestation and lactation on sow lactation changes in BW and back fat (BF) thickness, milk composition, piglet vitality, and lifetime growth of offspring. We hypothesized that sows fed a high-energy diet would have a higher lactation energy intake, consequently reducing their mobilization of body reserves. We also hypothesized that an increase in lactation energy intake would increase the concentration of nutrients in colostrum and milk, subsequently increasing the vitality and growth of offspring during the suckling period and throughout their lifetime.

Materials and Methods

This study was carried out between October 2017 and December 2018, at the Teagasc Pig Development Department, Moorepark, Fermoy, Co. Cork, Ireland. Ethical approval for this study was granted by the Teagasc Animal Ethics Committee (approval no. TAEC162/2017), and the project was authorized by the Health Products Regulatory Authority (project authorization no. AE19132/P071). The experiment was conducted in accordance with Irish legislation (SI no. 543/2012) and the EU Directive 2010/63/EU for animal experimentation.

Animals, housing, and treatments

One hundred sows with the same genetic background (Large White × Landrace; Hermitage Genetics, Sion Road, Co. Kilkenny,

Ireland) were used in the study. Sows selected from 7 weaning batches were artificially inseminated at the onset of standing estrus and again 24 h later using pooled semen (Danish Duroc; Hermitage Genetics, Ireland). Gestating sows were managed in a dynamic group pen which held 120 animals at any one time. The pen had two electronic sow feeders [ESF; Schauer Feeding System (Competent 6), Prambachkirchen, Austria], insulated concrete lying bays, and fully slatted floors. Water was available to sows ad libitum from single-bite drinkers in the ESF's and from five drinker bowls located around the pen. On day 105 of gestation, sows were blocked within batch into 25 blocks of 4 sows on the basis of parity (mean \pm SEM; 2.6 \pm 0.40), BW (277.4 \pm 6.96 kg) and BF thickness (18.0 \pm 0.60 mm). Sow parity distribution: parity 0 (10%), 1 (18%), 2 (11%), 3 (24%), 4 (34%), and 5 (3%).Within each block, sows were randomly assigned to 1 of 4 energy density diets at day 108 of gestation: (i) 13.8 MJ DE/kg, (ii) 14.5 MJ DE/kg, (iii) 15.2 MJ DE/kg, and (iv) 15.9 MJ DE/kg, denoted LL, L, H, and HH, respectively, until their subsequent service (day 6 ± 0.1 postweaning, PW). On day 108 of gestation, sows were moved into standard farrowing crates (pen dimensions: 2.5 m × 1.8 m). Farrowing rooms accommodated 7 or 14 animals per room. Artificial lighting was provided daily from 0800 to 1630 h. Farrowing room temperature was maintained at ~24 °C at farrowing and gradually reduced to 21 °C by day 7 of lactation. Where possible, litter size was standardized within treatment during the first 24 h after parturition, so that there was an average litter size of 13.8 ± 0.60 suckling piglets per sow. The final number of piglets remaining on each litter at 24 h postpartum was affected by the rearing capacity of each sow (i.e., the number of available functional teats), the availability of foster sows to take surplus piglets, and the time of farrowing. Piglets' teeth were clipped within 24 h postpartum and tails were docked on day 3 postpartum. All piglets received an iron injection on day 5 postpartum and males remained fully intact. Piglets were weaned on day 26 \pm 0.1 of lactation.

All pigs were grouped by sow treatment and sex at weaning, and a subsample of 312 pigs (156F and 156M) was monitored until slaughter at 141 d old. The pigs selected at weaning were those that represented the average weaning weight of each sow treatment. Then within each weaning group, pigs were randomly assigned to same sex pen groups of 12 pigs (N = 26 pens) and moved to weaner accommodation (pen dimensions: 2.1 m × 3.0 m). Sow treatments were represented in each pen, with 3 pigs per sow treatment per pen. Pens were equipped with a single-spaced automatic feeder and an individual pig recognition system (Schauer Agrotronic GmbH, Prambachkirchen, Austria). To allow pigs' time to adapt to the automatic feeding system, feeders were switched off for the first 7 d PW and then switched to training mode for a further 7 d. Each pig was fitted with a uniquely coded ear tag transponder and individual feed intake was recorded after the adaptation period, by the control software linked to each feeder (MLP; Schauer, Austria). Weaner room temperature was maintained at 28 °C for the first 7 d PW and gradually reduced to 22 °C by day 54 of age. On day 75 of age, pig groups were moved to finisher accommodation (pen dimensions: 4.0 m × 2.8 m) which had the same layout and feeding system as the weaner housing. Finisher room temperature was maintained at 20 to 22 °C. Pig growth and feed intake were monitored to slaughter. Pigs from each weaning batch were slaughtered on the same day, at an average age of 141.0 \pm 0.06 d. Pigs were transported 95 km to a commercial abattoir (Dawn Pork and Bacon, Co. Waterford, Ireland) where they were killed by exsanguination after CO, stunning.

Diets and feeding

Diets were formulated to meet or exceed NRC (2012) recommendations. The ingredient composition and chemical analyses of the experimental diets are presented in Table 1. All diets were manufactured on site and celite (1 g/kg) was added to each diet during the milling process as a source of acid and insoluble ash in order to measure the coefficient of apparent total tract digestibility (CATTD) of nutrients and energy (McCarthy et al., 1977). The ESF's in the group sow house (Schauer Feeding System) recognized individual sows by their transponder, which was programmed with the sows' daily feed allowance. During gestation, sows were fed a standard gestation diet at a feed allowance of 2.2 kg/d from days 0 to 90 of gestation. The gestation diet was formulated to have a total lysine content of 0.8% and an energy density of 13.2 MJ DE/kg. From day 90 of gestation to parturition, sow feed allowance was increased to 2.7kg/d and sows received their respective experimental diets from day 108 of gestation until subsequent service. In the farrowing room, diets were fed using a computerized feed delivery system (DryExact Pro, Big Dutchman, Vechta, Germany). All four experimental diets were formulated to contain the same level of total lysine (1.2%). Sows were fed twice daily from days 0 to 6 of lactation and three times daily thereafter until weaning

(~ day 26 of lactation). Sows were fed according to a lactation feed curve which started at 60 MJ DE/d at day 0 of lactation and gradually increased to 107, 125, 133, and 137 MJ DE/d at days 7, 14, 21, and 26 of lactation, respectively. However, feed troughs were checked once a day in the morning to assess sow feed intake and individual feeding curves were adjusted accordingly to ensure that intake was as close to ad libitum feeding as possible and to prevent feed wastage. Thus, some sows were fed below or above the curve, depending on the daily feed disappearance in each trough. Water was provided on an ad libitum basis to sows from a single-bite drinker in the feed trough and to suckling piglets from a bowl in the farrowing pen. During the weaning to service interval, sows remained on their respective experimental diet and were fed 3.5 kg/d in the morning. Water was provided to sows on an ad libitum basis from a single-bite drinker in the feed trough.

Suckling piglets did not receive creep feed. Following weaning (day 26), pigs were fed the following sequence of dry pelleted diets (3 mm in diameter): Starter diet (1.6% lysine, 16.2 MJ DE/kg) from days 26 to 33, link diet (1.5% lysine, 15.0 MJ DE/kg) from days 33 to 47, weaner diet (1.3% lysine, 14.4 MJ DE/kg) from days 47 to 75, and a finisher diet (1.1% lysine, 13.8 MJ DE/kg) from day 75 to slaughter (~ day 141). Water was available on an ad libitum

Table 1. Composition of experimental diets (on air dry basis as fed)

| Dietary treatment | LL | L | Н | HH | |
|------------------------------------|--------|--------|--------|--------|--|
| MJ DE/kg | 13.8 | 14.5 | 15.2 | 15.9 | |
| Ingredients, g/kg | | | | | |
| Wheat | 410.00 | 419.80 | 429.60 | 439.40 | |
| Barley | 372.50 | 320.60 | 268.80 | 217.10 | |
| Soya bean meal (480 g/kg CP) | 178.50 | 187.60 | 196.70 | 205.70 | |
| Soya oil | 0.00 | 33.00 | 66.00 | 99.00 | |
| Lysine HCL (78.8)1 | 4.71 | 4.59 | 4.47 | 4.36 | |
| DL-Methionine ¹ | 1.27 | 1.31 | 1.35 | 1.40 | |
| L-Threonine (98)1 | 2.48 | 2.46 | 2.45 | 2.43 | |
| L-Tryptophan ¹ | 0.72 | 0.72 | 0.71 | 0.71 | |
| Di-calcium phosphate | 8.50 | 8.50 | 8.50 | 8.50 | |
| Limestone flour | 11.50 | 11.50 | 11.50 | 11.50 | |
| Salt | 5.00 | 5.00 | 5.00 | 5.00 | |
| Minerals and vitamins ² | 1.50 | 1.50 | 1.50 | 1.50 | |
| Phytase 5,000 IU/g³ | 0.10 | 0.10 | 0.10 | 0.10 | |
| Celite ⁴ | 1.00 | 1.00 | 1.00 | 1.00 | |
| Chemical composition, g/kg | | | | | |
| DM ⁵ | 881.13 | 884.68 | 888.33 | 892.76 | |
| Ash⁵ | 44.50 | 45.12 | 45.59 | 44.78 | |
| CP ⁵ | 170.44 | 171.74 | 172.63 | 171.60 | |
| EE ⁵ | 18.99 | 43.46 | 72.35 | 90.69 | |
| NDF ⁵ | 136.18 | 131.01 | 120.70 | 111.16 | |
| GE, MJ/kg ^s | 16.0 | 16.7 | 17.2 | 17.8 | |
| DE, MJ DE/kg ⁶ | 13.8 | 14.5 | 15.2 | 15.9 | |
| NE, MJ NE/kg6 | 9.5 | 10.2 | 10.9 | 11.6 | |
| Total lysine ⁶ | 11.5 | 11.5 | 11.5 | 11.5 | |
| SID lysine ⁶ | 10.6 | 10.6 | 10.6 | 10.6 | |

EE, ether extract; NDF, neutral-detergent fiber; SID, standardized ileal digestible.

¹Synthetic AAs

² Lactation diet provided (mg/kg completed diet): Cu, 15 mg; Fe, 70 mg; Mn, 62 mg; Zn, 80 mg; I, 0.6 mg; Se, 0.2 mg; vitamin A as retinyl acetate, 3 mg; vitamin D_3 as cholecalciferol, 25 mg; vitamin E as DL-α-tocopheryl acetate, 100 mg; vitamin K, 2 mg; vitamin B_{12} , 15 mg; riboflavin, 5 mg; nicotinic acid, 12 mg; pantothenic acid, 10 mg; biotin, 200 mg; folic acid, 5 mg; thiamin, 2 mg; pyridoxine, 3 mg.

³Sow diets contained 500 phytase units (FYT) per kilogram finished feed from Natuphos 5000 (RONOZYME HiPhos, DSM, Belfast, UK).

⁴Celite (1 g/kg) was added to the lactation diets during the milling process in order to measure the coefficient of apparent total tract digestibility (CATTD) of nutrients and energy.

⁵Analyzed nutrient composition.

⁶Calculated nutrient composition (Sauvant et al., 2004).

basis from a single drinker bowl in each pen in both weaner and finisher accommodation (DRIK-O-MAT, Egebjerg International A/S, Egebjerg, Denmark).

Sow BW and BF thickness

Sow BW and BF were recorded on day 105 of gestation, on day 14 of lactation (BF only), at weaning, and again at their subsequent service (day 6 PW). Sow BW was recorded using an electronic sow scales (EziWeigh 7i, O'Donovan Engineering, Co. Cork, Ireland), and BF was measured using a digital BF indicator (Renco LEAN-MEATER, Renco Corporation, Golden Valley, MN) as previously described by Rooney et al. (2019).

Collection and analysis of sow blood samples

On day 108 of gestation and at weaning, blood samples for the analysis of IGF-1 and insulin were collected from a randomly selected subsample of sows by jugular venepuncture (n = 8 sows per treatment). Blood samples were collected into 9 mL EDTA collection tubes and into 9 mL serum clot activator collection tubes (VACUETTE, Labstock Microservices, Co. Meath, Ireland). Sow blood glucose concentration was determined using a hand held blood glucose monitor (IDIA Blood Glucose monitor, Arctic Medical, Folkestone, UK), by inserting a glucose test strip into a fresh droplet of blood. Blood samples were handled, stored, and then analyzed in duplicate for concentrations of IGF-1 and insulin, using commercial enzyme-linked immunosorbent assays (Mediagnost IGF-1 ELISA kit, Oxford Biosystems, Oxford, UK; Human Insulin ELISA Kit, Fisher Scientific, Co. Dublin, Ireland) as previously described by Rooney et al. (2019). The minimum detectable concentration of IGF-1 and insulin that could be distinguished from 0 was 0.09 µg/L and 0.17 µIU/mL, respectively. The intra-assay CVs were 5.9% and 6.0%, and the inter-assay CVs were 9.1% and 9.2% for IGF-1 and insulin, respectively. IGF-1 and insulin concentrations were quantified by interpolating absorbance readings from a standard curve generated in the same assay.

Collection and analysis of colostrum and milk samples

Colostrum samples (~15 mL) were collected from all sows within 2 h of the first piglet being born. On day 14 of lactation, milk samples were collected from a randomly selected subsample of sows (~30 mL; n = 14 sows per treatment) following a 1 mL (10 IU) intramuscular injection of Oxytocin (Eurovet Animal Health, Bladel, the Netherlands). Prior to milk sampling, litters were removed from the sow for 3 h to facilitate refill of the mammary gland. Colostrum and milk samples were manually collected from teats at the anterior, middle and posterior locations of the udder and immediately frozen at -20°C for subsequent analysis. Colostrum samples were diluted 1:4 with distilled deionized water prior to analysis and then analyzed in duplicate for the percentage of total solids, protein, fat, lactose, and ash on an infrared analyzer (Bentley DairySpec FT 89111, Bentley Instruments, Co. Tipperary, Ireland). Undiluted milk samples were analyzed in duplicate for the percentage of total solids, protein, fat, and lactose on another infrared analyzer (Milkoscan FT 6000, Foss Electric, Warrington, UK). Milk samples (~10 mL; n = 14 sows per treatment) were dried at 55 °C for 72 h and the GE content of milk was measured using an adiabatic bomb calorimeter (Parr Instruments, Moline, IL). Sow milk yield was estimated by assuming 4 kg of milk produced per kilogram of litter weight gain between day 1 postpartum and weaning (Boyd et al., 2002).

Total tract digestibility and laboratory analysis

Representative feed samples were collected at regular intervals throughout the experimental period and retained for chemical analysis. Fecal samples were collected from the pens of a subsample of sows (n = 10 sows per treatment) on days 13, 14, and 15 of lactation and promptly frozen at -20 °C for the determination of CATTD. Prior to analysis, fecal samples were dried at 55 °C for 72 h and feed and dried fecal samples were milled and passed through a 2 mm screen (Christy and Norris Hammer Mill, Chelmsford, England). Feed and fecal samples were analyzed in duplicate for DM, ash, CP, neutral detergent fiber (NDF), ether extract (EE), and GE. The DM content of feed and feces was determined after drying overnight at 105 °C (18 h minimum). The crude ash content was determined after ignition of a weighed sample in a muffle furnace (Nabertherm, Bremen, Germany) at 550 °C for 5.5 h (Thiex et al., 2012). The CP content was determined as nitrogen × 6.25 using a LECO FP 528 instrument (LECO Instruments UK LTD, Chesshire, UK) (Thiex, 2009). The NDF content was determined according to the method of Van Soest et al. (1991) using the Ankom 220 Fibre Analyser (Ankom Technology, Macedon, NY). The EE concentration was determined using light petroleum ether and Soxtec instrumentation (Tecator, Sweden). The GE of diets and fecal samples was measured using an adiabatic bomb calorimeter (Parr Instruments, Moline, IL). The concentration of acid and insoluble ash in feed and fecal samples was determined according to the method of McCarthy et al. (1977).

Lactation feed and energy intake

Individual lactation feed intake of sows was recorded daily, from which the total lactation feed intake and ADFI for each sow was calculated. The DE and NE intake of sows (total and mean daily) were determined using analyzed DE and calculated NE values, respectively.

Farrowing performance and preweaning piglet growth performance

Video cameras were installed above a subsample of sows (n = 10 sows per treatment) before the onset of farrowing so that farrowing duration, piglet birth interval, and the birth to suckle interval of the first born piglet could be recorded. As piglet vitality at birth was a variable of interest, management interventions such as drying off piglets postfarrowing or moving piglets away from the rear of the sow were not implemented. The number of piglets born (total, live, stillborn, and mummified) was recorded at birth, and each piglet was tagged for identification purposes. Subsequently, piglets were individually weighed on days 1, 6, 14, and 26 postpartum and these data were used to determine the number of suckling piglets at each weighing, the litter weight at each weighing, and piglet preweaning ADG. Piglet mortality between birth and weaning was also recorded.

Piglet vitality measures

Intra-uterine growth restriction (IUGR) score

At birth, piglets were scored for traits that are characteristic of IUGR according to the shape of their head (0 =normal shape, 1 = "dolphin" shape), presence or absence of bulging eyes (0 = absent, 1 = present), and presence or absence of wrinkles perpendicular to the mouth (0 = absent, 1 = present) (Hales et al., 2013). Scores were then summed so that piglets presenting none of the IUGR characteristics (i.e., a score of 0) were considered to be "normal" and scores between 1 and 3 were indicative of increasing levels of IUGR.

Muscle tone score

To test the vitality of piglets at birth, a simple test was performed to determine the muscle tone of each piglet using the following protocol. The piglet was lifted from the ground by placing one hand under the belly of the piglet, and one hand was then placed under the piglets' hind legs. A score of 1 was given if the piglet used its hind legs to push off the palm of the handlers' hand, and a score of 0 was given if the piglets' hind legs were limp, with no pressure being applied by the hind legs.

Tympanic ear temperature (TEMP)

Piglet TEMP was measured at birth and again 24 h later using a hand-held tympanic ear thermometer (Vet-Temp VT-150, Vet Direct, Newcastle, UK). All temperature recordings were taken from the piglets left eardrum. It should be noted that TEMP is not a measure of core piglet body temperature and therefore, the values obtained were lower than the previously reported values for piglet rectal temperature (Schmitt et al., 2019).

Blood glucose concentration

At 24 h postpartum, a blood sample by needle prick was obtained from the ear vein of a subsample of randomly selected piglets (N = 988 piglets) (30G/0.3 mm), and glucose concentration was determined from a droplet of blood using a hand held blood glucose monitor (IDIA Blood Glucose monitor, Arctic Medical, Folkestone, UK) and a glucose test strip.

Lactation efficiency

Lactation efficiency was calculated for each sow for days 1 to 26 of lactation and was expressed as the ratio between the output in litter growth [total litter weight gain between days 1 and 26 of lactation (g)] and the energy intake in sows [energy intake during lactation (MJ DE)]. The energy intake during lactation was calculated as total sow energy intake (MJ DE) minus the energy requirement for maternal tissue deposition during lactation (kg sow BW gain × 20.8 MJ DE/kg) or total sow energy intake (MJ DE) plus the energy contributed from maternal tissue mobilization during lactation (kg sow BW loss × 12.5 MJ DE) (NRC, 2012).

PW pig growth performance

Pigs were individually weighed on days 26, 33, 40, 54, 75, and 141 (slaughter) of age. Pigs were not fasted before weighing. Feed intakes were recorded on an individual basis from 2 wk PW (day 40 of age) to slaughter. These data were used to determine the ADG, ADFI, and feed conversion efficiency (FCE) for each individual pig. At the abattoir, carcass cold weight was calculated by multiplying the hot carcass weight, recorded within 45 min of the pig being exsanguinated, by 0.98. BF thickness and muscle depth, measured from the edge of the split back at the level of the third and fourth last rib, were determined using a Hennessy Grading Probe (Hennessy and Chong, Auckland, New Zealand). Lean meat content was estimated according to the following formula: Estimated lean meat content (%) = 60.3 - 0.847x + 0.147y, where x = fat depth (mm); y = muscle depth (mm) (Department of Agriculture and Food and Rural Development, 2001).

Statistical analysis

Statistical analysis was performed using the Statistical Analysis Systems statistical software package version 9.4 (SAS Institute Inc., 1989). All data were analyzed using the mixed model procedure (PROC MIXED), with the exception of IUGR and muscle tone score data which were analyzed using a generalized linear mixed model (PROC GLIMMIX). All data were tested for normality prior to analysis by examination of histograms

and normal distribution plots using the univariate procedure. Residuals were inspected in all models to confirm normality. Model fit was determined by choosing models with the minimum finite-sample corrected Akaike information criteria. Linear and quadratic effects of treatment were investigated in all models; however, we did not find any significant effects with regard to our experimental measures and as such, data were analyzed using the fixed effect of dietary treatment. Differences in least square means were investigated using the t-test after Tukey adjustment for multiple comparisons. Degrees of freedom were estimated using Satterthwaite adjustment. The sow/ litter was the experimental unit for sow and preweaning data analysis, and the pig was the experimental unit for PW growth performance data analysis. The statistical model included the main effect of sow treatment and sow batch as a fixed effect. Sow block was included as a random effect for analysis of sow and litter data. Weaner/finisher pen and sow were included as random effects for analysis of PW pig data. For measures repeated over time, the time of recording was included in the model in the repeated statement. Spearman rank correlations were used to investigate the associations between piglet IUGR and muscle tone scores at birth and piglet birth weight, TEMP at birth, piglet preweaning ADG, and weaning weight. Pearson correlations were used to investigate the associations between piglet birth weight and TEMP at birth and piglet preweaning ADG, and associations between piglet weight at 24 h postpartum and TEMP at 24 h postpartum, piglet glucose concentration, and piglet preweaning ADG. These were analyzed at the piglet level. Covariates used in the model included sow BW and BF at day 105 of gestation for analysis of subsequent sow BW and BF, lactation length for analysis of sow lactation intake, litter size at birth for analysis of individual piglet birth-weight, litter size post-crossfostering for analysis of preweaning piglet ADG and litter weight, number of pigs weaned for analysis of sow milk yield, and carcass cold weight at slaughter for analysis of carcass fat depth, muscle depth, and lean meat yield. The results are presented in the text and tables as the least square means together with the pooled standard error. Differences were considered significant at P < 0.05 and as tendencies at P < 0.10.

Results

Diet formulation

The chemical analysis of experimental diets is presented in Table 1. The analysis of DM, ash, CP, EE, NDF, and GE met the formulated dietary composition very closely.

Sow BW and back fat thickness

There was no effect of treatment on sow BW at farrowing, at weaning, or at subsequent service (Table 2; P > 0.05). Sow BF at day 14 of lactation, at weaning, and at subsequent service was also unaffected by treatment (P > 0.05). Similarly, sow BW and BF change during lactation and during the weaning to service interval was unaffected by treatment (P > 0.05; Table 2).

Sow insulin, IGF-1, and glucose concentration

Concentrations of sow plasma IGF-1, serum insulin, and blood glucose on day 108 of gestation and at weaning are presented in Table 3. Concentrations of plasma IGF-1 were unaffected by treatment on day 108 of gestation (P > 0.05), but subsequent to this, IGF-1 levels at weaning were greater for HH sows compared with LL sows (P < 0.05). Serum insulin concentrations on day 108 of gestation and at weaning were

| Dietary treatment | LL | L | н | НН | | |
|---------------------------------|-------|-------|-------|-------|------|----------------------|
| MJ DE/kg | 13.8 | 14.5 | 15.2 | 15.9 | SEM | P-value ¹ |
| Number of sows | 25 | 25 | 25 | 25 | | |
| BW, kg ¹ | | | | | | |
| Day 105 of gestation | 278.1 | 277.9 | 279.5 | 282.0 | 7.19 | 0.84 |
| Farrowing ² | 239.3 | 240.6 | 239.0 | 243.3 | 1.44 | 0.12 |
| Weaning ³ | 256.4 | 255.0 | 252.3 | 261.5 | 2.70 | 0.11 |
| Service ³ | 246.5 | 247.4 | 243.9 | 251.4 | 2.61 | 0.23 |
| BF, mm | | | | | | |
| Day 105 of gestation | 18.0 | 18.4 | 18.0 | 18.5 | 0.70 | 0.91 |
| Day 14 of lactation | 15.7 | 16.0 | 16.0 | 16.7 | 0.41 | 0.30 |
| Weaning | 14.8 | 14.9 | 14.8 | 15.6 | 0.41 | 0.40 |
| Service | 14.9 | 15.0 | 14.4 | 15.0 | 0.41 | 0.63 |
| Sow BW change, kg | | | | | | |
| Day 105 to weaning ⁴ | -19.9 | -21.6 | -24.1 | -18.2 | 2.61 | 0.40 |
| Farrowing to weaning⁴ | +17.7 | +13.9 | +13.7 | +18.9 | 2.92 | 0.44 |
| Weaning to service⁵ | -10.0 | -7.6 | -8.5 | -10.4 | 1.56 | 0.55 |
| Sow BF change, mm | | | | | | |
| Day 105 to weaning ⁶ | -3.1 | -3.2 | -3.0 | -2.7 | 0.44 | 0.88 |
| Weaning to service ⁷ | +0.1 | +0.1 | -0.5 | -0.7 | 0.43 | 0.60 |

Table 2. Effect of incremental dietary energy density during late gestation and lactation on sow BW and back fat thickness, and sow body condition changes during lactation

BF, back fat thickness.

¹Treatements with different superscript letters within a row are considered significantly different at P < 0.05 and as tendencies at P > 0.05 but less than P < 0.10. Sow BW and BF at day 105 was used as covariate for the analysis of subsequent sow BW and BF.

²Estimated value: empty farrowing weight = (sow weight at day 105 – (total born × 2.25)). The value of 2.25 kg is an estimate of the increased weight in the gravid uterus and in mammary tissue attributed to each pig in a litter (NRC, 1998).

³Weaning = day 26 ± 0.1 of lactation; service = day 6 ± 0.1 postweaning.

⁴Sow BW change = (sow BW at weaning - sow BW at day 105 of gestation or at farrowing).

⁵Sow BW change = (sow BW at service – sow BW at weaning).

⁶Sow BF change = (sow BF at weaning - sow BF at day 105 of gestation).

⁷Sow BF change = (sow BF at service – sow BF at weaning).

Table 3. Effect of incremental dietary energy density during late gestation and lactation on the concentrations of sow plasma IGF-1, serum insulin, and blood glucose on day 108 of gestation and at weaning

| Dietary treatment | LL | L | Н | НН | | |
|----------------------|-------|----------------------|----------------------|--------------------|-------|----------------------|
| MJ DE/kg | 13.8 | 14.5 | 15.2 | 15.9 | SEM | P-value ¹ |
| Number of sows | 8 | 8 | 8 | 8 | | |
| IGF-1, ng/mL | | | | | | |
| Day 108 | 37.0 | 46.3 | 42.0 | 44.1 | 7.59 | 0.86 |
| Weaning ² | 96.3ª | 113.9 ^{a,b} | 106.4 ^{a,b} | 136.3 ^b | 7.75 | 0.02 |
| Insulin, ng/mL | | | | | | |
| Day 108 | 0.34 | 0.47 | 0.30 | 0.33 | 0.07 | 0.31 |
| Weaning | 0.28 | 0.34 | 0.37 | 0.32 | 0.07 | 0.87 |
| Glucose, mmol/L | | | | | | |
| Day 108 | 3.05 | 2.98 | 2.91 | 2.89 | 0.194 | 0.93 |
| Weaning | 2.75 | 2.29 | 2.15 | 2.20 | 0.262 | 0.33 |

¹Treatements with different superscript letters within a row are considered significantly different at P < 0.05 and as tendencies at P > 0.05 but less than P < 0.10.

²Weaning = day 26 \pm 0.1 of lactation.

not affected by treatment (P > 0.05). Similarly, there was no effect of dietary treatment on sow blood glucose concentration on either sampling day (P > 0.05).

Sow colostrum and milk composition and milk yield

There was no effect of dietary energy density on the concentration of total solids (23.3 \pm 0.72%), protein (16.2 \pm 0.56%), fat (4.1 \pm 0.30%), lactose (2.3 \pm 0.12%), or ash (0.7 \pm 0.03%) in colostrum (P > 0.05). Milk composition on day 14 of lactation did not differ between treatments (P > 0.05). The average concentration of

milk total solids, protein, fat, and lactose was $17.5 \pm 0.29\%$, $4.5 \pm 0.09\%$, $7.5 \pm 0.32\%$, and $5.8 \pm 0.06\%$, respectively. The GE content of milk was also similar between treatments (25.9 ± 0.23 MJ/kg; P > 0.05). There was an overall tendency for an effect of treatment on estimated sow milk yield (calculated by assuming 4 kg of milk produced per kilogram of litter weight gain; P = 0.08); whereby HH sows tended to have a higher milk yield than L sows ($11.2 \text{ vs. } 10.1 \pm 0.34 \text{ kg/d}$; P = 0.08). The milk yield LL sows ($11.0 \pm 0.33 \text{ kg/d}$) and H sows ($10.5 \pm 0.36 \text{ kg/d}$) were not different to any of the other treatments (P > 0.05).

Coefficient of apparent total tract digestibility

The effect of incremental dietary energy density on the CATTD of nutrients and energy is presented in Table 4. An overall tendency of dietary energy density on the CATTD of DM was observed (P = 0.08); however, there were no pairwise differences between treatments (P > 0.05). Dietary energy density had no effect on the CATTD of OM (0.890 \pm 0.0045), ash (0.441 \pm 0.0187), or CP (0.885 \pm 0.0050). Sows on the HH treatment tended to have increased CATTD of NDF compared with H sows (0.570 vs. 0.481 \pm 0.0244; P = 0.07). Sows on the LL treatment had reduced CATTD of EE compared with L, H, and HH sows (P < 0.001). Dietary energy density had no effect on the CATTD of GE (0.875 \pm 0.0056; P > 0.05). The actual DE values of the experimental diets (MJ DE/kg) evaluated in this study matched very closely to those calculated from the diet formulation (Table 4).

Sow lactation feed intake and estimated energy intake

Voluntary feed intake during lactation did not differ between treatments (P > 0.05; Table 4). The average total feed intake during lactation was 184.5 ± 2.62 kg, equating to 7.1 ± 0.10 kg/d over a 26-d lactation period. As dietary energy density increased, there was an incremental increase in the calculated energy intake (analyzed dietary DE and calculated NE values) in sows during lactation (P < 0.001; Table 4).

Lactation efficiency

There was an overall effect of treatment on sow lactation efficiency (Table 4; P < 0.01). Lactation efficiency was highest for LL sows compared with L sows (32.0 vs. 27.5 ± 1.13 g/MJ DE; P = 0.03) and HH sows (32.0 vs. 26.2 ± 1.10 g/MJ DE; P < 0.01). The lactation efficiency of H sows was not different to any other treatment (28.6 ± 1.16 g/MJ DE).

Sow reproductive performance

Overall farrowing duration (hh:min:ss) was not affected by dietary treatment (average across all sow treatments was 04:54:53; P > 0.05). However, the birth interval between each piglet born was greater for piglets born to HH sows compared with piglets born to H sows (00:26:15 vs. 00:15:03 ± 00:02:44; P < 0.05). The birth interval of piglets from LL sows (00:18:23 \pm 00:02:47) and L (00:21:00 \pm 00:02:47) was similar to that of all other treatments (P > 0.05). The birth to first suckle interval for the first born piglet was unaffected by dietary treatment (00:41:00 \pm 00:05:48; P > 0.05). The total number of piglets born per litter (15.2 \pm 0.65) and the number of piglets live born (14.3 \pm 0.61) did not differ between treatments (P > 0.05). Neither litter weight at birth (total = 20.9 ± 0.92 kg or live = 20.0 ± 0.88 kg) or individual piglet birth weight differed between treatments (P > 0.05). The mean birth weight of total born piglets and of piglets born alive was 1.39 \pm 0.041 and 1.40 \pm 0.040 kg, respectively. The size of the sows' litter at the subsequent farrowing after this experiment was not affected by treatment (P > 0.05; Table 5).

Table 4. Effect of incremental dietary energy density during late gestation and lactation on the coefficient of apparent total tract digestibility of DM, OM, ash, CP, neutral detergent fiber (NDF), ether extract (EE), and GE, as well as DE concentration, sow feed and energy intake, and lactation efficiency

| Dietary treatment | LL | L | Н | НН | | |
|--|----------------------|------------------------|----------------------|----------------------|--------|----------------------|
| MJ DE/kg | 13.8 | 14.5 | 15.2 | 15.9 | SEM | P-value ¹ |
| Number of sows | 10 | 10 | 10 | 10 | | |
| Digestibility coefficients | | | | | | |
| DM | 0.857 | 0.863 | 0.859 | 0.873 | 0.0046 | 0.08 |
| OM | 0.886 | 0.891 | 0.889 | 0.895 | 0.0045 | 0.57 |
| Ash | 0.428 | 0.429 | 0.434 | 0.474 | 0.0187 | 0.27 |
| CP | 0.886 | 0.883 | 0.880 | 0.893 | 0.0055 | 0.39 |
| NDF | 0.545 ^{A,B} | 0.545 ^{A,B} | 0.481 ^A | 0.570 [₿] | 0.0246 | 0.07 |
| EE | 0.773ª | 0.885 ^b | 0.910 ^b | 0.933° | 0.0166 | < 0.001 |
| GE | 0.869 | 0.875 | 0.872 | 0.885 | 0.0056 | 0.22 |
| DE, MJ/kg ² | 13.9ª | 14.5 ^b | 15.0 ^b | 15.7° | 0.08 | < 0.001 |
| Number of sows | 25 | 25 | 25 | 25 | | |
| Lactation feed intake ¹ | | | | | | |
| Total, kg | 184.9 | 181.7 | 183.6 | 187.8 | 2.62 | 0.38 |
| Average, kg/d ³ | 7.2 | 7.1 | 7.1 | 7.3 | 0.10 | 0.49 |
| Total lactation energy intake | | | | | | |
| MJ DE ⁴ | 2,567.8ª | 2,639.3 ^{a,b} | 2,752.0 ^b | 2,939.2° | 38.94 | < 0.0001 |
| MJ NE ⁵ | 1,747.8ª | 1,854.7 ^b | 2,000.8° | 2,174.1 ^d | 27.70 | < 0.0001 |
| Average lactation energy intake | | | | | | |
| MJ DE/d ⁴ | 99.7ª | 102.3 ^{a,b} | 106.4 ^b | 113.7° | 1.50 | < 0.0001 |
| MJ NE/d⁵ | 67.9ª | 71.9 ^b | 77.4 ^c | 84.1 ^d | 1.07 | < 0.0001 |
| Lactation efficiency, g/MJ DE ⁶ | 32.0ª | 27.5 ^b | 28.6 ^{a,b} | 26.2 ^b | 1.14 | <0.01 |

¹Treatements with different superscript letters within a row are considered significantly different at P < 0.05 and as tendencies at P > 0.05 but less than P < 0.10. Lactation length (days) was used as a covariate for the analysis of sow lactation feed intake.

 $^2Calculated as DE = [analyzed dietary GE value (MJ/kg) <math display="inline">\times$ GE digestibility coefficient (%)].

³Average lactation length = day 26 \pm 0.1.

⁴Calculauted using analyzed dietary DE values.

⁵Calculated using calculated dietary NE values.

⁶Calculated as: lactation efficiency = [total litter weight gain between days 1 and 26 of lactation (kg) × 1,000/sow lactation energy intake (MJ DE)].

| Dietary treatment | LL | LL L H HH | | | | |
|----------------------------|------|-----------|------|------|-------|----------------------|
| MJ DE/kg | 13.8 | 14.5 | 15.2 | 15.9 | SEM | P-value ¹ |
| Number of sows | 25 | 25 | 25 | 25 | | |
| Litter size, number | | | | | | |
| Total born ² | 16.0 | 14.8 | 15.2 | 14.6 | 0.65 | 0.43 |
| Live born | 15.3 | 13.9 | 14.3 | 13.5 | 0.61 | 0.25 |
| Subsequent litter size, nu | mber | | | | | |
| Total born | 16.2 | 15.7 | 16.8 | 15.8 | 0.72 | 0.70 |
| Live born | 14.5 | 14.2 | 14.6 | 14.6 | 0.72 | 0.97 |
| Litter weight, kg | | | | | | |
| Total born ³ | 22.4 | 20.5 | 21.2 | 19.7 | 0.92 | 0.21 |
| Live born | 21.7 | 19.5 | 20.2 | 18.7 | 0.88 | 0.12 |
| Mean piglet birth weight, | kg1 | | | | | |
| Total born ³ | 1.42 | 1.38 | 1.39 | 1.34 | 0.041 | 0.48 |
| Live born | 1.44 | 1.40 | 1.41 | 1.36 | 0.040 | 0.53 |

 Table 5. Effect of incremental dietary energy density during late gestation and lactation on the number of piglets born, subsequent sow litter size, litter weight at birth, and individual piglet birth weight

¹Treatements with different superscript letters within a row are considered significantly different at P < 0.05 and as tendencies at P > 0.05 but less than P < 0.10. Sow litter size (total and live born) was used as a covariate for the analysis of individual piglet birth weight (total and live). ²Total number born = number of piglets born alive, stillborn, and mummified.

³Total litter weight and individual piglet birth weight = weight of piglets born alive and stillborn. Mummified piglets were not weighed.

Piglet vitality

IUGR score and muscle tone score

The energy density of the diet had an effect on both the IUGR score (P < 0.001) and the muscle tone score of piglets at birth (P < 0.01). The odds of a piglet having a high IUGR score (i.e., displaying a greater number of traits that are characteristic of IUGR) were greater in piglets from LL sows than piglets from L sows (odds ratio; OR = 1.55, confidence interval; CI = 1.16 to 2.07), H sows (OR = 1.67, CI = 1.25 to 2.24), and HH sows (OR = 1.62, CI = 2.20 to 2.17). Negative but weak correlations were found between piglet IUGR score and piglet birth weight (r = -0.216; P < 0.0001), piglet preweaning ADG (r = -0.059; P < 0.05), and piglet weaning weight (r = -0.079; P < 0.05). The odds of a piglet having a high muscle tone score (i.e., indicative of a more vital piglet) were greater in piglets from HH sows than in piglets from LL sows (OR = 1.96, CI = 1.35 to 2.87), L sows (OR = 1.56, CI = 1.06 to 2.28), and H sows (OR = 1.55, CI = 1.06 to 2.27). Positive but weak correlations were found between piglet muscle tone score and piglet birth weight (r = 0.228; P < 0.0001), piglet preweaning ADG (r = 0.053; P = 0.05), and piglet weaning weight (r = 0.090; P = 0.001).

Tympanic ear temperature

Piglet TEMP at birth was unaffected by treatment (35.07 \pm 0.052 °C; *P* > 0.05). However, positive but weak correlations were found between piglet birth TEMP and piglet birth weight (*r* = 0.103; *P* < 0.0001) and piglet preweaning ADG (*r* = 0.107; *P* < 0.001). Subsequent to this, TEMP at 24 h postpartum was higher in piglets from LL sows than in piglets from HH sows (35.48 vs. 35.32 \pm 0.051 °C; *P* < 0.01), and TEMP at this time was also higher in piglets from H sows than in piglets from both HH sows (35.50 vs. 35.32 \pm 0.051 °C; *P* < 0.01) and L sows (35.50 vs. 35.35 \pm 0.051 °C; *P* = 0.07). Similarly, there was a positive but weak correlation between 24 h TEMP and piglet preweaning ADG (*r* = 0.073; P < 0.05).

Glucose concentration

The concentration of glucose in the blood of piglets at 24 h postpartum was greater in piglets from L sows than piglets

from HH sows (4.64 vs. 4.18 ± 0.189 nmol/L; P < 0.05). There was no difference in glucose concentration between piglets from LL sows (4.31 ± 0.189 nmol/L) and H sows (4.52 ± 0.196 nmol/L) compared with any other treatment (P > 0.05). A positive but weak correlation was found between piglet glucose concentration and piglet BW at 24 h postpartum (r = 0.356; P < 0.001).

Piglet preweaning growth

There was no effect of treatment on the BW of piglets on days 1, 6, 14, and 26 of lactation (P > 0.05). A tendency for an overall effect of treatment on piglet ADG was observed between days 0 and 26 of lactation (P = 0.06); piglet ADG tended to be higher for piglets from HH sows than L sows (P = 0.07); however, the ADG of piglets from LL and H sows did not differ between any other treatment (P > 0.05; Table 6). There was an overall effect of treatment on litter ADG between days 1 and 26 of lactation (P = 0.05); litter ADG tended to be higher for LL sows (P = 0.06)and for H sows (P = 0.10) than L sows. The number of suckling piglets per litter was unaffected by treatment on days 1 and 6 of lactation. At day 14 of lactation, there was an overall effect of treatment (P = 0.04), although no pairwise differences were observed between treatments. At weaning, H sows weaned a greater number of piglets than both L sows (P < 0.05) and HH sows (P < 0.01), and LL sows tended to wean a greater number of piglets than HH sows (P = 0.08; superscript not shown in Table 6). Sows in the LL treatment group (P < 0.05) and sows in the H treatment group (P < 0.05) weaned a heavier litter than sows in the L treatment group (Table 6).

PW pig growth

Results for pig BW, ADG, ADFI, and FCE are presented in Table 7. Pig BW on day 26 (weaning; 7.2 \pm 0.35 kg), day 33 (8.6 \pm 0.35 kg), day 40 (11.5 \pm 0.35 kg), day 54 (18.5 \pm 0.35 kg), and day 75 of age (32.7 \pm 0.36 kg), as well as pig live weight at slaughter (103.4 \pm 1.20 kg) was unaffected by treatment (P > 0.05). Similarly, pig ADG from day 26 of age to slaughter and pig ADFI and FCE from day 40 of age to slaughter was unaffected by sow treatment (P > 0.05).

Table 6. Effect of incremental dietary energy density during late gestation and lactation on the number of piglet's cross-fostered, piglet mortality, litter size, litter ADG, litter weight at weaning, individual piglet body weight, and piglet ADG to weaning

| Dietary treatment | LL | L | н | НН | | |
|--------------------------------|---------------------|-------------------|--------------------|---------------------|-------|----------------------|
| MJ DE/kg | 13.8 | 14.5 | 15.2 | 15.9 | SEM | P-value ¹ |
| Number of sows | 25 | 25 | 25 | 25 | | |
| Number of piglets born alive | 15.3 | 13.9 | 14.3 | 13.5 | 0.61 | 0.25 |
| Piglets CF off ² | 2.4 | 2.7 | 2.0 | 3.1 | 0.37 | 0.23 |
| Piglets CF on ² | 2.1 | 3.1 | 2.7 | 3.3 | 0.65 | 0.25 |
| Piglet mortality ³ | 2.2 | 2.0 | 1.9 | 2.2 | 0.35 | 0.91 |
| Litter size ⁴ | | | | | | |
| Day 1 | 14.4 | 13.5 | 14.3 | 13.2 | 0.60 | 0.41 |
| Day 6 | 13.2 | 12.7 | 13.3 | 12.3 | 0.35 | 0.14 |
| Day 14 | 13.0 | 12.5 | 13.2 | 12.2 | 0.31 | 0.04 |
| Day 26⁵ | 12.7 ^{a,b} | 12.0ª | 13.2 ^b | 11.6ª | 0.33 | < 0.01 |
| Litter ADG, kg/d ⁶ | 2.8 ^A | 2.5 [₿] | 2.8 ^A | 2.7 ^{A,B} | 0.10 | 0.05 |
| Litter weaned, kg1 | 92.3ª | 81.6 ^b | 93.5ª | 85.9 ^{a,b} | 2.95 | 0.01 |
| Piglet BW, kg | | | | | | |
| Day 1 | 1.51 | 1.48 | 1.51 | 1.48 | 0.049 | 0.95 |
| Day 6 | 2.5 | 2.3 | 2.3 | 2.3 | 0.08 | 0.44 |
| Day 14 | 4.2 | 3.9 | 3.9 | 4.1 | 0.14 | 0.43 |
| Day 26⁵ | 7.3 | 6.9 | 7.0 | 7.4 | 0.17 | 0.11 |
| Piglet ADG, g/d ^{1,7} | | | | | | |
| Days 0 to 1 | 63 | 58 | 69 | 66 | 8.6 | 0.80 |
| Days 1 to 6 | 182 | 163 | 160 | 175 | 7.4 | 0.13 |
| Days 6 to 14 | 242 | 217 | 232 | 246 | 9.6 | 0.12 |
| Days 14 to 26 | 226 | 215 | 219 | 227 | 9.2 | 0.74 |
| Days 0 to 26 | 225 ^{A,B} | 209 ^A | 215 ^{A,B} | 230 ^B | 6.2 | 0.06 |

ADG, average daily gain; CF, cross fostered.

¹Treatements with different superscript letters within a row are considered significantly different at P < 0.05 and as tendencies at P > 0.05 but less than P < 0.10. Sow litter size on day 1 of lactation was used as a covariate for the analysis of piglet ADG and litter weight between days 1 and 26 of lactation.

²Litter size was standardized within the first 24 h after parturition where possible.

³Piglet mortality = number of piglets that died between days 0 and 26 of lactation.

⁴Litter size = number of suckling piglets in the litter at each weighing.

⁵Day 26 = average age at weaning.

⁶Litter ADG = litter ADG between days 1 and 26 of lactation.

⁷Piglet ADG is calculated on the basis of individual piglet BW at specific time points during the suckling period/number of days between each time point.

Carcass measures at slaughter

There was no effect of treatment on the carcass weight (76.3 \pm 0.93 kg), fat depth (11.9 \pm 0.23 mm), muscle depth (43.4 \pm 0.55 mm), lean meat yield (56.6 \pm 0.21%), or kill out yield (73.6 \pm 0.22%) of progeny at slaughter (P > 0.05; Table 8). Carcass ADG (calculated from day 75 to slaughter; 914 \pm 11.5 g/d), carcass FCE (calculated from day 75 to slaughter; 2.62 \pm 0.019 g/g), and lean ADG (calculated from birth to slaughter; 306 \pm 3.7 g/d) were also unaffected by treatment (P > 0.05; Table 8).

Discussion

Lactation feed intake and energy intake

The energy concentration of lactating sow diets is a primary determinant of energy intake in sows and this is typically modified by the addition of fats and oils to the diet (Tokach et al., 2019). Increasing dietary energy density is normally associated with an increase in sow energy intake at the same level of physical feed intake; until a level is reached whereby voluntary feed intake is negatively impacted by dietary energy density (Van den Brand et al., 2000; Park et al., 2008; Quiniou et al., 2008). However as reviewed by Rosero et al. (2016), the addition of fats and oils (2% to 11%) to lactating sow diets, which compares well with the current study, increased the energy intake of multiparous sows by 7% per day on average. In our study, energy intake in sows was incrementally increased through dietary soya oil inclusion (3.3%, 6.6%, and 9.9% extra in the experimental diets relative to the control diet) without depressing voluntary feed intake. Therefore, the addition of dietary soya oil, at least up to an inclusion rate of 9.9%, is a viable feeding strategy to increase the energy intake in sows during lactation, as it does not depress voluntary feed intake.

Sow weight, back fat, and body reserve losses

After parturition, the sow has to maintain a high volume of milk output to support her litter. However, this is not always attainable by dietary feed intake alone and sows will often mobilize their own body fat and protein reserves in a bid to sustain milk production (Tokach et al., 2019). We observed no difference between dietary treatments with regard to sow BW and BF change during lactation, and thus the mobilization of sow body tissue reserves were similar. According to previous studies, commercial sows may lose between 15 and 40 kg of BW during lactation due to limited nutrient intake during lactation (Beyer et al., 2007; Hansen, 2012; Cools et al., 2014). It was therefore surprising to observe that sows in all treatment groups in the present study gained weight (numerically) between parturition

| Dietary treatment | LL | L | н | нн | | |
|----------------------------|-------|-------|-------|-------|-------|----------------------|
| MJ DE/kg | 13.8 | 14.5 | 15.2 | 15.9 | SEM | P-value ¹ |
| Number of pigs | 78 | 78 | 78 | 78 | | |
| Pig BW, kg | | | | | | |
| Day 26 ² | 7.5 | 6.8 | 7.3 | 7.3 | 0.35 | 0.55 |
| Day 33 | 8.8 | 8.2 | 8.6 | 8.7 | 0.35 | 0.71 |
| Day 40 | 11.8 | 11.1 | 11.4 | 11.7 | 0.35 | 0.52 |
| Day 54 | 18.8 | 18.2 | 18.7 | 18.3 | 0.35 | 0.64 |
| Day 75 ² | 32.9 | 32.4 | 32.9 | 32.5 | 0.36 | 0.62 |
| Day 141 ² | 103.1 | 103.1 | 105.3 | 102.2 | 1.20 | 0.32 |
| Pig ADG, g/d | | | | | | |
| Days 26 to 75 | 509 | 512 | 517 | 510 | 10.6 | 0.93 |
| Days 75 to 141 | 1,179 | 1,186 | 1,201 | 1,163 | 14.2 | 0.31 |
| Pig ADFI, g/d ³ | | | | | | |
| Days 40 to 75 | 900 | 882 | 902 | 881 | 15.0 | 0.67 |
| Days 75 to 141 | 2,413 | 2,389 | 2,405 | 2,357 | 32.1 | 0.63 |
| Pig FCR, g/g ³ | | | | | | |
| Days 40 to 141 | 1.52 | 1.47 | 1.51 | 1.51 | 0.024 | 0.50 |
| Days 75 to 141 | 2.06 | 2.02 | 2.01 | 2.04 | 0.017 | 0.22 |

Table 7. Effect of incremental dietary energy density during late gestation and lactation on pig BW and ADG from days 26 to 141 of age, and pig ADFI and FCE from days 40 to 141 of age

ADFI, average daily feed intake; ADG, average daily gain; FCE, feed conversion efficiency.

¹Treatements with different superscript letters within a row are considered significantly different at P < 0.05 and as tendencies at P > 0.05 but less than P < 0.10.

²Day 26 = weaning; Day 75 = pig age at transfer from the weaner accommodation to finisher accommodation; Day 141 = average pig age at slaughter.

³ADFI and FCE could not be calculated between days 26 and 40 of age as individual pig feed intake data were not available during this period. Therefore, values for ADFI and FCR are calculated between day 40 of age and slaughter.

and weaning. This would suggest that once energy requirements for maintenance were satisfied, the remaining energy from the diet was used for their own body reserves and maternal growth, as opposed to increasing milk production and litter growth. Our results are comparable to those of previous sow studies (Tilton et al., 1999; Choi et al., 2017).

A BF thickness of ~17 mm at farrowing and 13 mm or greater at the subsequent service is desirable for sows (Young et al., 2004). In the present study, sows in all treatment groups maintained a BF depth in excess of 14 mm throughout lactation and at the subsequent service, with only marginal losses in BF during lactation (< 3.2 mm). Our data imply that the energy requirements of lactating sows in all treatment groups were met, given that all sows maintained an optimum BF depth after parturition and avoided excessive mobilization of body tissue reserves, irrespective of the energy density of the diet fed.

At the dietary energy intakes observed in the current study (~106 MJ DE/d), some maternal tissue loss during lactation would have been expected based on the models of Close and Cole (2000). However, more recent lactating sow models of NRC (2012) depict a significantly lower sow energy requirement for an average sow from the current study than the models of Close and Cole (2000). From the models of NRC (2012), a 241 kg multiparous sow with a litter gain of 2.7 kg/d and a maternal weight gain of 16.1 kg during lactation would require an energy intake of 107 MJ DE/d during lactation to meet its requirements for: maintenance (0.402 MJ DE \times 241 kg^{0.75} = 24.5 MJ DE), milk production [(milk energy output)/0.7 = 69.9 MJ DE], and maternal weight gain (16.1 kg × 20.8 MJ DE/lactation length = 13.3 MJ DE) (NRC, 2012). Therefore, based on the sow energy intakes achieved during lactation in the current study, sows in all treatment groups had a sufficient energy intake to meet their above energy requirements.

Colostrum and milk composition

It was surprising to observe no difference in colostrum composition in the present study, given previous findings (Heo et al., 2008; Che et al., 2019). Heo et al. (2008) assigned sows to diets with increasing energy density during late gestation and lactation (13.1, 13.4, and 13.7 MJ DE/kg), and fat and lactose percentage increased in sow colostrum with increasing dietary energy density. Similarly, colostrum fat percentage was higher in sows that had a higher energy intake (33.8 MJ/d intake of NE) than sows with a lower energy intake (28.2 MJ/d intake of NE) in the study of Che et al. (2019). Colostrogenesis is defined as "the synthesis of milk-specific constituents and the transfer of IgG into lacteal secretions" (Quesnel and Farmer, 2019). Milk components are synthesized during late pregnancy and the first lipid droplets become visible in the milk at day 105 of gestation (Kensinger et al., 1986). Therefore, it is likely that the lack of dietary effect on colostrum composition in our study is because the period of experimental feeding prior to parturition, beginning on day 108 of gestation, was too late for the dietary treatment to impose any compositional changes in colostrum (Shi et al., 2019). The above-mentioned studies assigned their sows to treatment on days 80 (Heo et al., 2008) and 90 of gestation (Che et al., 2019).

Research on the effect of increased dietary energy density and energy intake in sows on milk composition has yielded variable results. Lauridsen and Danielsen (2004) reported no difference in milk composition between control sows and sows fed a control diet with 8% supplemental fat; even when the energy intake in sows fed the high-energy dense diet was significantly greater than that of control sows. Leonard et al. (2010) also observed similar concentrations of nutrients in the milk of sows which were supplemented with (100 g/d) or without (0 g/d) fish oil

| Dietary treatment | LL | L | н | НН | | |
|-------------------------------|--------|--------------------|--------------------|--------------------|-------|----------------------|
| MJ DE/kg | 13.8 | 14.5 | 15.2 | 15.9 | SEM | P-value ¹ |
| Number of pigs | 76 | 68 | 70 | 73 | | |
| Age at slaughter | 141.3ª | 140.9 ^b | 141.0 ^b | 141.0 ^b | 0.05 | < 0.001 |
| Live-weight at slaughter, kg | 103.1 | 103.1 | 105.3 | 102.2 | 1.20 | 0.32 |
| Carcass measures ¹ | | | | | | |
| Weight, kg | 76.1 | 76.1 | 77.5 | 75.7 | 0.93 | 0.55 |
| Fat depth, mm | 12.2 | 11.9 | 11.7 | 11.9 | 0.23 | 0.36 |
| Muscle, mm | 43.4 | 43.4 | 43.5 | 43.2 | 0.55 | 0.97 |
| Lean meat, % | 56.3 | 56.7 | 56.7 | 56.6 | 0.21 | 0.43 |
| Kill out, % | 73.7 | 73.7 | 73.3 | 73.7 | 0.22 | 0.53 |
| Carcass ADG, g/d² | 912 | 916 | 925 | 903 | 11.4 | 0.62 |
| Carcass FCE, g/g ³ | 2.64 | 2.61 | 2.60 | 2.63 | 0.019 | 0.55 |
| Lean ADG, g/d ⁴ | 303 | 306 | 311 | 303 | 3.7 | 0.42 |

Table 8. Effect of incremental dietary energy density during late gestation and lactation on pig age and carcass quality at slaughter, carcass ADG, carcass FCE, and carcass lean ADG

ADG, average daily gain; FCE, feed conversion efficiency.

¹Treatements with different superscript letters within a row are considered significantly different at *P* < 0.05 and as tendencies at *P* > 0.05 but less than *P* < 0.10. Carcass cold weight at slaughter was used as a covariate for the analysis of carcass fat depth, muscle depth, and lean meat yield.

 2 Carcass ADG (from day 75 to slaughter) = [(carcass weight in kg – day 75 weight in kg × 0.65) × 1,000/number of days from day 75 to slaughter] (Lawlor and Lynch, 2005).

³Carcass FCE (from day 75 to slaughter) = [daily feed intake (g)/carcass ADG (g)].

⁴Lean ADG (from birth to slaughter) = [(carcass weight × carcass lean meat percentage × 10)/number of days to slaughter] (Lawlor and Lynch, 2005).

from day 109 of gestation until weaning. Thus, our results are consistent with those of the aforementioned studies. However, several other researchers have reported higher concentrations of milk fat and lactose in response to increased dietary energy density and energy intake in sows, and proposed that intrinsic sow factors such as energy status around parturition and dietary oil and fat content improved the nutrient composition of milk (Heo et al., 2008; Kim et al., 2018; Che et al., 2019).

Given the finding for increased maternal weight gain during lactation, we can assume that sows partitioned any energy that was left after meeting energy requirements for maintenance into their own maternal tissue reserves, rather than into increasing milk production and nutrient composition. Pluske et al. (1998) provided sows with a high-energy diet during lactation (15.4 MJ DE/kg) and sows were fed according to one of three feeding regimes (restricted, ad libitum, and superalimented). Despite super-alimented sows receiving 38% more energy and achieving exceptionally high-energy intakes of 111 MJ DE/d during lactation, these sows did not produce more milk or support superior piglet growth than ad libitum fed sows. Pluske et al. (1998) conclude that sows partitioned the additional energy from the diet into their own body growth, rather than into increasing milk production, and it could be surmised that a similar phenomenon occurred in our study.

Daily lysine intake is a key determinant of milk production and litter growth during lactation, as lysine is the first-limiting AA in most lactation sow diets (Yang et al., 2000). According to the lactating sow models proposed by NRC (2012), a multiparous sow has an SID lysine requirement of 52 g/d to meet its requirements for maintenance, milk production, and maternal gain (using the same above-mentioned sow and litter assumptions). This would suggest that we oversupplied lysine in all treatment groups, given that sows in the current study had an average SID lysine intake of 77 g/d during lactation (average lactation feed intake of 7.2 kg/d of a diet containing 10.6 g SID Lys/kg). Therefore, sows may have been depositing excess lysine as body protein and this hypothesis may support the lack of any difference observed in sow BF loss during lactation in our study. The lysine content of all experimental diets in the current study was kept constant (10.6 g SID Lys/kg), so that it was not a confounding factor when investigating the effect of increasing dietary energy content. As such, SID lysine to energy ratios decreased with each increment in dietary energy density and SID lysine (g/kg) to DE (MJ DE/ kg) ratios were 0.77, 0.74, 0.71, and 0.68 in the LL, L, H, and HH dietary treatments, respectively. NRC (2012) recommend an SID lysine to DE ratio of between 0.51 and 0.61, depending on sow parity and litter growth. It is therefore evident that the lysineto-energy ratio was above that recommended and as such, is unlikely to have impacted performance in the present study.

Piglet vitality

In the current study, the diet which was most energy dense was most effective at increasing piglet vitality at birth, as measured by the piglets' motivation to push back when pressure was applied to the hind feet. Thus, our hypothesis that feeding maternal diets high in energy to improve indicators of piglet vitality is confirmed. On the other hand, maternal deficit in either protein or energy intake during gestation can result in a higher occurrence of IUGR (Costa et al., 2019). This was demonstrated in our study also, as piglets with the greatest likelihood of presenting a greater number of traits characteristic of IUGR were from litters of LL sows. However, it was then surprising that these piglets had a greater thermoregulatory ability (higher mean TEMP at 24 h) than piglets born to sows in the HH treatment group. Our finding contradicts the findings of previous studies, in which lower piglet vitality at birth was associated with reduced thermoregulation (Pedersen et al., 2013; Mota-Rojas et al., 2018; Santiago et al., 2019). It is also interesting to note that in the treatments where piglet temperature at 24 h was highest (LL and H treatments), a greater number of piglets was reared to weaning. Thus, piglet temperature at 24 h postpartum might be considered as an indicator of survival. This finding is in line with previous, more detailed work on piglet vitality, where an association between piglet temperature postpartum and preweaning piglet survival has been documented (Baxter et al., 2009; Panzardi et al., 2013).

Offspring growth

According to recent literature, the benefit of increased energy intake in sows is seen through an increase in litter growth. As sow milk yield is relatively unresponsive to altered dietary fat supply (Pedersen et al., 2016), this increase in litter growth rate is attributed to a greater supply of energy and nutrients to suckling piglets through an increase in milk fat composition (Rosero et al., 2015; Rosero et al., 2016). However in the current study, the percentage of fat in colostrum and milk did not increase with increasing dietary energy density. According to Eissen et al. (2003), the use of feed for increasing litter weight gain is less efficient at higher levels (>11 piglets) than lower levels of litter size (< 11 piglets); thus providing a possible explanation for the lack of effect of increased energy intake in sows on litter growth, given the average litter size in the present study. Lactation efficiency is defined as the energy efficiency of sows during lactation (Bergsma et al., 2009). Interestingly, LL sows had higher lactation efficiency than both L sows and HH sows, indicating that LL sows were more efficient at utilizing the available energy from the diet for litter growth; and this may be able to partly explain the higher litter ADG of LL sows. The finding of increased lactation efficiency and therefore increased litter ADG suggests that it may be more beneficial to target an increase in sow feed intake of diets that have moderate energy density than feeding sows a high-energy dense diets during lactation.

Conclusion

Increasing dietary soya oil inclusion is an effective feeding strategy to increase energy intake in sows during lactation, as this practice did not depress the voluntary feed intake of sows during lactation. Feeding sows a high-energy dense diet (> 14.5 MJ DE/kg) also improved some indicators of postnatal piglet vitality. However, we did not see a response to increased dietary energy density for other measures of piglet vitality or for preweaning litter growth performance. Based on the findings in the current study, it can also be concluded that the energy intake in sows is used more efficiently for piglet growth when sows are fed a low-energy dense diet than a high-energy dense diet.

Acknowledgments

The authors thank Tomas Ryan, David Clarke, our visiting summer student Emma Gourlez and the farm staff at the Teagasc Pig Development Department for their continued assistance with pig management and data collection during this study. In particular, we wish to thank John Walsh, Pat Magnier, Henry Allen, John Heffernan, and Dan O'Donovan. The authors thank Jimmy Flynn and Anne Marie McAuliffe for their help with the analysis of colostrum and milk (Teagasc). The authors also wish to express sincere thanks to Bernie Flynn, Gaurav Rajauria, Patrick Reilly, and Denise Cunningham for their help with the analysis of feed and fecal samples (University College Dublin).

Funding

The authors of this research would like to acknowledge the funding from the DAFM FIRM/RSF/CoFoRD 2013 Research Call (grant number 13S428).

Conflict of interest statement

The authors have no conflicts of interest to declare.

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