

Article

The Impacts of Feeding a Reduced Energy and Lysine Balance in Lactation on Sow Body Composition, Litter Growth, and Markers of Subsequent Reproductive Performance

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Abstract

This experiment examined whether multiparous sows fed a diet lower in energy and lysine at a reduced feed allowance would still mobilise fat and (or) protein to support piglet growth and negatively impact subsequent reproductive performance. A total of 152 multiparous sows was allocated in a 2 × 2 factorial design with the respective factors being diet type fed in lactation (gestation, 13.0 MJ digestible energy (DE)/kg, 0.42 g standardised ileal digestible (SID) lysine/MJ DE; or lactation, 14.3 MJ DE/kg, 0.62 g SID lysine/MJ DE) and feed allowance (ad libitum or 7.5 kg/d, ~15% reduction on ad libitum intake). Body composition was estimated on the day after farrowing (day 2) and at weaning (day 21). Blood was collected on days 2, 21 and at standing heat, for the analysis of insulin and insulin-like growth factor 1 (IGF-1). Diet type did not alter ($p > 0.05$) bodyweight or P2 backfat depth change in lactation, estimated body fat and protein changes, litter growth, or subsequent total piglets born. Ad libitum-fed sows showed a significant gain in girth compared to sows offered 7.5 kg/d (2.9 versus −0.4 mm, $p = 0.015$) and had a tendency for a shorter wean-to-service interval ($p < 0.10$). Sows fed the lactation diet had higher insulin concentrations at weaning ($p < 0.05$), but levels were the same ($p > 0.10$) by heat detection; IGF-1 concentrations remained unaffected. These data indicate that imposing a calculated negative energy and lysine balance on lactating sows had a limited impact on lactation or subsequent reproductive performance, supporting the notion that the modern sow may be more resilient to nutritional impositions than has been historically reported.

Keywords: sow; lactation; piglet survival; feed allowance; diet type; litter growth; protein; fat; girth; wean-to-service interval



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1. Introduction

The nutrient and energy requirements of multiparous lactating sows are determined predominantly by their milk production, suckling intensity, and hence the extent of tissue mobilisation [1]. Furthermore, genetic selection has paved the way for the modern sows to produce larger litters [2], resulting in, typically, a loss of body protein at weaning [3]. A loss of sow body fat mass has also been shown to negatively impact wean-to-service interval [4]

and the percentage of stillborn piglets in the subsequent parity [5]. Sows experiencing a reduction in nutrient and/or energy balance during lactation can maintain milk production by using body reserves [2,6], whilst an oversupply can result in sows releasing nitrogen and phosphorus in excreta [7] and depositing body fat and protein.

Providing insufficient dietary lysine (Lys) to lactating sows can reduce piglet performance and the subsequent reproductive performance of sows. Dietary Lys requirements largely depend on milk production [8], which becomes important later in lactation at the time of peak milk demand and litter growth. The increased nutrient and energy requirements for maintaining milk production, especially for Lys, means that the diet fed typically has more energy and Lys compared to a gestation diet. Lysine intake during lactation is a strong driver of milk production [3], and consequently piglet litter weight, and sows fed more Lys lose less weight [9]. The increase in Lys content of the lactation diet also aims to improve litter gain, but as with energy, a threshold is reached at which energy and Lys inputs do not result in further growth [10]. Increased Lys intake during lactation has been associated with higher insulin concentrations at weaning [4], which influences subsequent ovulation and embryo survival. Furthermore, insulin-like growth factor 1 (IGF-1) plays an important role in follicular development and concentrations are affected by short-term periods of reduced feed intake [11].

In order to separate the effects of energy and Lys intakes from feed intake in lactation per se, and in view of the modern sow potentially being more resilient to nutritional challenges in lactation than in the past [12,13], this experiment tested the hypothesis that sows fed a diet lower in energy and Lys during lactation, at a reduced allowance, would still experience a loss in body fat and protein that would in turn negatively impact sow and litter performance.

2. Materials and Methods

2.1. Animals and Animal Management

The Murdoch University Animal Ethics Committee (protocol no. CHM/SAFS/SCMB/407/16) and PIRSA Animal Ethics Committee approved the protocol for this experiment (Project #19/18) in accordance with the Australian Code for the Care and Use of Animals for Scientific Purposes (National Health and Medical Research Council, 2013, Canberra, Australia). As part of these approvals, a statistical Power analysis was conducted using an alpha value of 0.05 with a power to detect statistically significant differences set to 0.8. This analysis revealed that a minimum of 35 sows and their litters per treatment was required.

This experiment was conducted at a commercial breeder unit (SunPork Group, South Australia, Australia). On day 106.9 ± 2.1 (mean $\pm$ SD) of gestation, 152 multiparous pregnant sows, (parity 3.0 ± 1.0) (Camborough[®] 42, PIC Australia, Grong Grong, NSW, Australia), were moved into the farrowing shed over three time periods (October–November) and offered 2.5 kg of a standard dry sow diet at 0700 h daily. Diets were formulated to provide 13.0 MJ digestible energy (DE)/kg, 14.8% crude protein, and 0.42 g standardised ileal digestible (SID) Lys/MJ DE. Sows were housed in a naturally cross-ventilated shed, which consisted of four rooms each housing 60 individual farrowing crates (2.4 m $\times$ 1.8 m) with fully slatted plastic flooring. Shed lighting occurred on a 16 h:8 h (light/dark) cycle. Each farrowing crate was fitted with a heating lamp over the creep area to create a microclimate for piglets. Water was available to sows and piglets ad libitum throughout the experiment via two nipple drinkers. Creep feed was not made available to the litters. Sows farrowed naturally without any assistance or intervention, including any post-partum management, and were managed according to standard farm practices, including standardisation within 24 h of birth to a litter size of ~ 11 piglets (11.3 ± 1.2 piglets per sow) to ensure an even suckling pressure. Piglets were administered an oral coccidiostat (Baycox

Coccidiocide; Bayer Australia Ltd., New South Wales, Australia) and 1 mL of combined iron plus cyanocobalamin (Feron™ 200 + B12; Bayer Australia Ltd., New South Wales, Australia) on day 3 of lactation and underwent tail docking at this time.

Sows were weaned at the end of lactation (21.0 ± 2.2 d) into group housing and offered a wean-to-service diet (13.4 MJ DE/kg, 0.72 SID g Lys/MJ DE) on an ad libitum basis. Sows were tested once daily at 0800 h for the onset of standing oestrus using fence-line exposure to a vasectomised boar for 10 min. Each sow was removed from its group pen and housed in a detection mating area for the duration of testing, before being returned to its original group pen. On the first sign of oestrus, the sows were temporarily housed in individual stalls and mated twice through post-cervical artificial insemination before being housed in group pens for the remainder of gestation.

2.2. Experimental Design

A 2×2 factorial arrangement of treatments comprising two diets fed in lactation (G: Gestation; L: Lactation) and two feeding allowances (R: allowance of 7.5 kg/d; AL: ad libitum) was used. Diets are subsequently categorised as GR, GAL, LR and LAL. The G diet was formulated to contain 13.0 MJ DE/kg and 0.42 g SID lysine/MJ DE, and the L diet was formulated to contain 14.3 MJ DE/kg and 0.62 g SID lysine/MJ DE (Table 1), according to the feeding standards for this genotype in this production system.

Table 1. Composition of experimental diets (as-fed basis) *.

Item	Gestation (G) Diet	Lactation (L) Diet
Ingredients (g/kg)		
Barley	202.0	-
Wheat	437.2	514.0
Grape marc crimped	6.8	13.5
Millrun	210.0	70.0
Peas-field	-	118.0
Lentils	72.0	-
Pulse offal	6.0	-
Soybean meal	-	33.0
Full-fat soybean	-	19.3
Blood meal	-	5.0
Canola meal	-	100.0
Meat meal	22.0	66.0
Salmon oil	-	4.3
Vegetable oil blend	14.0	35.0
Poultry tallow	0.4	1.1
Limestone fine	12.8	5.1
Monocalcium phosphate	4.0	0.6
Salt	3.0	4.2
DL-Methionine	1.08	0.68
Lysine HCl	1.68	1.81
L-Threonine	1.0	0.6
L-Tryptophan	0.12	0.12
L-Valine	-	0.23
Betaine (liquid) 40%	3.6	4.8
Flavour	-	0.3
Levucell SB10 ME Titan	0.1	0.1
Phytase	0.2	0.2
Vitamin/Mineral Premix *	2.0	2.0

Table 1. Cont.

Item	Gestation (G) Diet	Lactation (L) Diet
Calculated analysis		
Digestible energy (MJ/kg)	13.0	14.3
Crude protein, %	14.8	19.8
SID Lysine, %	0.55	0.89
Crude fibre, %	4.80	4.51
SID Lys:DE, g MJ	0.42	0.62
Calcium, %	0.88	0.95
Available phosphorus, %	0.45	0.50

* premix (per tonne of feed): Vitamin A, 11 milli-international Units (miu); Vitamin D3, 1.5 miu; 25 Hydroxy D3, 50 mg; Vitamin E, 80 g; Vitamin K, 2 g; Vitamin B1, 1.5 g; Vitamin B2, 6 g; Vitamin B6, 6 g; Vitamin B12, 100 mg; Pantothenate, 15 g; Niacin, 20 g; Biotin, 400 mg; Folate, 8 g; Fe (total), 100 g; Zn (total), 120 g; Mn (total), 50 g; Cu (total), 15 g; Se (total), 0.3 g; Cr (as picolinate), 0.2 g; Co (as carbonate), 0.5 g; I (as KI), 2 g; L-Carnitine, 50 g; Antioxidant (total), 150 g.

Sows were allocated to treatments based on parity, backfat depth measured at the P2 location (17.0 ± 2.2 mm), and a body condition score (3.0 ± 0.5) collected upon entry to the farrowing house. This resulted in 35, 40, 38 and 39 sows and their litters for treatments GR, GAL, LR and LAL, respectively. Sows that were ad libitum-fed were offered 7.5 kg at 0700 h and again at 1530 h, and the sows with a reduced feed allowance of 7.5 kg/d were capped at 5.0 kg at 0700 h and 2.5 kg at 1530 h. Each morning before feeding, feed residue was removed and weighed, with individual sow feed refusal recorded.

The reduced feed allowance of 7.5 kg/d was based on the recorded individual daily intake of 210 sows in the same herd over a 21 d lactation (*unpublished data*). These sows had an average daily feed intake (ADFI) of 8.8 kg/d by day 21 of lactation. A percentage reduction of 15% was used to apply the reduced feed allowance treatment in the current experiment of 7.5 kg/d, similar to that previously used by Craig et al. (2017) [14] where a 13% difference in ADFI (6.99 kg/d versus 6.09 kg/d) pertained to lactating sows experiencing a significant body weight (BW) loss.

2.3. Sow Body Condition and Composition Measures

Sow body condition scoring was assessed using a numerical rating of 1 to 5, to provide an assessment of bone prominence indicating body and rib fat [15]. Back-fat depth at the P2 location (P2) was measured using ultrasonography (ImaGo S, BCF Ultrasound, Victoria, Australia) by taking measurements 65 mm from the midline and directly above the last rib on the left and right sides of the sow until measurements differed by <1 mm [16]. Sows were weighed using livestock scales (Iconix FX Series; A1 Weighing & Equipment, QLD). Sow's girth circumference was measured whilst sows were standing during inactivity directly behind the front legs, to not include the udder, using a measuring tape. Sow body fat and body protein change were estimated using sow BW and P2 measured on the day after farrowing (day 2) and at weaning (day 21) according to the equations of Dourmad et al. (1997) [17], found previously to be a good predictor using the same genotype [18].

$$\text{Fat, kg} = -26.4 + 0.221 \times \text{BW} + 1.331 \times \text{P2}$$

$$\text{Protein, kg} = 2.28 + 0.178 \times \text{BW} - 0.333 \times \text{P2}$$

Sow reproductive performance was based on the wean-to-service interval and total piglets born in the subsequent litter, which included pigs born alive and stillborn.

2.4. Litter Growth Performance

Litter size and litter weight were recorded on day 1 after cross-fostering (farrowing), and day 21 of lactation (weaning). The number of dead piglets was recorded, and each dead piglet was weighed. Litter weight on day 21 included the weight of all dead piglets as well as those alive. Sow milk production was calculated for the 21 d lactation period using litter average daily gain (ADG) and litter size multiplied by a factor of 4.2 [19], with this constant representing the conversion of milk production (g) to piglet gain (g) over a 24 d lactation period.

2.5. Blood Sampling and Analyses

Blood samples were taken on a sub-sample of sows (LAL = 23; LR = 22; GAL = 25 and GR = 20) and analysed for concentrations of IGF-1 and insulin. All sows were fasted for 6 h, and blood samples were collected by jugular venipuncture on days 2 and 21 of lactation and at standing heat after weaning (4.0 ± 0.9 d). An 18 g needle was used to collect the sample into a 5 mL EDTA tube (Provet; Brisbane, QLD, Australia) and immediately put on ice. Samples were centrifuged within 4 h of collection at $3000 \times g$ for 15 min in a bench centrifuge. Plasma was decanted and stored at -20 °C until all samples were sent to the laboratory (Adelaide Research Assay Facility, North Adelaide, SA, Australia) and analysed for IGF-1 and insulin. Concentrations of IGF-1 were measured using a commercial RIA kit for humans (ALPCO Diagnostics, Salem, NH, USA); intra- and inter-assay CVs were 7.9% and 10.1%, respectively. Insulin was measured using a porcine insulin commercial RIA kit (Millipore, St-Charles, MO, USA) with intra- and inter-assay CVs of 7.5% and 3.9%, respectively. Validation was carried out on the dilution of pig serum pools with different hormone concentrations, with extraction prior to assaying for IGF-1 assays.

2.6. Statistical Analyses

Of the final dataset, only sows which weaned ≥ 7 piglets and did not refuse feed for ≥ 2 d were included for analyses. As a result, the final dataset included 37 GAL sows, 34 GR sows, 34 LAL sows and 35 LR sows. Days on which the subset sows were fasted for blood sampling were removed from the feed intake data. Statistical analysis of data was performed with SPSS (IBM SPSS V25.0; IBM, Chicago, IL, USA). Data are expressed as least-square means $\pm$ standard error of the mean (SEM).

Data for dependent variables of sow BW, P2 backfat, fat, protein, girth, ADFI, milk production, litter gain, IGF-1, insulin, wean-to-service interval, and total piglets born in the subsequent litter were analysed according to a 2×2 factorial design of treatments using diet type and feed allowance as independent variables, and their interaction, and room fitted as a random effect, using a linear mixed model. Where necessary, variables measured on day 1 were fitted as covariates for the same measure at day 21, and data were then further analysed for change between these two time points. Piglet removals and mortality were not normally distributed and therefore analysed using a generalised linear mixed model with Poisson distribution with day 1 litter size, diet type, feed allowance and the interaction of diet type and feed allowance, fitted as fixed terms, with room fitted as a random effect. Percent sows bred by <7 days and farrowing rate were analysed using a generalised linear model with binary distribution with treatment and parity as independent variables.

All feed consumption data were determined on an as-fed basis twice daily at 0700 h and 1530 h. Feed intake data were analysed as repeated measures using a linear mixed model, which incorporated sow as the random term and day as the repeated measure. Day, diet type, feed allowance and the interaction of day $\times$ diet type, day $\times$ feed allowance, and day $\times$ diet type $\times$ feed allowance, were fitted as fixed terms. A value of $p \leq 0.05$ was considered statistically significant in all tests. A value of $p \leq 0.10$ was considered a trend.

3. Results

3.1. Sow Performance

Average daily feed intake for sows offered feed ad libitum was higher for sows offered the G diet on most days of lactation ($p < 0.05$) (Figure 1). Sows offered both the G and L diets followed a similar energy intake ($p > 0.10$) (Figure 2). The calculated SID Lys intake between the two groups was significantly higher in sows offered the L diet on all days excluding day 4 ($p < 0.05$) (Figure 3).

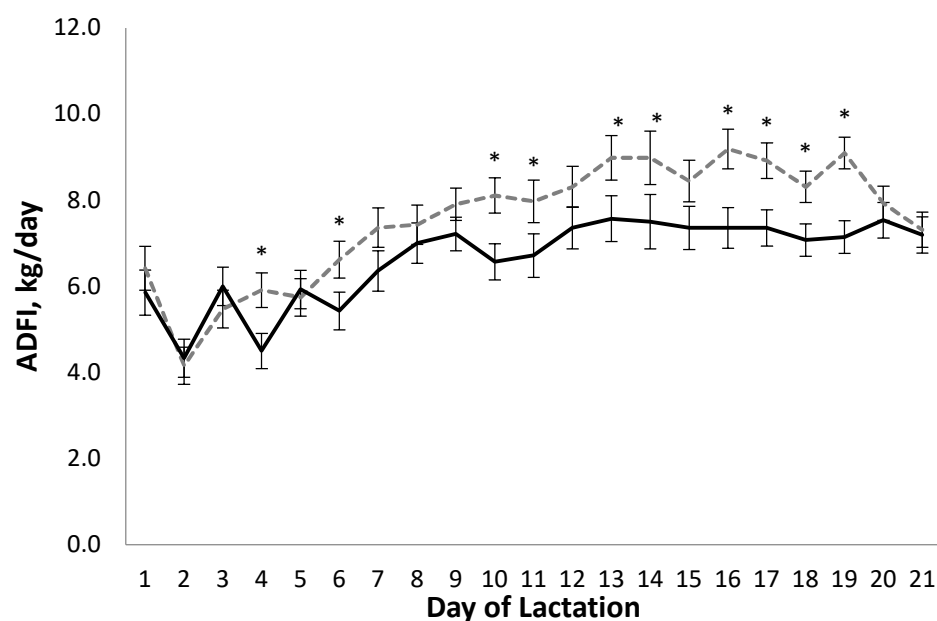


Figure 1. Average daily feed intake (ADFI) for sows offered a gestation (dashed line) or lactation (solid line) diet, ad libitum, during lactation. * $p < 0.05$.

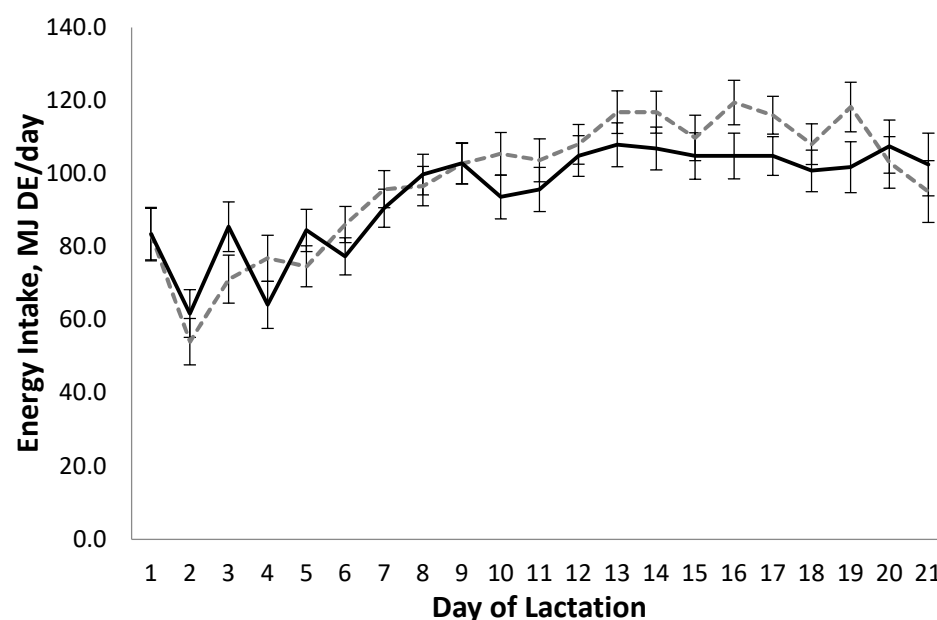


Figure 2. Calculated DE intake for sows offered a gestation (dashed line) or lactation (solid line) diet, ad libitum, during lactation.

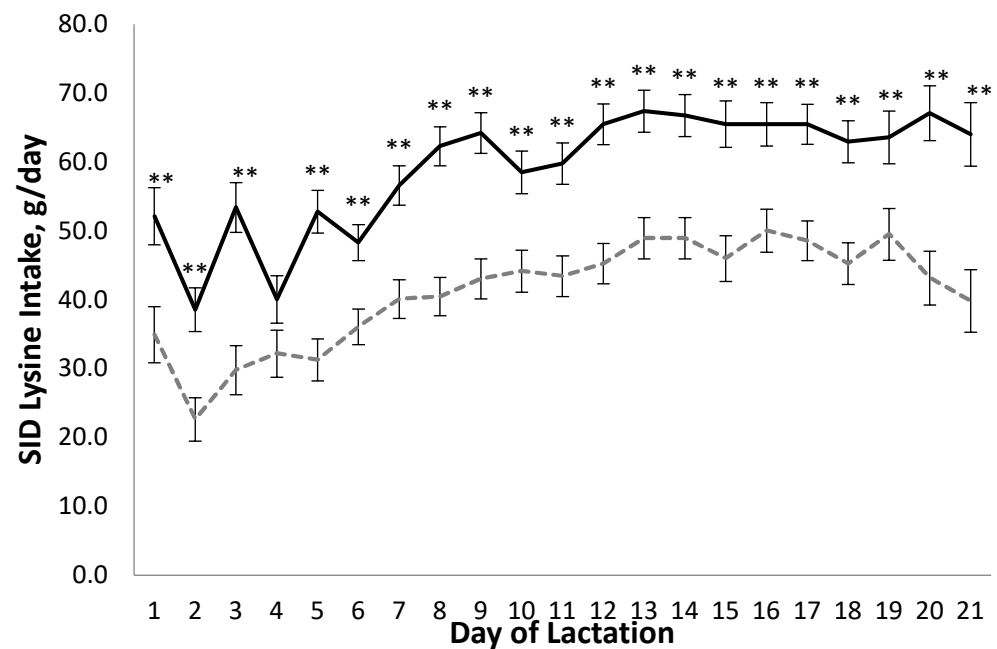


Figure 3. Calculated SID Lys intake for sows offered a gestation (dashed line) or lactation (solid line) diet, ad libitum, during lactation. ** $p < 0.001$.

Sows in the GAL treatment had the highest ADFI ($p < 0.05$) while sows in the R treatments had the lowest, with LAL being intermediate (Table 2). The interaction between diet type and feed allowance was significant for DE intake ($p < 0.05$), with sows in the GR treatment recording the lowest and sows in the GAL treatment recording the highest DE intake. Sows offered diets ad libitum had a higher SID Lys intake compared to sows offered the diet at a reduced level (50.8 versus 45.4 g/day, $p < 0.001$). Diet type influenced calculated SID Lys balance with sows offered the G diet experiencing a negative balance (-14.2 g/d; $p < 0.05$), whilst feed allowance influenced energy balance with sows offered feed ad libitum experiencing a higher balance over lactation (-5.2 MJ/d; $p < 0.05$). Sow BW, P2, and calculated body fat and protein at farrowing and weaning were similar ($p > 0.05$). By weaning, sows in the AL treatment experienced a significant gain in girth (2.9 mm; $p < 0.05$) compared to the sows in the R treatments, which showed an average loss of -0.4 mm (Table 2).

Table 2. Effects of diet type and feed allowance on average daily feed intake (ADFI), digestible energy (DE) and/or standardised ileal digestible (SID) lysine (Lys) intake and balance during lactation (d1–21) on sow body composition on the day after farrowing (day 2), at weaning (day 21) and change between these two time points. Data are presented as means with a pooled standard error (SEM).

Diet Type	Gestation		Lactation		<i>p</i> Value			
Feed Allowance	Ad Libitum	Reduced	Ad Libitum	Reduced	SEM	Diet Type	Feed Allowance	Diet Type × Feed Allowance
ADFI, kg/d	7.7 ^a	6.4 ^c	6.7 ^b	6.3 ^c	0.01	0.009	<0.001	0.015
DE								
Intake, MJ/d	100.0 ^a	82.6 ^c	95.5 ^a	90.0 ^b	28.21	0.596	<0.001	0.023
Requirement ¹ , MJ/d	104.4	97.7	101.6	104.1	32.81	0.540	0.461	0.105
Balance ³ , MJ/d	−3.4	−15.7	−6.9	−13.3	47.2	0.867	0.007	0.384
SID lysine								
Intake, g/d	41.9	34.6	59.7	56.2	7.40	<0.001	<0.001	0.149
Requirement ² , g/d	56.6	52	54.4	55.8	17.73	0.682	0.436	0.145
Balance ³ , g/d	−14.2	−17.6	4.5	0.7	21.19	<0.001	0.118	0.934

Table 2. Cont.

Diet Type	Gestation		Lactation		p Value			
Feed Allowance	Ad Libitum	Reduced	Ad Libitum	Reduced	SEM	Diet Type	Feed Allowance	Diet Type × Feed Allowance
Body weight, kg								
Farrowing	223.0	224.4	224.3	228.2	4.77	0.647	0.636	0.822
Weaning	226.6	223.5	229.0	230.7	4.26	0.340	0.894	0.625
Change	3.7	−1.4	7.9	4.8	2.41	0.135	0.236	0.769
Backfat P2 ⁴ , mm								
Farrowing	17.1	16.8	17.2	17.1	0.62	0.581	0.731	0.686
Weaning	15	15.1	14.7	14.8	0.55	0.334	0.746	0.939
Change	−1.7	−1.6	−2.2	−2.3	0.61	0.124	0.941	0.821
Girth circumference, cm								
Farrowing	144.1	146.1	140.9	144.1	10.89	0.103	0.106	0.713
Weaning	146.6	144.9	144.2	143.8	11.82	0.304	0.552	0.697
Change	1.8	−0.9	4.1	0.1	7.50	0.226	0.015	0.659
Fat ⁵ , kg								
Farrowing	43.7	43.8	43.3	45.3	9.33	0.728	0.525	0.537
Weaning	41.7	40.9	41.5	42	6.81	0.724	0.908	0.639
Change	−2.2	−2.8	−1.6	−2.8	5.44	0.782	0.452	0.775
Protein ⁶ , kg								
Farrowing	36.4	36.7	36.7	37.5	3.88	0.544	0.544	0.794
Weaning	37.6	37.1	37.7	38.3	3.01	0.475	0.965	0.515
Change	1.2	0.3	1	1.2	2.55	0.683	0.690	0.480

^{a,b,c} superscript letters within a row indicate a significant difference. ¹ energy requirement was calculated based on the total requirement of the sow for maintenance and milk production from farrowing to weaning [20,21]. ² lysine requirement was calculated based on the total requirement of the sow for maintenance and milk production from farrowing to weaning [22]. ³ energy and lysine balance was calculated based on intake and total requirement of the sow from farrowing to weaning. ⁴ back-fat depth measured at the P2 location. ⁵ fat mass was estimated using BW and P2 [17]. ⁶ protein was estimated using BW and P2 [17].

3.2. Litter Performance and Subsequent Reproductive Performance

There was a trend for litter size after farrowing (post-fostering) to be lower in the LAL sows ($p < 0.10$). Litter size at weaning was greater in sows fed diet G than sows fed diet L (10.4 ± 0.2 versus 9.8 ± 0.2 ; $p < 0.05$). Additionally, a tendency for sows from the AL treatment to have more piglets at weaning compared with the R treatment was identified (10.3 ± 0.2 versus 9.9 ± 0.2 ; $p < 0.10$). The total number of piglet removals was highest in the litters of the sows offered the lower feed allowance (1.7 ± 0.3). There was a greater incidence of piglet mortality, in particular, piglet overlays, in the litters of sows offered the lower feed allowance (0.4 ± 0.1) ($p < 0.05$). Litter weight at weaning, litter gain and milk production were consistent across all treatments (Table 3).

Table 3. Effects of diet type and feed allowance on sow and litter performance the day after farrowing (day 2), at weaning (day 21) and at standing heat. Data are presented as means with a pooled standard error (SEM).

Diet Type	Gestation		Lactation		p Value			
Feed Allowance	Ad Libitum	Reduced	Ad Libitum	Reduced	SEM	Diet Type	Feed Allowance	Diet Type × Feed Allowance
Litter size								
Farrowing	11.6	11.3	10.9	11.4	0.21	0.170	0.770	0.068
Weaning	10.8	10.0	9.8	9.8	0.36	0.033	0.091	0.144
Mortality								
Total removals	1.1	1.4	1.3	1.9	0.26	0.182	0.037	0.636
Overlays	0.7	0.9	0.6	1.3	0.22	0.544	0.021	0.302
Litter weight, kg								
Farrowing	17.6	17.9	17.8	16.7	0.96	0.298	0.455	0.160
Weaning ¹	62.9	59.5	61.2	60.9	12.29	0.933	0.284	0.374
Litter gain, kg ¹	45.3	41.6	43.6	44.7	11.33	0.682	0.436	0.145
Milk output ³ , kg/day ²	9.5	8.7	9.1	9.4	0.51	0.684	0.436	0.145

Table 3. Cont.

Diet Type	Gestation		Lactation		p Value			
Feed Allowance	Ad Libitum	Reduced	Ad Libitum	Reduced	SEM	Diet Type	Feed Allowance	Diet Type × Feed Allowance
Litter ADG, kg/d ¹	2.3	2.1	2.2	2.2	0.11	0.682	0.436	0.145
Wean-to-service interval, days	4.1	4.6	4.2	4.4	0.28	0.825	0.085	0.547
Bred < 7 days ⁴ , %	85.7	82.7	87.5	85.7	1.14	0.341	0.594	0.659
Farrowing rate ⁴ , %	97.0	96.6	100	91.4	0.88	0.633	0.664	0.742
Total piglets born in the subsequent litter	12.9	12.6	12.5	13.3	1.31	0.796	0.661	0.288

¹ for litter weight at weaning, litter gain and litter ADG, day 1 litter size was used as a covariate in the model.

² milk output was estimated using equations from Hojgaard et al. (2020) [19]. ³ measured on a subset of litters.

⁴ 95% confidence intervals rather than SEM are presented for binary data.

Wean-to-service interval tended to be lower by 0.3 days in sows offered feed AL compared to those from the R treatment (4.2 ± 0.1 versus 4.5 ± 0.1 ; $p < 0.10$); however, the total piglets born in the subsequent litter was unaffected by diet type and feed allowance or the interaction (Table 3).

3.3. Plasma Metabolites

At weaning, insulin concentration was lowest ($p < 0.05$) in sows fed diet G (9.8 ± 2.1 uU/mL) compared to sows fed diet L (14.8 ± 2.1 uU/mL). However, the change in plasma insulin concentration from farrowing to weaning was not different between groups, nor were the levels measured at standing heat ($p > 0.05$).

There was no significant difference ($p > 0.05$) between treatment groups for IGF-1 at farrowing, weaning or standing heat or as a change from farrowing to weaning (Table 4).

Table 4. Effects of diet type and feed allowance on changes in plasma metabolites, insulin and IGF-1, measured the day after farrowing (day 2), at weaning (day 21) and at standing heat. Data are presented as means with a pooled standard error (SEM).

Diet Type	Gestation		Lactation		p Value			
Feed Allowance	Ad Libitum	Reduced	Ad Libitum	Reduced	SEM	Diet Type	Feed Allowance	Diet × Feed Allowance
Insulin, uU/mL								
Farrowing	29.6	20	29.8	30.3	3.26	0.137	0.194	0.151
Weaning	10.1	9.5	14.9	14.6	2.11	0.030	0.825	0.942
Change	−19.3	−10.5	−14.8	−15.1	4.02	0.997	0.293	0.267
Standing heat	17.3	19.3	14.2	13.6	2.55	0.106	0.848	0.152
IGF-1, ng/mL								
Day 1 lactation	158.1	133.9	130.8	122.9	12.9	0.146	0.221	0.534
Weaning	158	149.7	152.6	163.7	16.4	0.797	0.935	0.560
Change	−0.1	15.8	21.7	40.8	16.2	0.154	0.287	0.922
Standing heat	128.1	123.1	114.7	131.4	10.6	0.817	0.585	0.313

4. Discussion

The two diets offered at two different feed allowances applied in this experiment were chosen to test the hypothesis that sows fed a diet lower in energy and SID Lys content, at a reduced allowance, would still mobilise body fat and body protein to a greater extent that would, in turn, negatively impact litter growth and subsequent reproduction. The treatments applied were successful at establishing divergent DE and SID Lys intakes, but these differences were not sufficient to adversely impact litter growth. A reduced feed allowance in lactation resulted in sows whose piglets suffered a higher pre-weaning mortality, lost girth circumference, and exhibited a tendency for a longer wean-to-service interval, but no treatment effects were seen in any of the endocrine markers of reproductive

function or total piglets born in the subsequent litter. Thus, restricted feeding of sows reduced energy and SID Lys balances in lactation and impacted piglet overlays with a tendency to extend the time from weaning to oestrus. However, in contrast to the proposition examined, sows did not experience any significant changes in estimated body composition over the 21 d lactation period.

4.1. Sow Performance

Management of lactation feeding regimes for multiparous sows typically follows a feeding curve designed to support productivity during lactation, which, in turn, drives litter growth [2]. Feed is generally offered ad libitum from early lactation to meet Lys and energy requirements, which is important to support and sustain milk production while also reducing the extent of tissue mobilisation, which in turn is regarded to negatively impact subsequent reproductive success. The energy requirement of lactating sows increases from week one to three of lactation and declines in week four, while the Lys requirement typically decreases from week one to two, before gradually increasing with litter growth to week four [23]. Watzeck and Huber [24] and Gregory and Huber [25] reported that maternal nitrogen retention was unaffected by a SID Lys-to-net energy (NE) ratio ranging between 2.79 and 5.50 g SID Lys/Mcal NE in multiparous sows; however, piglet growth rate increased with an increasing ratio. As such, in multiparous sows, Huber [26] remarked that the optimum SID Lys:NE ratio is dynamic in lactation and that maternal nitrogen retention becomes positive in weeks two and three of lactation. This indicated a repartitioning of nutrients towards maternal growth, or the reconstitution of maternal protein previously mobilised in late gestation or early lactation. Data from the present study is consistent with either, or both, of these mechanisms.

Feed intake is obviously an important determinant of energy and Lys intake. The ADFI and energy intake curve analysis of the AL treatments revealed that sows were consuming feed to meet the energy demands of lactation over the ~3-week period. When considering the ADFI and SID Lys intake curves, the ADFI of sows offered diet L reached a plateau lower than that of sows fed diet G. Feed intake could possibly have been limited by the SID Lys content of the diet, or sows were eating to a maximum energy level rather than a feed intake level. In this regard, Boler et al. [27] reported that lactating sows fed a low lysine diet (0.85% SID Lys) consumed 0.29 kg more feed per day compared with sows fed a high lysine diet (1.11% SID Lys). Although there was a significant difference in ADFI during this period of lactation, overall dietary treatments did not impair energy and nutrient supply to a level that led to excessive body protein mobilisation or changes in litter growth.

It was not anticipated that sows fed diet G would experience a negative Lys balance over the 21 d lactation period yet maintain reserves of estimated body protein. Similarly, sows which experienced a reduced energy balance showed no difference in loss of P2 backfat and no change in litter weight relative to that of sows fed diet L by day 21. A contributing factor could have been that although the ADFI in late lactation of sows offered diet L was lower, the reduced feed allowance of ~15% to 7.5 kg may not have been limiting in this experiment. It is also possible that sows experienced a nutrient oversupply, particularly Lys, in early lactation to that required for milk production, followed by a period of insufficiency once peak milk production was reached later in lactation. With energy requirements of lactating sows decreasing around week four of lactation [23], it is possible that sows experienced a period of depositing energy in early lactation and a loss in later lactation. Sows in the current experiment experienced an overall loss in estimated body fat, but this was found not to be statistically significant.

In support, Pedersen et al. (2016) [28] reported that a two-diet feeding regime improved milk production and litter growth as lactation progressed, while sow BW loss was

minimised in late lactation. These results are supported by Feyera and Theil (2017) [29] and Watzeck and Huber [24], who both demonstrated that the calculated ME or NE and SID Lys requirements changed depending on the stage of lactation, with energy potentially limited in the first week of lactation while the reverse is true for Lys in the remainder of lactation. Litter growth rate may adjust accordingly to periods of oversupply and inefficiency, contributing to two distinct stages of the lactation period. In the present experiment, sows fed diet G may have experienced a period of oversupply of Lys and/or energy in early lactation, followed by an insufficiency later that translated to an early period of depositing body protein, counterbalanced by mobilisation in late lactation [3]. However, this could not be determined in the present experiment as sow body composition was measured only after farrowing and at the point of weaning.

In the present experiment, litter weight at weaning was not different between sows experiencing either a 0.8% (G) or 3.2% (L) protein gain in lactation. Hojgaard et al. (2019) [3] investigated varying levels of SID crude protein content of lactating diets and showed that sows with an average SID Lys intake of 50 g/d and nursing 13 piglets over a 26 d lactation mobilised 0.9% body protein. Sows in the present experiment offered the L diet, with a SID Lys intake of 57.9 g/kg and nursing 10.4 piglets over a 21 d lactation, deposited 3.3% protein. In this regard, the finding that sows offered diet G, with a lower SID Lys intake of 38.3 g/day and nursing 9.8 piglets, deposited 0.8% protein, was unexpected. Muller et al. (2021) [18], using sows of a similar genotype over a 21 d lactation period, showed that sows experienced a BW gain when offered ad libitum a similarly formulated lactation diet to that used in the present study, despite having a lower ADFI of 5.0–5.4 kg/d. It is possible that sows which experience a negative Lys balance are more efficient at using body protein and the excess Lys in the diet after parturition [27,28,30]. Sows suckling only ~10 piglets per litter may also have contributed to this finding.

As reviewed by Tokach et al. (2019) [12] and Muller et al. [13] and in accordance with other work [31–33], these findings indicate that the modern sow is possibly more resilient to nutritional impositions and do not mobilise body tissues in lactation to support milk production and piglet growth, to the same degree as has been historically reported. Even if lean and fat tissues are mobilised, negligible (commercial) impacts on reproductive traits such as wean-to-service interval, farrowing rate and litter size are seemingly identified, at least in a 21-day lactation, and this seems especially true for multiparous sows [13,25]. As such, the mobilisation of energy and protein in lactation to support the piglets' needs are not completely independent [12], and hence, the interactions between Lys and energy requirements are more complex and subject to factors involved in nutrient deficit, including energy and protein intake, energy and protein output in milk, growth rate of the litter, and lactation length [19,25].

4.2. Litter Performance

Milk production and milk composition are critical factors for stimulating and supporting improvements in litter growth rate; therefore, considerable focus on energy and protein (Lys) levels in lactation diets has occurred. Despite a considerable body of research being conducted, both under research and commercial production conditions, the influence of dietary Lys intake on milk production and composition is equivocal [12]. Previous research has demonstrated that an increase in litter growth of up to 9% occurs in response to increasing Lys intake from 77 to 89 g/kg for sows nursing litter sizes of 13 piglets [14,34]. The response of litter growth to an increase in protein can be seen in early lactation up to day 4 [35] and late lactation from day 12–18 [36]. Hojgaard et al. (2020) [19] found that when sows were fed 96–152 g/kg of SID crude protein, piglet gain was limited by milk

intake and protein concentration from day 10 of lactation, whereas up to this point, only milk intake was limiting in litters of 13 piglets.

The average sow Lys intakes of the G and L diets (38.2 versus 58.0 g/kg) in the current experiment were generally lower than previous reports; lactation length was 4–8 days shorter, and on average, sows were nursing two piglets less. Given these disparities, our results cannot truly be compared with previous studies where sows typically supported more piglets and lactation length was longer. Nevertheless, in terms of Lys requirements, the estimated requirements (Table 2) were in general agreement with those reported previously [12], although it is recognised that estimation of Lys requirements for litter growth rate requires a multifactorial approach by taking into account parity, lactation curve, daily Lys intake, growth rate of the litter, milk production, and milk composition, as these factors affect how Lys is required and partitioned by lactating sows [12].

Generally, in response to milk protein, litter growth seems to slow down beyond day 10 of lactation [34]. In the current study, litters of sows fed diet G may have grown better in the first 10 d of lactation, whilst litter growth may have slowed in later lactation, but this was not possible to verify. Changes in litter growth and milk intake throughout lactation between the litters of sows fed the G and L diets may explain similar litter weights at weaning. In this regard, it has been estimated that the amount of daily digestible Lys intake per kilogram of litter daily gain is consistent around 24 to 25 g [9,32], but Tokach et al. [12] updated this regression and predicted an increase to 27 g per day in the amount of digestible Lys intake required for each 1 kg of litter growth, and also an increase to 13 g per day in the expected mobilisation of Lys from body protein reserves. In the present study, sows fed the L diet had an intake of 26.4 g SID Lys per day for 1 kg of litter growth, whereas for sows fed the G diet, only 17.5 g SID Lys per day was required to support 1 kg of daily litter growth. Litter growth rate was unaffected by diet type (Table 3), and (calculated) body protein mobilisation did not occur (Table 4), adding further credence to the modern Australian sow, at least of this genotype, appears to be more resilient to nutritional impositions during lactation.

Litter size at weaning was impacted by diet and feed allowance, with the sows offered the L diet and sows fed restrictively (trend, $p = 0.091$) weaning fewer piglets. It is not known why sows fed diet L weaned fewer piglets, as the total removals were the same. The specific causes of piglet mortality were investigated to ascertain possible reasons for these differences. Sows offered a reduced feed allowance experienced more piglet overlays. The relationship between higher pre-weaning mortality and feed restriction has been demonstrated previously as sows offered less feed experience less satiation [37]. This, then, can result in increasing sow movement and consequently a higher risk of piglet overlays [38]. One possible explanation for the higher piglet mortality figure may be the extended period from the last feed drop for the day (0–2.5 kg, given at 1400 h) and the first feed drop the following day (5.0–7.5 kg, given at 0700 h). As piglet overlays were recorded and weighed at 0700 h each day, the lack of access by sows to feed during this period (~17 h) may have contributed to the higher mortality figure in this treatment.

4.3. Reproductive Performance

A sow's nutritional status at weaning is an important determinant of subsequent reproductive performance as insufficient dietary energy and Lys intakes fuel a change in metabolic status, which ultimately causes changes in endocrine function, specifically follicular developmental competence. Impairments in the developmental competence of follicles as established during lactation may at least partially explain the reduced reproductive performance in the next reproductive cycle, and lower piglet birth weights [39]. Insulin

and (or) IGF-1 have been implicated in this process given their various roles in metabolic status, although results tend to be ambiguous [40].

In the current study, and despite a ~20 g/d increase in SID Lys intake during lactation in sows fed the L diet, only a higher insulin concentration was observed at weaning, with no differences seen at standing heat. The relationships between the metabolic state of sows during lactation and at weaning, circulating endocrine markers, and subsequent reproductive performance are ambivalent, with recent studies using modern-day sows being scarce. Previously, Yang et al. (2000) [36] conducted a study in primiparous sows that recorded Lys intakes over an 18 d lactation of 16, 36 or 56 g/d. Increasing Lys intake increased serum urea nitrogen and postprandial insulin concentrations ($p < 0.05$) during lactation, and sows fed more Lys had greater serum IGF-I concentrations on days 6 and 18 ($p < 0.05$). However, these increases did not increase secretion of oestradiol and luteinising hormone compared with a medium Lys intake, and no impacts of higher Lys intake on the wean-to-service interval were found. Heo et al. (2008) [41] found similar results with respect to insulin, also in gilts, although a shorter wean-to-oestrus interval was observed. Earlier, a diet with 0.5% SID Lys fed to primiparous sows in lactation, compared to a diet with 1.08% SID Lys, was found to alter circulating concentrations of somatotrophic hormones and insulin at the end of lactation and had a negative impact on post-weaning ovulation rate, albeit that no obvious relationships between reproductive traits and metabolic hormone data were observed [42].

Levels of IGF-1 are influenced by a change in feed intake, that is, a restriction, or withdrawal of feed. Gilts which experienced a period of ad libitum feeding followed by feeding at maintenance requirement had significantly reduced levels of IGF-1 compared to gilts which were restrictively fed, followed by a period of ad libitum feeding [11]. These results were supported by Zak et al. (1997) [43], where sows restrictively fed 50% of their 'appetite' from day 22 to 28 of lactation had reduced IGF-1 levels by day 28. Therefore, the lack of effect of a reduced feed allowance on IGF-1 levels in the current experiment is not surprising, given that sows may not have been sufficiently restricted in their intake of energy and protein. Moreover, the current study used multiparous sows, whereas many previous studies have used primiparous sows, which are seemingly more sensitive to nutritional perturbations in lactation.

The consequences of tissue mobilisation in lactation on subsequent sow reproductive success are well studied, e.g., [4,39,44]. In the present experiment, despite varying energy and SID Lys intakes during lactation, sows experienced little to no BW loss or estimated body protein change. Given these results, it is also not surprising that there were no adverse impacts on subsequent reproductive performance. In support of these findings, studies have shown that significant changes in the SID crude protein content of the diet [3], as well as restrictively feeding sows 60% less during lactation, bore little impact on the total piglets born in the subsequent litter [13]. However, results of the present experiment indicated that sows offered a reduced feed allowance tended to have a slightly longer wean-to-service interval, by ~0.3 d, but this is unlikely to be of commercial significance. Nevertheless, periods of insufficient energy intake during lactation, or the time from weaning to oestrous, have been shown to impact fertility and ovulation in other studies, e.g., [22,39].

5. Conclusions

Results from this experiment, conducted under commercial conditions, showed that diets formulated to either gestation or lactation specifications, or restricting the feed allowance of lactating sows (~6.35 kg/d over a 21 d lactation compared to an ad libitum intake of ~7.2 kg/d), had little to no impacts on litter performance and subsequent reproductive performance, concomitant with no significant changes in (estimated) body protein

and fat mass. Sows in all treatments gained (estimated) body protein mass during lactation and lost 1.6–2.8 kg of (estimated) fat mass. Sows offered feed ad libitum gained more girth in lactation. These findings occurred despite a ~20 g/d difference in SID Lys intake between sows fed a gestation or lactation diet. Despite insulin levels being reduced in sows fed the gestation diet, levels were the same by standing heat. Collectively, in association with other recent studies, these data suggest that the modern sow is more resilient to nutritional impositions in lactation, and does not mobilise body tissues in lactation to support milk production and piglet growth, to the same degree as has been historically reported. As such, the consideration of different feeding strategies for multiparous lactating sows to meet the dynamic SID Lys and energy requirements throughout lactation is suggested, although commercially, logistical constraints associated with feed delivery systems and (or) sow flow need to be carefully balanced.

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