Impact of sow lactation feed intake on the growth and suckling behavior of low and average birthweight pigs to 10 weeks of age

Samuel J. Hawe, †,‡,1 Nigel Scollan,‡ Alan Gordon,† and Elizabeth Magowan†,‡

[†]Agri-Food and Biosciences Institute, Livestock Production Sciences Unit, Hillsborough, Northern Ireland BT26 6DR, UK; and [‡]Queens University Belfast, Institute for Global Food Security, Belfast, Northern Ireland, BT7 1NN, UK

ABSTRACT: Improved genetics in commercial pig production have resulted in larger litter sizes. However this has increased the prevalence of compromised pigs exhibiting inferior birthweights, weaning weights, and lifetime performance. This study aimed to determine the effects of increased sow lactation feed intake on growth of low and average birthweight piglets until 10 wk of age. Low (Low BW; <1 kg) and average (Av BW; 1.3–1.7 kg) birthweight animals were reared in uniformly weighted litters comprising 14 piglets on a foster mother offered either a low (Low FA; max 7.5 kg/d) or high (High FA; max 11 kg/d) feed allowance over a 28- ± 1-d lactation. Piglet performance was monitored from birth until 10 wk of age. Sows offered a High FA consumed 42.4 kg more feed on average than those offered Low FA, resulting in a greater derived milk yield (P < 0.05). Animals of Av BW remained heavier than Low BW pigs throughout the trial (P < 0.05). Piglets reared by High FA sows were heavier at weeks 3, 4, 5, and 7 (P < 0.05) but not week 10 (P > 0.05). Growth rate of piglets relative to their birthweight was significantly greater for Low BW piglets than those of Av BW during lactation (P < 0.001). Piglets reared by sows offered

a High FA expressed greater relative growth preweaning (P < 0.05); however, postweaning relative growth for piglets reared on sows offered a Low FA was greater (P < 0.05) suggesting compensatory growth. Neither birthweight nor sow feed allowance significantly affected preweaning mortality (P > 0.05). However, Low BW animals on sows with a High FA recorded half the preweaning mortality of Low BW pigs on sows with a Low FA. During week 1 of lactation, Av BW litters recorded a greater total suckling duration compared to Low BW litters (P < 0.05) but there was no difference in suckling frequency (P > 0.05). During week 3 of lactation, High FA litters displayed a significantly lower suckling frequency (P < 0.05) yet a greater total suckling duration (P < 0.001). Average daily gain was greater for Av BW pigs during weeks 4-7 (P < 0.001) but no difference was recorded between weeks 7 and 10 (P > 0.05). Average daily feed intake was greater for Av BW pigs throughout the nursery period (P < 0.05) but feed–conversion ratio did not differ compared to Low BW pens (P>0.05). In conclusion, offering sows a High FA increased weaning weight of all animals; however, birthweight was the major determinant of postweaning performance.

Key words: compromised pigs, growth, mortality, suckling behavior, weaning

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¹Corresponding author: shawe02@qub.ac.uk Received March 25, 2020. Accepted May 2, 2020.

INTRODUCTION

Advances in genetics, combined with improved management, has resulted in significant increases in litter sizes within commercial pig production (Bruns et al., 2018). This has been accompanied by an increase in the number of low birthweight (Low BW) and potentially unviable piglets, largely due to intrauterine growth retardation (IUGR) (Antonides et al., 2015). Quiniou et al. (2002) showed that large litters (>16 piglets) demonstrated an average reduction of 330 g in piglet birthweight and that Low BW pigs occupied a significantly greater proportion of these larger litters (23% of piglets <1 kg compared to 7% in litters <11 piglets). These compromised animals commonly have elevated levels of preweaning mortality, as well as impaired weaning weights and lifetime performance (Beaulieu et al., 2010). With litter sizes continuing to increase, it is imperative that effective postnatal intervention strategies are developed to maximize the performance of these compromised animals to ensure the sustainability of the industry. Multiple studies have shown how Low BW pigs have the potential to achieve improved growth rates when effective intervention strategies are employed. For example, Douglas et al. (2014) reported that Low BW pigs fostered into uniformly weighted litters recorded greater weaning weights than those in mixed weight litters (7.34 vs. 6.8 kg; P = 0.045). Increased nutrient availability during the suckling period through sow lactation feed intake has been highlighted as a potential approach to support sufficient growth of piglets reared in large litters during the nursing phase. Indeed. Sulabo et al. (2014) found that litters reared by sows fed ad libitum during lactation exhibit superior total (46.7 vs. 43.0 kg; P < 0.04) and daily (2.56 vs. 2.36 kg; P < 0.04) litter weight gain compared to those fed a standard diet. However, much of the existing work has been conducted on litter sizes of fewer than 12 pigs and does not focus on the specific impact of treatment on Low BW piglets, resulting in the published data not adequately reflecting modern commercial practice.

The objective of this study was, therefore, to determine the effects of increased nutrient supply to piglets through sow lactation feed intake on the performance of compromised (<1 kg) and "normal" (~1.5 kg) birthweight pigs reared in large litter sizes of 14 piglets during a 28- ± 1-d lactation and up until 10 wk of age. It was hypothesized that increased lactation feed intake would improve the milk yield of sows and result in increased

weight gain and reduced mortality of all piglets during lactation. A key focus of the work was to then investigate if any improvements in performance preweaning were carried through significantly postweaning.

MATERIALS AND METHODS

This study was conducted at the Agri-Food and Biosciences Institute (AFBI), Hillsborough, Northern Ireland, UK. The work was carried out in accordance with the Animals (Scientific Procedures) Act 1986 (The Parliament of the United Kingdom, 1986). All AFBI research and equipment was externally checked and/or calibrated and work was ISO 9001 certified.

Animals

Existing literature frequently defines Low BW as 1.25 kg or below (Wolter et al., 2002; Douglas et al., 2014; Muns et al., 2014, 2017). However, recent analysis from the commercial setting has shown that 25% of piglets record a birthweight under 1.1 kg (Wang et al., 2017), with up to 23% born under 1 kg in large litters (Quiniou et al., 2002). For this reason, an upper limit of 1 kg was set for Low BW piglets in this study to reflect compromised pigs in the commercial environment. It is also accepted that the majority of piglets are born within a weight range of 1.4 and 1.6 kg (Quiniou et al., 2002). Therefore, the weight profile of the average birthweight (Av BW) pig population employed in this study approximated 1.5 kg and ranged from 1.3 to 1.7 kg. A total of 448 crossbred piglets [Duroc × (Large White × Landrace)] were selected from 71 sows at birth over 8 time replicates. Sows were induced to farrow with 2 mL of Planate (cloprostenol, Intervet/Schering-Plough Animal Health, Boxmeer, Netherlands) on day 114 of gestation and all sows within each replicate farrowed within a 24-h period. Within this cohort, 224 piglets had a birthweight under 1 kg and the remaining 224 piglets had a birthweight between 1.3 and 1.7 kg. At farrowing, four sows per time replication were selected as foster mothers. As such, all piglets were reared on a total of 32 foster sows, which ranged from parity 2 to 4. Therefore, two experimental litters of 14 Low BW piglets and two experimental litters of 14 Av BW piglets were established per time replicate. Weight, parity, and body condition of foster sows was balanced across each treatment group. Each litter was also balanced for sex.

Treatments and Lactation Feeding Regime

The trial represented a 2×2 factorial arrangement where two levels of lactation feed allowance, namely high feed allowance (HIGH FA) and low feed allowance (LOW FA), were offered to sows rearing litters of either a Low BW or Av BW. All sows were offered 3 kg/d of the lactation diet from day 108 ± 1 of gestation until the day of farrowing. When the litters were established, sows assigned to the Low FA treatment received increasing increments of 0.3 kg/d up to a maximum of 7.5 kg/d. The Low FA regime was designed after consultation with industry to reflect intake on commercial farms. Sows assigned to a High FA regimen were offered increasing increments of 0.5 kg/d to a maximum of 11 kg/d. Intake was capped at 11 kg/d to reduce the likelihood of sows overeating and becoming "sickened," leading to food refusal and reduced lactation intake. The lactation period lasted for a duration of 28 ± 1 d.

Animal Management

At day 108 ± 1 of gestation, sows were placed in farrowing accommodation where the temperature was maintained at 19 °C and reduced to 17.5 °C on completion of farrowing. Each sow was allocated to an individual farrowing crate $(0.5 \times 2.2 \text{ m})$, located at the center of the farrowing pen (2.3 \times 1.5 m). Sows were fed a commercial lactation diet [14.5 MJ digestible energy (DE)/kg, 17.4% crude protein (CP), 1.2% total lysine (Lys)] twice daily using a wet and dry feeder. Farrowing crates were equipped with individual heat lamps, as well as an enclosed heated creep area at the front (1.5×0.6) m). Temperature of the creep area was maintained at 30 °C until piglets had reached 1 wk of age when it was gradually reduced to 23 °C. Piglets were teeth clipped, tail docked, and given a 2-mL iron injection (Uniferon; Virbac Ltd., Suffolk, UK) within 12 h of birth. Piglets were also assigned a unique electronic ear tag to allow health and performance to be monitored on an individual basis. Piglets remained with their birthmother for a minimum of 12 h after birth to allow for colostrum intake. Cross fostering was then completed within 36 h of farrowing to establish two litters containing only 14 Low BW piglets (<1 kg) and two litters containing only 14 Av BW piglets (1.3–1.7 kg). Each litter was then randomly assigned to a foster sow. Fostered litters were designed such that no litter contained any more than three siblings and no piglets were reared by their birth mother. Litters were also balanced for sex. Each piglet was vaccinated for Mycoplasma hypopneumoniae with Ingelvac MycoFLEX and PCV2 with Ingelvac CircoFLEX (Boehringer Ingelheim Ltd, Bracknell, UK) on day 27 \pm 1. Piglets were offered no creep feed during lactation. All piglets were weaned at 28 \pm 1 d of age.

At weaning, 10 piglets were selected from each experimental litter on the basis of weight. Selection was undertaken such that the group of 10 was representative of the originating litter in terms of average weight and variation in weight. Sex remained balanced. Surplus animals were removed from trial. All trial pigs were then moved to the nursery accommodation at 28 ± 1 d of age and remained there until day 69 \pm 1. In the nursery accommodation, pigs were housed in plastic slatted pens (0.38 m² per pig), remaining in their litter group of 10. Temperature was initially fixed at 28 °C but was reduced to 18 °C in daily increments of 0.5 °C. Animals were fed using dry multispace feeders (Etra Feeders Ltd., Dungannon, UK) with an average feeding space of 6.6 cm per pig. In the nursery accommodation, feed allowance was offered on a per pen basis. The nursery dietary regime consisted of 30 kg of Starter Diet 1 (16.5 MJ/kg DE, 22.5% CP, 1.70% Lys) per pen followed by 60 kg of Starter Diet 2 (15.8 MJ/kg DE, 22.0% CP, 1.55% Lys) per pen. When each pen had consumed their starter diet allocation, a grower diet (13.5 MJ/kg DE, 17.4% CP, 0.32% Lys) was offered ad-lib to 10 wk of age.

Measurements

Sow body weight was recorded at day 108 of gestation and day 28 ± 1 of lactation (weaning). Sow back-fat depth at the P₂ position (65 mm from the midline at the level of the last rib) was also recorded using an ultrasonic scanner (Pig Scan-A-Mode backfat scanner, SFK Technology, Denmark). Lactation feed intake was recorded daily as a measure of feed offered minus any refusals. Feed allowance was managed to minimize refusals. At birth, piglets had rectal temperatures recorded using a digital thermometer (Brannan 11/064/2; ±0.1 °C; RS-Components Ltd, UK). Birth order within birth litter was also recorded for each animal. Pigs were individually weighed at birth and 7, 14, 21 and 28 d of age. A 24-h video recording was taken of each farrowing pen under trial at days 8, 15, and 22 to allow the analysis of suckling behavior. In each video, the total number and duration of suckling bouts were quantified. A suckling bout was considered to begin when at least 50% of the piglets were actively stimulating the udder and

was considered to end when more than 50% of the piglets had left the udder or were no longer actively massaging the udder (Berkeveld et al., 2007). All fallen experimental animals had a death date, weight, and cause recorded. Preweaning mortality was calculated as the percentage of the litter that died or were euthanized before weaning. Sow milk yield was calculated as piglet gain × 4.2 (van derr Peet-Schwering et al., 1998). Sow lactation efficiency was calculated by dividing sow energy input during lactation by total litter gain (kilograms) after cross-fostering, where energy input was calculated by adding the total energy intake from feed during lactation to energy gained from sow weight lost during lactation (assuming every 1 kg loss = 12.5 MJ DE; Close and Cole, 2000). When calculating sow lactation efficiency, sow empty bodyweight was calculated using the formula: sow empty weight (kilograms) = sow weight prefarrowing [day 108 (kilograms)] - (total number of piglets born × 2.28) (National Research Council, 1998). Relative growth over a given time was calculated by subtracting the initial weight from the current weight and then dividing this figure by the initial weight.

In the nursery accommodation, feed intake was manually recorded for each pen on a daily basis for the 9 d after weaning. Relative feed intake for this period was calculated as pen feed intake for a given day divided by pen weaning weight. Total pen feed intake was also recorded at days 49 and 69. The average daily feed intake (ADFI), average daily gain (ADG), and feed—conversion ratio (FCR) of all treatment groups were calculated on a per pen basis. All pigs were individually weighed at days 35, 49, and 69.

Statistical Analysis

A linear mixed model was employed to analyze pig performance at an individual and litter level (body weight, relative growth, litter gain, mortality, suckling duration, feed intake, ADG, and FCR) with replicate, birth mother or foster mother incorporated as a random effect. Birthweight and feed allowance were fitted as fixed effects, with the first order interaction forming four treatment groups. Significance was defined as P < 0.05, with tendencies defined as P < 0.1. The experimental unit for piglet weights, ADG and relative growth was the individual pig. The experimental unit for ADFI, FCR, and suckling behavior was the pen of pigs. Detailed calculations are shown in Supplementary Material S1. All statistical analysis was carried out using Genstat 16th Edition (Lawes Agricultural Trust, Rothamsted Experimental Station).

RESULTS

Sow Lactation Performance

There were no significant interactions between litter birthweight and lactation feed allowance on sow feed intake, back-fat loss, weight loss, lactation efficiency, or derived milk yield during the lactation period (Table 1). Sows offered the High FA regimen consumed an average of 42.4 kg more feed than those offered a Low FA (P < 0.001). There was no difference in sow weight loss during lactation between sows offered Low FA or High FA (P > 0.05) but absolute and percentage weight loss was significantly greater in sows rearing Av BW piglets than those rearing Low BW animals (P < 0.05, respectively). Sows rearing Av

Table 1. Effect of litter birthweight and lactation feed allowance on sow feed intake, body condition, and derived milk yield during lactation

	Low BW		Av	BW		P-value			
	Low FA	High FA	Low FA	High FA	SEM	Birthweight	Feed allowance	Birthweight × feed allowance	
Sow feed intake, kg	173.3	212.2	175	220.9	6.98	0.465	< 0.001	0.622	
Sow P ₂ loss, mm	1.96	1.68	4.25	2.69	0.571	0.009	0.122	0.275	
Prefarrowing weight, kg	267.1	254.6	255.6	272	10.03	0.773	0.849	0.165	
Postfarrowing weight, kg	254.6	248.6	230.4	252.6	10.28	0.336	0.438	0.184	
Sow weight loss, kg	12.5	6.0	25.2	19.4	6.14	0.045	0.325	0.96	
Sow weight loss, %	4.72	2.23	9.68	7.06	2.236	0.04	0.266	0.977	
Lactation efficiency	37.11	32.93	30.79	32.19	1.904	0.078	0.473	0.157	
Derived milk yield, kg									
Week 1	44.2	56.7	63.6	64.5	7.01	0.067	0.352	0.418	
Week 2	80.1	101.4	96.9	106.0	7.09	0.147	0.044	0.398	
Week 3	72.7	100.8	86.4	107.5	7.55	0.191	0.004	0.648	
Week 4	80.8	101.0	89.0	103.8	5.86	0.364	0.007	0.646	
Weeks 1-4	277.8	359.9	335.8	381.7	23.00	0.097	0.011	0.439	

BW litters also recorded significantly greater back-fat loss (P < 0.01). Milk yield was greater in weeks 2, 3, and 4 of lactation and overall from birth to weaning (P < 0.05, respectively) for sows offered a High FA compared to those offered a Low FA. Sow lactation efficiency was not affected by sow lactation feed allowance (P > 0.05). There was a tendency for sows rearing Low BW piglets to record a superior lactation efficiency (P < 0.1).

Animal Performance From Birth to 28 d of Age

No interactions between birthweight and feed allowance were significant for parameters of preweaning weight, growth rate, or mortality rate (P > 0.05; Table 2). Pigs of Av BW recorded a significantly greater rectal temperature at birth than Low BW animals (P < 0.001). Pigs of Av BW also tended to be born later in the litter (P = 0.071). Litter weight was not affected by sow feed allowance at week 1 (P > 0.05) but was significantly heavier for High FA animals at weeks 2, 3 and 4 compared to Low FA pigs (P < 0.05, respectively). Litters of Av BW were significantly heavier than those of a Low BW throughout lactation (P < 0.001). During the lactation period, litter gain was significantly greater for litters of an

Av BW (P < 0.001) and for those reared by a sow offered a High FA (P < 0.01). Preweaning mortality was significantly greater for Low BW litters than Av BW (P < 0.01) resulting in a smaller litter size weaned (P < 0.01). However preweaning mortality of Low BW animals reared on sows offered a High FA was half that of Low BW animals reared on sows offered a Low FA. Animals of a Low BW that died during lactation were lighter at time of death than Av BW mortalities (P < 0.001). However, weight and age of preweaning deaths were not affected by feed allowance (P > 0.05). Relative growth during lactation was greater for Low BW animals (P < 0.001) and for animals reared by sows offered a High FA (P < 0.001). The covariance of "within-litter" piglet weights at weaning was not affected by birthweight or feed allowance (P > 0.05, respectively).

Effect of Birthweight and Feed Allowance on Suckling Behavior

No interactive effects between birthweight and feed allowance were recorded for suckling behavior during the lactation period (P > 0.05; Table 3). Total suckling duration was significantly greater for Av BW litters than those of Low BW

Table 2. Effect of birthweight and sow lactation feed allowance on litter and piglet preweaning performance from birth until day 28

	Lov	BW	Av BW			P-value			
	Low FA	High FA	Low FA	High FA	SEM	Birthweight	Feed allowance	Birthweight × feed allowance	
Rectal temp (birth), °C	36.36	'	37.15	'	0.109	< 0.001	_	_	
Birth order	7.08		8.15		0.453	0.019	_	_	
Piglet weight, kg									
Birth	0.93	0.92	1.51	1.51	0.013	< 0.001	0.923	0.846	
Week 1	1.80	1.95	2.72	2.78	0.114	< 0.001	0.223	0.601	
Week 2	3.46	3.83	4.57	4.75	0.208	< 0.001	0.074	0.533	
Week 3	5.26	5.86	6.25	6.75	0.324	< 0.001	0.025	0.841	
Week 4	7.00	7.87	7.94	8.63	0.363	0.003	0.005	0.715	
Relative growth weaning:birth, kg/kg	6.48	7.50	4.28	4.71	0.245	< 0.001	<0.001	0.105	
Litter weight, kg									
Birth	12.8	12.9	21.1	21.2	0.11	< 0.001	0.69	0.933	
Week 1	21.8	25.0	37.8	37.8	1.26	< 0.001	0.209	0.211	
Week 2	39.4	49.3	62.4	63.0	2.50	< 0.001	0.048	0.076	
Week 3	56.6	73.3	83.1	88.6	3.84	< 0.001	0.009	0.159	
Week 4	75.6	97.4	104.5	113.2	4.89	< 0.001	0.005	0.195	
Covariance of wean weights	0.206	0.175	0.175	0.155	0.0192	0.215	0.198	0.777	
Preweaning mortality, %	22.3	11.6	6.3	6.3	3.53	0.006	0.144	0.144	
Average age of death, d	10	9	18	8	0.4	0.175	0.228	0.123	
Average weight of death, kg	1.0	1.5	2.8	2.0	0.53	< 0.001	0.712	0.078	
Litter gain, kg	62.7	84.5	83.4	92.1	4.86	0.009	0.005	0.193	
Litter size weaned	10.9	12.4	13.1	13.1	0.49	0.006	0.144	0.144	

at week 1 of lactation (P < 0.05) but there was no significant difference in suckling frequency or average bout duration (P > 0.05, respectively). Birthweight had no effect on suckling behavior at weeks 2 or 3 of lactation (P > 0.05, respectively). Feed allowance had no impact on suckling behavior at weeks 1 or 2 of lactation (P > 0.05, respectively). However, at week 3, High FA litters recorded a significantly greater total suckling duration (P < 0.001) and average bout duration (P < 0.001) but a lower suckling frequency (P < 0.01) than Low FA litters.

Pen Performance From 28 to 69 d of Age

No interactive effects between birthweight and feed allowance on live weight, ADG, ADFI, or FCR were recorded in the nursery stage (Table 4). Pigs of Av BW were significantly heavier than those of Low BW at weeks 5, 7, and 10 (P < 0.001, respectively). Pigs reared by High FA sows were heavier than those of Low FA at weeks 5 and 7 (P < 0.05, respectively) but there was no significant difference at week 10 (P > 0.05). Pig ADG was significantly greater for Av BW animals than those

Table 3. Effect of birthweight and sow lactation feed allowance on piglet litter suckling behavior during lactation

	Low	BW	Av	BW			·	
	Low FA	High FA	Low FA	High FA	SEM	Birthweight	Feed allowance	Birthweight × feed allowance
Sucklink free	quency, total bo	uts/d				,		
Week 1	43	46	50	46	2.0	0.099	0.887	0.137
Week 2	42	44	45	48	2.0	0.101	0.343	0.772
Week 3	43	36	48	38	2.5	0.24	0.005	0.561
Total sucklin	g duration, min	ı/d						
Week 1	172.1	160.1	201.7	192.8	11.43	0.019	0.379	0.89
Week 2	136.7	140.2	135.2	147.6	12.51	0.816	0.538	0.73
Week 3	129.7	151.2	130.4	172.1	5.99	0.096	< 0.001	0.117
Average bour	t duration, min/	'd						
Week 1	4.09	3.52	4.09	4.20	0.346	0.346	0.519	0.347
Week 2	3.21	3.21	2.99	3.07	0.239	0.467	0.858	0.869
Week 3	3.04	4.19	2.77	4.65	0.229	0.693	< 0.001	0.131

Table 4. Effect of birthweight and sow lactation feed allowance on piglet growth performance from weaning until day 69

	Lov	v BW	Av	BW				
	Low FA	High FA	Low FA	High FA	SEM	Birthweight	Feed allowance	Birthweight × feed allowance
Piglet weight, kg								
Week 5	7.7	8.6	8.9	9.7	0.39	< 0.001	0.005	0.89
Week 7	13.9	14.6	16.0	16.9	0.55	< 0.001	0.049	0.776
Week 10	24.4	25.3	26.8	27.8	0.79	< 0.001	0.101	0.966
Piglet weight gain weaning—10 weeks, kg	17.3	17.4	19.0	19.1	0.61	< 0.001	0.91	0.948
Relative growth week 10:week 4, kg/kg	2.53	2.22	2.53	2.23	0.140	0.958	0.006	0.911
Pig average daily gain, g								
Weeks 4–7	328	316	387	388	14.4	< 0.001	0.717	0.667
Weeks 7–10	533	535	543	546	20.0	0.502	0.861	0.995
Weeks 4–10	427	423	463	465	10.0	< 0.001	0.892	0.749
Pig average daily feed intake	e, g							
Weeks 4–7	324	321	376	379	19.4	0.012	0.982	0.887
Weeks 7–10	926	984	1060	1057	30.0	0.002	0.353	0.295
Weeks 4–10	607	632	691	698	20.0	0.006	0.498	0.717
Pen FCR								
Weeks 4–7	1.10	1.06	1.02	1.04	0.041	0.187	0.841	0.486
Weeks 7–10	1.82	1.87	1.97	1.97	0.063	0.066	0.719	0.714
Weeks 4–10	1.53	1.55	1.53	1.57	0.034	0.756	0.39	0.685

of Low BW between weeks 4 and 7 (P < 0.001) but there was no significant difference present from weeks 7 to 10 (P > 0.05). Pig ADG did not differ throughout the nursery stage between those reared by sows on High FA or Low FA (P > 0.05). Piglet weight gain from week 4 to 10 was significantly greater for Av BW pigs than those of a Low BW (P < 0.001) but feed allowance had no effect (P > 0.05). Relative growth between birth and week 4 was significantly greater for Low BW pigs (P < 0.001) and for animals reared by sows offered a High FA (P < 0.001). However, between weeks 4 and 10, there was no significant difference in relative growth of Low BW and Av BW animals (P > 0.05, respectively) and relative growth was significantly greater for animals reared by sows offered a Low FA (P < 0.01).

The ADFI per pig was greater for Av BW than Low BW animals during the growing period (P < 0.05) but did not differ between High FA and Low FA pen groups (P > 0.05). The feed intake for Av BW pens was significantly greater than those of Low BW each day in the immediate postweaning period (P < 0.05), with the exception of days 1 and 5 where there was no significant difference (P >0.05, respectively). However, when pen feed intake was calculated relative to pen weaning weight, there was no significant difference in relative feed intake between Low BW and Av BW pens (P > 0.05), with the exception of days 2 and 6 where intake was significantly greater in Av BW pens (P < 0.05, respectively; Table 5). There was no difference in daily feed intake during days 1–9 postweaning between pens of Low FA or High FA pigs (P > 0.05). Table 4 shows that between weeks 4 and 10, no differences in pen FCR were recorded between Low BW and Av BW pigs (P > 0.05) or between High FA or Low FA pen groups (P > 0.05).

DISCUSSION

Impact on Sow Condition and Performance

Sows rearing litters with an Av BW lost 13 kg more weight and 1.65 mm more back-fat than those rearing litters of a Low BW. This is in agreement with literature showing that heavier birthweight pigs increase sow weight loss during lactation (Tantasuparuk et al., 2001) and may have been caused by a greater mobilization of sow body reserves to accommodate a greater milk demand associated with heavier litters (Eissen et al., 2003). The tendency for sows rearing Low BW litters to record a greater lactation efficiency could be due to reduced fat losses, which was highlighted by Bergsma et al (2009) as a distinguishable feature of efficient sows.

Results from this study suggest that the birthweight of piglets was a greater driver in loss of sow weight and body condition than sow feed allowance, with week 1 of lactation being highlighted of significant importance. However, as expected, feed allowance was the major determinant of feed intake and derived milk yield.

Impact of Birthweight on Animal Weight, Suckling Behavior, Feed Intake, and Feeding Efficiency

In this study, the rectal temperature of Low BW animals was 0.8 °C lower than Av BW counterparts, which indicates an increased susceptibility to potentially lethal conditions, such as postnatal hypothermia, starvation, and crushing (Muns et al., 2016; Vande Pol et al., 2019). This finding is in agreement with previous work showing compromised pigs to be particularly at risk of low body temperatures in the immediate postpartum period, contributing to their increased mortality rate (Malmkvist et al., 2006). Conflicting findings relating to birthweight

Table 5. Pen daily feed intake relative to wean weight in the 9 d after weaning (days 28–			M/HOHH	1111 111	112 9 (1	1 21161	$\mathbf{L} \mathbf{W} = \mathbf{W} + $	$10131/8 /\Delta$	30° K 07 K 0 I
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	Low	BW	Av	BW				
	Low FA	High FA	Low FA	High FA	SEM	Birthweight	Feed allowance	Birthweight × feed allowance
Relative feed in	itake, g/kg							
Day 1	1.2	0.4	2.3	0.8	0.65	0.258	0.094	0.542
Day 2	2.2	3.0	9.2	5.9	1.91	0.021	0.52	0.302
Day 3	9.2	10.8	17.5	14.4	2.87	0.056	0.805	0.421
Day 4	15.3	15.7	22.6	17.9	3.00	0.134	0.488	0.41
Day 5	14.9	15.2	18.0	16.5	3.10	0.483	0.858	0.787
Day 6	19.4	17.4	24.4	21.8	2.14	0.045	0.298	0.876
Day 7	29.1	25.9	30.3	30.4	2.27	0.231	0.52	0.469
Day 8	37.6	31.9	40.8	37.4	3.37	0.214	0.198	0.744
Day 9	41.6	37.3	44.6	41.6	3.55	0.326	0.327	0.86
Days 1–9	170.3	157.6	209.6	186.6	18.12	0.079	0.342	0.781

and order are reported in literature, with initial studies indicating that piglets born later in the litter tended to be lighter (Hartsock and Graves, 1976), whereas more recent work is in agreement with this study in which birth order and birthweight were positively correlated (Beaulieu et al., 2010).

Litters of Av BW litters were significantly heavier each week throughout lactation, resulting in greater litter gain and weaning weight. These findings could suggest an innate inferiority in compromised pigs, which hinders their growth performance. However, further analysis showed Low BW animals to express a relative growth rate 1.6 times greater than those of Av BW during lactation. This demonstrates how compromised pigs may not necessarily be biologically inferior and that their lower weaning weights are purely a consequence of a low birthweight. Results here are in agreement with literature that shows a clear association between Low BW and a subsequent inferior growth rate (Douglas et al., 2014). A variety of prenatal and postnatal factors have been attributed to this. First, compromised pigs have been shown to possess fewer total and primary muscle fibers than their Av BW counterparts at birth (Rehfeldt and Kuhn, 2006), with animals relying on the increasing size of existing muscle fibers at birth for future growth. Second, multiple experiments have demonstrated a positive relationship between an increased birthweight and adoption of the more productive anterior teats, facilitating acquisition of vital energy and maternal antibodies (Cabrera et al., 2012). The effects of reduced colostrum and milk intake in disadvantaged pigs, combined with lower growth capacity due to an inferior muscle fiber network, results in lighter weights at weaning. Despite this, Low BW pigs recorded a greater relative growth than those in the Av BW groups. Hence, in spite of their already compromised nature, Low BW animals appear to "work harder" in relation to their heavier counterparts to achieve an acceptable weaning weight.

Pigs of Av BW were significantly heavier than those of Low BW at weeks 5, 7, and 10. This is in agreement with literature showing that differences in weight at weaning only increase further in the growing and finishing periods (Fix et al., 2010). These findings are partially reflected in the results from this study with the 0.9 kg difference in individual animal bodyweight of Low and Av BW pigs at weaning increasing to 1.2 kg by week 5 and 2.2 kg by week 7, showing a linear divergence during this period.

Suckling behavior of piglets is key to understand and maximize preweaning growth and development. During this trial, Av BW litters suckled for 31 min/d longer compared to Low BW litters at week 1 of lactation. This reduced total suckling duration of Low BW litters at week 1 could be linked to postnatal hypothermia, which describes the significant reduction in piglet body temperature postparturition (Tuchsherer et al., 2000). The high surface area:body weight ratio and limited body fat reserves in Low BW pigs restricts their thermoregulatory capacity, impairing vitality at birth and limiting their ability to stimulate effective milk ejection (Yuan et al., 2015; Muns et al., 2016). This can contribute to delayed colostrum uptake, as well as the reduced growth performance and increased preweaning mortality. Postnatal hypothermia can also contribute to disease, starvation, and crushing (Caldara et al., 2014). The above is in agreement with the significantly greater preweaning mortality recorded in Low BW litters compared to Av BW litters in this study, as well as the majority of these deaths occurring in the first 2 d postfarrowing. With regard to later in lactation, it was interesting that the suckling frequency, total suckling duration, and average bout duration were similar between Low BW and Av BW piglets. It is noted that by weeks 2 and 3 of lactation, only the strongest of the Low BW had survived and these animals were able to adequately stimulate the udder and suckle in a manner similar to their Av BW counterparts.

This trial showed that the feed intake of Av BW pens of pigs was greater than that of Low BW pens in seven of the nine immediate postweaning pig weighings, which mirrors findings in literature (Cabrera et al., 2010). Whilst piglets of all birthweights can struggle to adapt to solid feeding, impairment of gastrointestinal development and digestive capacity have been shown to be more pronounced in low weight pigs (Pluske et al., 2003). It is possible that this contributed to the reduced postweaning feed intake of Low BW animals in the current study. When calculated relative to weaning weight, Av BW pigs only recorded a significantly greater relative feed intake on two of the nine immediate postweaning pig weighings. This illustrates how Low BW must actually outperform heavier littermates in order to attain an "average" level of performance. Whilst disadvantaged pigs have been found to display an inferior FCR than heavier littermates postweaning (Gondret et al., 2006), this was not observed in the current study.

Impact of Lactation Feed Allowance on Animal Weight, Suckling Behavior, Feed Intake, and Feeding Efficiency

It is accepted that the Low FA regime employed in this study offered a greater daily feed intake to sows than that shown to achieve satisfactory litter growth in previous studies (Sulabo et al., 2014; De Bettio et al., 2016). However, it must be recognized that previous work has been conducted on significantly smaller litter sizes than that employed in the current study, increasing the nutrient requirements of the sow. Furthermore, a key aim of this study was to determine whether improving sow intakes beyond levels seen commercially would significantly improve litter growth. By extrapolating the nutrient requirements of lactating sows outlined by Whittemore (2003), it is predicted that sows rearing a litter of 14 piglets, with similar birthweights to that recorded in the current study, over a 28-d lactation and targeting an average weaning weight of 8 kg (339 g/d litter growth rate) would require a DE intake of 131.5 MJ/d and a total Lys intake of 90 g/d. In the current study, Low FA sows recorded a DE intake of 90 MJ/d and total Lys intake of 75 g/d. In contrast, High FA sows recorded a DE intake and total Lys intake of 112 MJ/d and 93 g/d, respectively. As such, Low FA sows only met 68% of the recommended DE intake and 83% of the recommended total Lys intake. In contrast, High FA sows consumed 85% of the recommended DE requirements and exceeded the recommended Lys intake by 3%. The performance of the litters reared by sows offered each regime was, therefore, as expected per the requirements outlined by Whittemore (2003), with High FA piglets recording a 10% greater weaning weight on average compared to Low FA pigs.

During week 1 of lactation, sow feed allowance was similar for both regimes offered. This, in combination with sow body reserves dictating the rate of milk production during early lactation (Beyer, 2007), explains the equivalent weight of litters in this trial at week 1 regardless of sow lactation feed allowance. However, as lactation progressed, it would appear that the reduced feed intake and, hence, energy and Lys intake in sows offered a Low FA was a limiting factor for the growth of piglets in these litters. Whilst mobilization of sow body fat reserves can help meet the nutrient requirements of milk production (Quesnel et al., 1995; Beyer, 2007), results indicate that this was not sufficient to match the litter growth achieved in litters reared by sows with a High FA. It is likely that the demand placed

on the sow for milk dramatically increased during this period, depleting body reserves and forcing the mother to become reliant on feed intake for milk production. Indeed, sows offered a High FA were able to generate a greater derived milk yield during weeks 2, 3, and 4 of lactation, supporting increased weights and weight gains on both an individual and litter basis at weaning.

In the current study, the impact of lactation feed allowance on postweaning growth trajectory became less pronounced as animals grew. Despite the 0.85 kg weight advantage held by High FA animals being significant at week 5, this only increased to 0.96 kg at week 10 where heavier animal weights meant that this differential was no longer significant. This concurs with literature showing that the preweaning benefits of lactation intervention confer no advantage on postweaning growth performance (Douglas et al., 2014). Although Wolter et al. (2002) found that animals offered superior lactation nutrition expressed superior ADG and ADFI postweaning, this was not the case during the current experiment. It is interesting to note that relative growth from weaning to 10 wk of age was significantly greater for animals reared by sows offered a Low FA. This may be explained by a phenomenon known as compensatory growth whereby animals exhibit an accelerated growth rate after a period of restriction (Heyer and Lebret, 2007).

The increased milk yield recorded by High FA sows in later lactation could explain the suckling behavior of litters at week 3. Indeed, the longer, yet less frequent, suckling bouts recorded for High FA litters compared to Low FA litters during late lactation indicate a greater success rate in udder stimulation (Beyer, 2007). Conversely, the behavior of Low FA litters suggests that these animals exhausted sow milk resources, resulting in premature termination of the suckling bout.

Whilst no significant interactions between birthweight and feed allowance were found during this study, it was interesting from a commercial standpoint to note that Low BW litters reared by sows offered a High FA recorded half the mortality of those with an equivalent birthweight reared on sows offered a Low FA, resulting in extra 1.5 piglets weaned per litter. Although the average age of Low BW preweaning deaths was not affected by sow feed allowance, 40% of mortalities for Low BW pigs on sows offered a Low FA occurred after the first week of lactation. In contrast, only 23% of mortalities for Low BW animals on sows with a High FA occurred after week 1 of lactation. It could be suggested that the increased feed intake

and, hence, milk yield of sows offered a High FA promoted the survival of Low BW pigs as lactation progressed, ensuring a greater number reached weaning. In addition, Low BW pigs on a High FA sow numerically matched the weaning weight of heavier counterparts reared under commercial conditions. This could suggest that rearing Low BW pigs on sows offered a High FA may help to minimize weight variation at weaning compared with heavier birthweight animals.

CONCLUSION

This study has shown that the careful management of sow feeding during lactation can markedly increase feed intake and facilitate greater milk yields. This represents an opportunity commercially to maximize the weaning weights of all piglets, including low birth weight piglets. Furthermore, improved sow lactation nutrition can significantly reduce preweaning mortality of low birthweight animals. This, in turn, will greatly increase the number of animals weaned, improving output and profitability at farm level.

SUPPLEMENTARY DATA

Supplementary data are available at *Translational Animal Science* online.

Conflict of interest statement. The authors declare there are no conflicts of interest.

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