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Running head: Compensatory feeding in gestating sows

Compensatory feeding during early gestation for sows with a high weight loss after a summer lactation increased piglet birth weight but reduced litter size[1,2]

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ABSTRACT

Sows mated in summer produce a greater proportion of born-light piglets (<1.1 kg) which contributes to increased carcass fatness in the progeny population. The reasons for the low birth weight of these piglets remain unclear, and there have been few successful mitigation strategies identified. We hypothesized that: (1) the low birth weight of progeny born to sows mated in summer may be associated with weight loss during the previous summer lactation; and (2) increasing early gestation feed allowance for the sows with high lactational weight loss in summer can help weight recovery and improve progeny birth weight. Sows were classified as having either low (av. 1%) or high (av. 7%) lactational weight loss in their summer lactation. All the sows with low lactational weight loss (LLStd) and half of the sows with high lactational weight loss received a standard gestation feeding regime (HLStd) (2.6 kg/d; d 0-30 gestation), whereas the rest of the sows with high lactational weight loss received a compensatory feed allowance (HLComp) (3.5 kg/d; d 0-30 gestation). A comparison of LLStd (n=75) vs HLStd sows (n=78) showed that this magnitude of weight loss over summer lactation did not affect the average piglet or litter birth weight, but such results may be influenced by the higher litter size ($P = 0.032$) observed in LLStd sows. A comparison of HLStd vs HLComp (n=81) sows showed that the compensatory feeding increased ($P = 0.021$) weight gain of gestating sows by 6 kg, increased ($P = 0.009$) average piglet birth weight by 0.11 kg, tended to reduce ($P = 0.054$) the percentage of born-light piglets from 23.5% to 17.1% but reduced the litter size by 1.4 ($P = 0.014$). A sub-group of progeny stratified as born-light (0.8-1.1 kg) or -normal (1.3-1.7 kg) from each sow treatment were monitored for growth performance from weaning until 100 kg weight. The growth performance and carcass backfat of progeny were not affected by sow treatments. Born-light progeny had lower feed intake, lower growth rate, higher G:F, and higher carcass backfat than born-normal progeny (all $P < 0.05$). In summary, compensatory feeding from d 0-30 gestation in the sows with high weight loss during summer lactation reduced the

percentage of born-light progeny at the cost of a lower litter size, which should improve growth rate and carcass leanness in the progeny population born to sows with high lactational weight loss.

Key Words: backfat, birth weight, feeding, gestation, sows, summer

List of Abbreviations

ADG, average daily gain; ADFI, average daily feed intake; BA; born alive piglets; CV, coefficient of variation; DE, digestible energy; G:F, gain: feed; HOMA-IR, homeostatic model assessment of insulin resistance; IGF-1, insulin -like growth factor 1; MUM, mummified fetuses; SB, stillborn piglets; TB, total number of piglets born.

INTRODUCTION

Carcass backfat of finisher pigs peaks in late winter and spring (Trezona et al., 2004). This seasonal increase in carcass fatness creates complications for pig producers in the supply of consistent pork products to markets where high backfat is penalized. As a novel explanation of the seasonality of carcass fatness, our recent study showed that sows mated in summer produce a greater proportion of born-light piglets (≤ 1.1 kg) than those mated at other times of the year, which contribute to the higher carcass fatness observed in the following spring (Liu et al., 2020). However, reasons for the greater proportion of born-light piglets born to sows mated in summer remain unclear and thus no mitigation strategies have been developed. Excess lactational weight loss during summer may contribute to reduced progeny birth weight in the subsequent parity, as weight loss is common in sows during a summer lactation (Renaudeau et al., 2003; Liu et al., 2020), and severe lactational weight loss can reduce embryo development in the subsequent gestation (Vinsky et al., 2006). To understand the influence of lactational weight loss during summer on subsequent piglet birth weight and carcass fatness, we categorized weaned sows based on lactational bodyweight loss over summer (high vs low) and compared their progeny's birth weight, lifetime growth performance (stratified as born-light vs -normal) and carcass backfat. Additionally, sows classified as having high lactational weight loss, and that received either a standard or a compensatory gestation feeding regime during early gestation, were compared. We hypothesized that (1) sows that had high lactational weight loss in summer would have a greater proportion of born-light piglets than those that had low lactational weight loss; (2) increasing feed allowance during d 0-30 gestation for the sows that had high lactational weight loss would reduce the proportion of born-light piglets thus reducing carcass backfat in their progeny population.

MATERIALS AND METHODS

Animals and Experimental Design

All procedures that involved animals in the current experiment were in accordance with the Australian Code for the Care and Use of Animals for Scientific Purposes (8th edition, 2013), and the protocol (ID:18N079C) was approved by the Animal Ethics Committee of Rivalea Australia Pty Ltd, Corowa, NSW, Australia.

A flowchart of the experimental design is illustrated in Fig. 1. The lactation period for sows included in the study was between the 5th February and the 27th March 2019 (summer dry season in southern Australia). The daily outdoor maximum temperature was 29.8 ± 4.70 °C and 26.2 ± 4.43 °C (mean ± standard deviation) for the summer lactation period and the first month of the subsequent gestation period, respectively. The relative humidity was 45 ± 15.8% and 54 ± 15.9% (mean ± standard deviation) for the summer lactation period and the first month of the subsequent gestation period, respectively. Data were retrieved from the Bureau of Meteorology, Australia (Station ID: 074034). Lactating sows were weighed on the third day post-farrowing and at weaning so that the maternal bodyweight loss could be calculated. Sows were ranked by lactational weight loss from low to high within each parity. The top 33% of sows in the rank from each parity were allocated to the low lactational weight loss group and received a standard feeding regime (2.6 kg feed/d as fed basis in the first 30 d of gestation; **LLStd**; n=96 sows). The rest of the sows in each parity group were allocated to the high lactational weight loss group. This group was then randomly and evenly split, with half the group receiving a standard feeding regime similar to the low lactational weight loss group (**HLStd**; n=102 sows); with the other half receiving a compensatory feeding regime (3.5 kg feed/d during the first 30 d of gestation; **HLComp**; n=102 sows). Sows that had a reproductive failure or health issues were removed from the experiment, resulting in n=75 LLStd sows, n=78 HLStd sows, and n=81

HLComp sows farrowing in the subsequent parity. A frequency chart of lactational bodyweight change of LLStd, HLStd and HLComp sows that farrowed in the subsequent parity is illustrated in Supplementary Fig. 1. The standard feeding levels for gestating sows on the farm were developed based on the energy and amino acid requirements recommended by NRC (2012). All sows were restrictively fed 2.0 kg/d from d 31 until d 90 of gestation and then 2.4 kg/d from d 91 until farrowing. The increased feeding amount was designed to allow sows to recover approximately 14 kg maternal bodyweight within 30 d post-mating. The following parameters were entered in the nutrition model for gestating sows (NRC, 2012) for calculating the amount of feed required: digestible energy content (3,128 kcal/kg), fermentable fiber content (9.0%), sow bodyweight at breeding (252 kg), parity (4), gestational length (115), anticipated litter size (12), anticipated birth weight (1.50 kg), feed wastage (5%). Early gestation was chosen for compensatory feeding as it was expected that the extra nutrients during this period would help sows recover from lactation weight loss sooner and thus spare nutrients for fetal development. For example, an early study showed that increasing early gestation feeding allowance from 2.50 kg to 3.25 kg for young parity sows improved the recovery of sow bodyweight loss and increased litter size in the subsequent parity (Hoving et al., 2011). Mid or late gestation was not chosen, because increasing feeding levels during mid (Lawlor et al., 2007) and late gestation (Mallmann et al., 2019) were reported to increase the number of stillborn piglets. All the sows were housed in groups and fed *ad libitum* during the weaning-to-estrus interval, then the sows were mated using post-cervical artificial insemination at the first detected estrus post-weaning. The gestation shed was naturally ventilated with an uninsulated roof. Cooling equipment such as fans and water sprinklers were installed in the gestation shed and were automatically operated when air temperature increased beyond 28 °C. The gestation diet contained 13.1 MJ/kg digestible energy (DE) and 0.54% standardized ileal digestible lysine (Supplementary Table 1). The sows from the three gestation treatments were mixed in pens of 40 during gestation. Sows were fed using electronic sow feeders whilst in the gestation pens, with each feeding station (40 sows per feeding station) allowing for individual feeding. Bodyweight and backfat thickness were recorded at weaning, d 0, 30, 60 and 108 of gestation. The backfat thickness of sows was measured using an ultrasound machine (CTS-900 V; Shantou Institute of Ultrasonic Instruments, Shantou, Guangdong, China) at the P2 site (65 mm from the midline over the last rib). Twenty-four gestating sows (n=8 sows per gestational treatment; two sows from parity 2, 3, 4 and 5 were randomly selected for each gestational treatment) were monitored for physiological signs of heat stress including respiration rate and rectal temperature at 09:00 h and 16:00 h one day per week until the fifth week of gestation (Supplementary Fig. 2 A and B). On d 108 of gestation, all the sows were moved to farrowing houses. Sows farrowed in an individual farrowing crate, and the number of piglets born-alive, stillborn piglets, and mummified fetuses were recorded within the first 24 h post-farrowing. Meanwhile, the newborn piglets were individually weighed using a digital scale. The birth weight of live and stillborn piglets was individually recorded for all litters.

Progesterone Measurement in Gestating Sows

Blood samples were obtained from 15 sows from each treatment group (three sows from parity 2, 3, 4, 5 and 6 were randomly selected) via jugular venipuncture on d 30, 60 and 90 of gestation. Blood samples were collected in heparinized vacutainers (BD Vacutainers, 4 mL, Item Number 367883, BD Diagnostics, Preanalytical Systems, Oxford, UK) and then plasma samples were separated after centrifugation at 1600 × *g* for 10 min at 4°C (Heraeus Megafuge 16R, Item Number 50122064, Thermo Fisher Scientific, North Ryde, NSW, Australia). The plasma samples were stored at -20 °C and later used to measure progesterone concentrations using a commercial kit (Progesterone enzyme-linked immunosorbent assay kit, Item Number 582601, Cayman Chemical, Ann Arbor, MI, USA). The assay was conducted in duplicate, and the intra- and inter-plate CV were 8.2% and 18.1%, respectively.

Blood IGF-1 Measurement in New-born Piglets

Blood samples were taken from new-born piglets via jugular venipuncture at 24 h after birth (n=20 born-light and n=20 born-normal piglets from each sow treatment group; half male and half female pigs). The blood sample was collected via heparinized vacutainers (BD Vacutainers, 4 mL, Item Number 367883, BD Diagnostics, Preanalytical Systems, Oxford, UK) and a drop of whole blood sample was stained on an IGF-1 sample card (Primegro, Corowa, NSW Australia). The measurement of blood IGF-1 concentration was conducted in singlicate and completed in one assay (Quantikine Human IGF-1 immunoassay kit, Item Number SG100B, R and D Systems, Minneapolis, MN, USA).

Growth Performance and Carcass Traits of Progeny Pigs

Born-light piglets and born-normal piglets were defined as those that weighed between 0.8 kg and 1.1 kg and between 1.3 kg and 1.7 kg, respectively, on the first day after birth. No more than one born-light and one born-normal piglet from a litter were selected and ear-tagged, and sex was balanced in the tagged pigs. Six progeny treatment groups were formed: three sow treatments (LLStd, HLStd and HLComp) × two birth weight classes of progeny (born-light and born-normal). On the weaning day (24 ± 2.9 d age for mean ± standard deviation), 16 male (uncastrated) and 16 female piglets were randomly selected from the tagged piglets in the six progeny treatment groups and then housed in the weaner facility (4-10 weeks of age). Birth weights of the selected weaners were similar among treatment groups within each birth weight class. Piglets were housed two per pen (1.8 × 0.8 m^2) within sow treatments and birth weight class during the weaner phase, resulting in 16 born-light pens and 16 born-normal pens for each sow treatment group (half number of male and half number of female pens). A pen was classed as an experimental unit for studying growth performance during the weaner phase (n=96 pens in total). One born-normal pen and one born-light pen from the LLStd group were removed from the weaner phase of the experiment due to health issues. The weaner shed was climatically controlled, and the temperature was set at 28°C in the first week then decreased by 2°C weekly until 10 weeks of age.

At 10 weeks of age, each weaner pen contributed at least one pig for the grower/finisher phase (from 10 weeks of age to approximately 100 kg live weight). Fifty-four born-light and 54 born-normal pigs were selected from the weaner shed and then moved to the grower/finisher facility and housed individually (n=18 born-light and 18 born-normal pigs for each sow treatment group; half were male and half were female pigs;). A pig was the experimental unit during the grower/finisher phase of the experiment (n=108 pigs in total). Each individual grower/finisher pen was 2.35 × 1.77 m^2. A total of seven pigs were removed from the grower/finisher phase of the experiment due to health issues. The shed for the grower/finisher phase was semi-climatically controlled. The cooling system including water fans and water drippers, which were activated when the air temperature exceeded 30ºC. The air temperature was recorded every hour using a temperature logger (Hygrochron, Item Number DS1923, OnSolution Pty, Baulkham Hills, NSW, Australia). The air temperature inside the grower/finisher shed was 22.0 ± 3.51ºC (mean ± standard deviation). Feed delivery, refusal, and bodyweight were recorded weekly. Average daily feed intake (ADFI), growth rate (ADG), and gain: feed ratio (G:F) were calculated separately for the weaner and grower/finisher phases. Pigs had *ad libitum* access to water and feed in all production phases. Pigs were sent to a commercial abattoir when they reached approximately 100 kg liveweight. Hot standard carcass weight (Australian Trim 1 standard (Australian Pork Limited, 2018), visceral tissues off, head on and trotters on), backfat thickness (P2 site: 65 mm from the midline over the last rib; Hennessey Chong's probe method), and loin depth (P2 site; Hennessey Chong's probe method) were recorded for each pig.

Fasting Glucose and Insulin in Progeny Pigs

A blood sample was taken from a sub-group of pigs (n=10 born-light and 10 born-normal pigs randomly selected from each sow treatment; half were female and half were male pigs) when they reached 18 weeks of age. The pigs were fasted from 15:00 h until blood sampling at 09:00 h the next morning. Blood was collected via jugular venipuncture using heparinized vacutainers (BD Vacutainers, 4 mL, Item Number 367883, BD Diagnostics, Preanalytical Systems, Oxford, UK), and then plasma samples were separated after centrifugation at 1600 × *g* for 10 min at 4°C (Heraeus Megafuge 16R, Item Number 50122064, Thermo Fisher Scientific, North Ryde, NSW, Australia). Plasma samples were analyzed for glucose and insulin. One sample from a born-normal pig born to the HLComp was lost before analysis. Glucose was measured in duplicate in one assay using a glucose oxidase kit (Infinity, Item Number TR15221, Thermo Fisher Scientific, Waltham, MA, USA) with an intra-assay CV of 1.7%. Insulin was measured in duplicate in one assay using a porcine insulin radioimmunoassay kit (Item Number PI-12K, EMD Millipore Corporation, St Louis, MO, USA) with an intra-assay CV of 2.5%. Homeostatic Model Assessment of Insulin Resistance (HOMA-IR) was calculated using the following equation (Matthews et al., 1985; Liu et al., 2017):

$$HOMA-IR = Fasting\ glucose\ concentration\ (mmol\ per\ litre)\ /22.5 \times Fasting\ Insulin\ concentration\ (micro\ units\ per\ litre)$$

Statistical Analysis

Retrospective data on lactation performance during summer and the subsequent farrowing outcomes of sows were analyzed using the UNIVARIATE procedure of SPSS (IBM SPSS Statistics for Windows, v25, Armonk, NY, USA) for the main effect of sow treatments (LLStd, HLStd and HLComp) with the parity of sows (defined as 2, 3, 4, 5, 6, 7 and 8+) as a blocking factor. The percentage of piglets that weighed ≤ 1.1 kg at birth and the within-litter coefficient of variation (CV) were calculated for each litter, and the data were analyzed using the above statistical method with and without litter size as a covariate. Growth performance and carcass traits of progeny pigs were analyzed using the UNIVARIATE procedure for the main effects of sow treatments, piglet birth weight class (born-light vs born-normal), and their interactions with the sex of progeny as a blocking factor. Fisher's Least Significance Difference test was used for comparing LLStd vs HLStd and HLStd vs HLComp among the sow treatments. Continuous outcome variables are presented as mean ± standard error (SE). Farrowing rate of sows (defined as farrowed or not farrowed) was analyzed by Pearson's *Chi*-square analysis and reported as a percentage of the total distribution. Means were considered to be significantly different when $P \leq 0.05$, and a trend was considered to exist when $P \leq 0.10$.

RESULTS

Retrospective Data Analysis on Summer Lactation Performance of Sows

As expected, the sows allocated to the LLStd group had less lactational weight loss than the sows allocated to high weight loss groups (-3.1 kg, -18.9 kg and -19.4 kg for LLStd, HLStd, HLComp groups respectively; $P < 0.001$) as sows were allocated to these treatments based on this variable (Table 1). The parity of sows, body weight measured on the third day of lactation, and change in backfat thickness of sows were similar ($P > 0.10$) among the treatment groups. Retrospective analysis of lactation performance data from the three treatment groups showed that the lactation length, average daily feed intake, number of piglets post-foster, number of piglets on the third day of lactation, number of piglets weaned, and litter weight gain were all similar ($P > 0.10$) among treatment groups. The total number of piglets born to the sows (at the start of the summer lactation) that classified as LLStd was greater ($P = 0.030$) than those born to the groups classified as HLStd. Similarly, the number of piglets born alive (at the start of the summer lactation) from the LLStd sows was greater ($P = 0.016$) than from the HLComp sows. Our further analysis showed that the bodyweight change of sows over the summer lactation was positively correlated with the total number of piglets born before the summer lactation (linear, $r^2 = 0.038$. $P = 0.004$; data are not shown). The number of total piglets born and the number of piglets born alive were both similar ($P > 0.10$) between HLStd and HLComp sows before the summer lactation.

Body Condition Change of Sows During Gestation

The LLStd sows had a higher body weight at weaning than HLStd and HLComp sows ($P = 0.011$) (Table 2). On d 0 of gestation, sows with high lactational weight loss that were destined to receive compensatory feeding during early gestation tended to be lighter than the sows with low weight loss ($P = 0.068$). Bodyweight measured on d 30 and d 108 was not different among treatment groups. Bodyweight gain between d 0 and d 30 of gestation was greater in HLComp sows than in LLStd and HLStd sows (both $P < 0.05$). After the period of compensatory feeding, body weight gain of sows between d 30 and d 108 was similar among treatments. Backfat thickness measured at weaning, d 0, 30 and 108 of gestation did not differ among the treatments. Change in backfat thickness from weaning to d 0, d 0 to 30, or d 30 to 108 of gestation were not significantly different ($P > 0.10$) between the LLStd and HLStd sows. A planned comparison showed that the increase in backfat thickness from d 30 to 108 and d 0 to 108 of gestation were greater in the HLComp sows than in the HLStd sows (both $P < 0.05$).

Plasma Progesterone of Gestating Sows

Plasma progesterone concentrations did not significantly differ ($P > 0.10$) among the sow treatment groups (Fig. 2). The plasma progesterone concentration was lower at d 30 compared with d 60 and d 90 of gestation (Day, $P < 0.001$). The interaction between the sow treatment group and the day of gestation was not significant ($P > 0.10$).

Farrowing Outcomes of Sows Mated After a Summer Lactation

The farrowing rate was similar ($P > 0.10$) among sow treatment groups (Table 3). The gestation length of HLComp sows was longer than that of HLStd (116.4 vs 115.9 d, $P = 0.046$), whereas LLStd and HLStd had the same gestation length (both 115.9 d). The total number of piglets born to HLComp sows was lower than that of HLStd sows (13.0 vs 14.4, $P = 0.015$). The total number of piglets born was lower in HLStd sows than in LLStd sows (14.4 vs 15.9, $P = 0.032$). The number of piglets born alive was not significantly different ($P = 0.16$) between HLStd and HLComp sows, and this number was not different ($P > 0.10$) between HLStd and LLStd sows. The number of stillborn piglets was lower in litters from HLComp sows than in those from HLStd sows (0.9 vs 1.6, $P = 0.009$), and HLStd sows had a lower number of stillborn piglets than did LLStd sows (2.4 vs 1.6, $P = 0.010$). The number of mummified fetuses was not affected by sow treatment (P > 0.10). Litter birth weight (including stillborn piglets) was similar (P > 0.10) among sow treatment groups. Average piglet birth weight (including stillborn piglets) was greater in HLComp sows than HLStd sows (1.49 vs 1.37 kg, P = 0.009), but there was no difference (P > 0.10) between LLStd and HLStd sows. The HLComp sows tended to have a lower within-litter percentage of born-light (≤ 1.1 kg) piglets than HLStd sows (17.1% vs 23.5%, P = 0.054), whereas there was no significant difference between the LLStd sows and HLStd sows (P > 0.10). The effect of sow treatments on the percentage of born-light piglets in the litter diminished when the sum number of the current born alive and stillborn was used as a covariate. The within-litter CV of progeny birth weight was not affected (P > 0.10) by the treatment groups of sows whether or not if the sum of the current born alive and stillborn was used as a covariate.

Blood IGF-1 of Progeny at Birth

Blood IGF-1 concentration of the selected progeny pigs was not affected by sow treatment (Fig. 3). Born-light progeny pigs had lower blood IGF-1 concentrations than born-normal piglets (24.9 vs 36.5 ng/mL, P < 0.001). The interaction between sow treatment and progeny birth weight class was not significant (P > 0.10).

Progeny Growth Performance

Sow treatment did not significantly affect weaning weight, ADFI, ADG or G:F of progeny pigs during the weaner phase (4-10 weeks age; $P \geq 0.10$) (Table 4). Born-light progeny had a lower weaning weight (5.78 vs 7.92 kg), ADFI (620 vs 762 g), ADG (445 vs 519 g), and 10-week bodyweight (25.4 vs 30.8 kg) and a higher G:F (0.73 vs 0.69) than born-normal progeny pigs (all P < 0.01). The interaction between sow treatment and progeny birth weight class was not significant (P > 0.10) for any of the above measurements.

Sow treatment did not affect ADFI, ADG, G:F or days required to reach 100 kg live weight during the grower/finisher phase (10 weeks of age to slaughter) (Table 5). Born-light progeny were lighter than born-normal progeny (26.4 vs 30.8 kg; $P < 0.001$) at entry to the grower/finisher facility. Born-light progeny had a lower ADFI (2.08 vs 2.41 kg), lower ADG (937 vs 1032 g) and higher G:F (0.46 vs 0.43) than born-normal progeny (all $P < 0.01$) during the grower/finisher phase (10 weeks of age to slaughter). Born-light progeny took more days from birth to reach a 100 kg live weight than born-normal progeny (148.8 vs 138.8 d; $P < 0.001$).

Carcass Traits of Progeny

Dressing percentage and hot standard carcass weight were similar ($P > 0.10$) among sow treatments and between progeny birth weight classes (Table 6). Backfat thickness was not significantly affected by sow treatment ($P > 0.10$). Born-light pigs had a greater backfat thickness than born-normal pigs (14.9 vs 13.9 mm, $P = 0.049$; 78.0 kg carcass weight was used as the covariate for every pig). Loin depth was not affected by sow treatments or progeny birth weight class ($P > 0.10$). The interaction between sow treatment and progeny birth weight class was not significant $P > 0.10$) for any of the carcass traits measured.

Fasting Glucose and Insulin of Progeny

Plasma concentrations of fasting glucose, insulin and the calculated HOMA insulin resistance index were not affected by sow treatment, progeny birth weight class or their interactions ($P > 0.10$; Table 7).

DISCUSSION

Understanding the reason for a higher proportion of born-light piglets born to sows mated in summer will help to develop strategies that may improve growth performance and reduce carcass fatness of these progeny. The current experiment had two important findings. First, these data showed that the litter birth weight, average piglet birth weight, progeny growth performance and carcass backfat of progeny pigs did not differ between sows that were classified as HLStd (average 7% weight loss) and LLStd (average 1% weight loss). Cautions need to be taken when interpreting the birth weight results from the comparison between LLStd and HLStd sows, because the LLStd sows had higher litter size, which potentially influenced the birth weight. Second, increasing feeding allowance from 2.6 to 3.5 kg/d during d 0-30 gestation for the sows within the high lactational weight loss group improved average piglet birth weight from 1.41 kg to 1.52 kg, and reduced the percentage of born-light piglets (≤ 1.1 kg) from 23.5% to 17.1%, at a cost of reduced litter size. As expected, born-light progeny had a poorer growth rate and higher carcass backfat thickness than born-normal progeny during their lifetime. Although the progeny growth performance or carcass traits stratified by birth weight class did not differ between HLStd and HLComp sows, the reduction in the proportion of born-light progeny through compensatory feeding should improve the overall growth performance and carcass leanness of the progeny population that born to the sows with high lactational weight loss.

Providing those high lactational weight loss sows an increased amount of feed in the first 30 d of gestation improved average birth weight, but at the cost of reduced litter size, when compared to HLStd sows. Specifically, it reduced the percentage of born-light piglets from 23.5% to 17.1%, increased average piglet birth weight from 1.37 to 1.49 kg. Although growth performance of progeny (stratified by birth weight class) was not affected by the sow treatment group, the reduction in the proportion of born-light piglets should improve the overall growth performance and carcass leanness in the progeny population because, as shown in our current experiment, the born-light piglets had 9% lower growth rate, required an extra 10 d to reach 100 kg and had a 1.0 mm greater carcass backfat thickness (at a fixed weight) compared with the born-normal pigs. In some countries, including Australia, a 1.0 mm increase in carcass backfat thickness can attract significant penalties on the whole carcass value (Morgan, 2019), so the high carcass backfat in the born-light pigs can be an economic concern in some pig industries. The reduction in the proportion of born-light piglets through compensatory feeding diminished when using litter size as a covariate in the statistical model, and the litter birth weight was similar between the two feeding levels, suggesting that the improvement of average birth weight was due to the reduced litter size.

The reduction in litter size (from 14.4 to 13.0) in the sows received the compensatory feeding was in agreement with a recent study that found increasing feeding levels from 2.5 to 3.2 kg from d 6 to 30 of gestation reduced the number of total born from 14.6 to 13.5 (Mallmann et al., 2020). The number of piglets born alive was not significantly affected by the compensatory feeding in the current experiment (12.5 and 11.7 for HLStd and HLComp). However, the numerical difference should draw attention, because the non-significant difference might be due to the limited sample size and high variance in this study. Retrospective data analysis showed that the body weight gain of gestating sows was negatively related to the total number of piglets born in the subsequent parity (Wientjes et al., 2013). In our experiment, the HLComp sows gained 7.4 kg and 5.9 kg more weight than HLStd sows during 0-30 d of gestation and the whole gestation period, respectively. It may be that the reduction in litter size seen in the current study was due to the reduced embryo survival rate which was associated with high feed allowance during early gestation (discussed below).

The effects of feeding levels on embryo survival rate varied in previous studies. Some early studies showed that a high feeding level during early gestation can reduce circulating progesterone concentration and negatively impact embryo survival rate in sows (Jindal et al., 1997; Virolainen et al., 2005; De et al., 2009). The reduction in circulating progesterone as a result of a high feeding level was believed to be caused by increased progesterone clearance by the liver (Prime and Symonds, 2009). In the current experiment plasma progesterone concentrations measured on d 30, 60 and 90 during gestation were not affected by increased feeding levels, but this may be because the sampling day points were not early enough to reflect the difference in progesterone concentrations in sow treatment groups. For example, the reduction in venous progesterone concentration was observed in the sows that received high feeding allowance (52 MJ DE/d vs 26 MJ DE/d from d 0-35 of gestation) during the first 15 d of gestation then the reduction diminished afterward (Virolainen et al., 2005). Conversely, some studies showed that litter size was not reduced in young parity sows that received additional feeding during early gestation. For example, high feeding levels in gilts during early gestation did not affect embryo survival rate, and the ovary-produced progesterone increased in the local circulation although peripheral progesterone was reduced (Athorn et al., 2012). Hoving et al. (2011) reported that increasing feeding levels from 2.50 kg to 3.25 kg from d 3 to 32 of gestation increased subsequent litter size from 13.2 to 15.2 in parity 1 and 2 sows with a 10% lactational weight loss. The HLStd and HLComp sows used in our current experiment had a similar magnitude of bodyweight loss as the above study (7%) but these results were observed in higher parity sows (parity 2 to 8), so the disparity of the results may be due to the different parity structure used in the experiments. The inconsistent results may also be due to the different genetics used in various studies. It may be worthwhile to revisit the relationship between early gestational feeding levels and litter size in various modern genetics.

The disadvantage in lifetime growth performance of born-light piglets agreed with results from previous studies (Beaulieu et al., 2010; Liu et al., 2020). The observation that born-light pigs finished with greater carcass fatness than born-normal pigs is also supported by previous studies (Bee, 2004; Schinckel et al., 2010; Liu et al., 2020). A compromised somatotropin-IGF-1 axis in the born-light piglets may explain their poorer lifetime growth performance and increased adiposity. Similar to previous reports (Schoknecht et al., 1997; Liu et al., 2020), the current study showed that the born-light piglets had 50% lower blood IGF-1 concentration at birth compared with the born-normal pigs. The increased carcass adiposity of the born-light piglets was unlikely to be caused by insulin resistance, because fasting glucose, insulin concentration, and HOMA-insulin resistance index that were measured at 18 weeks of age were not affected by birth weight class of progeny in the current study. Similarly, Poore and Fowden (2004) found no difference in fasting insulin or glucose concentrations between low and high birth weight piglets (average 1.13 vs 1.90 kg birth weight) at three months age, but rather these indicative measurements of insulin sensitivity were found to be correlated with postnatal growth. The greater adiposity of born-light progeny may also be a consequence of changes to dietary energy partitioning. Although born-light progeny had a lower ADFI compared to born-normal progeny, the relative partitioning of net energy to adipose versus muscle may have been greater in these pigs due to their lower capacity for muscle deposition (Powell and Aberle, 1981; Gondret et al., 2005). Partitioning energy towards increased fat deposition at a given energy intake usually results in lower feed efficiency (G:F) (Campbell and Taverner, 1988; Schinckel et al., 2008), because more energy is required for depositing one gram of fat than lean tissue (considering lean tissue consists of approximately 70% water; energy requirements for fat and protein deposition are referenced from Tess et al. (1984)). But, interestingly, the born-light progeny exhibited a greater feed efficiency than the born-normal ones even their carcasses were fatter in the current experiment. Similar findings have recently been reported elsewhere (Camp Montoro et al., 2020; Hawe et al., 2020). The reason for the greater feed efficiency in the born-light progeny remains to be investigated. It is suspected that the born-light pigs may have less maintenance energy requirement than the pigs born with normal weights. For example, born-light lambs had lower maintenance energy requirement per unit of metabolic body weight, higher fat deposition rate, and greater G:F than born-normal lambs from birth to approximately 10 kg liveweight (Greenwood et al., 1998), but similar evidence has not been reported in pigs.

The feasibility of using the compensatory gestation feeding regime to boost piglet birth weight should be evaluated on each farm for each market situation. In a scenario when there is a greater pork-to-feed margin, the reduction in litter size may make the strategy less economically viable. By contrast, in a market where increased carcass backfat can cause heavy price penalties and when the margin between pork and feed is less favored, it may be worthwhile to prioritize the production of leaner carcasses at the cost of lower overall carcass numbers and increased gestation feed usage. It is worthwhile to mention that the greater G:F observed in the born-light progeny may offset their carcass fatness-related penalties depending on markets. The longevity of the sows was not evaluated in this experiment, but it may increase the economic return if sows continue to be productive in subsequent parities. It is known that greater backfat loss during lactation is associated with a shorter productive lifetime (Serenius et al., 2006), so recovery of the previous lactation weight loss during the subsequent early gestation may be beneficial to sow longevity. In the current study, sows that lost 7% of their body weight over a summer lactation were able to recover within the first 30 d of gestation via the use of the compensatory feeding regime.

Whether body weight loss over the summer lactation affects subsequent fetal development is less conclusive from this experiment. Similar litter birth weight and average piglet birth weight were found between the sows classified as LLStd and HLStd in the current experiment. But this outcome might have been influenced by the naturally higher litter size observed in LLStd sows compared with HLStd sows, because it is known that litter size is usually negatively correlated with average birth weight (Vázquez-Gómez et al., 2020). The reason for the naturally higher litter size observed in LLStd sows remains unknown. A previous study showed that 50% restriction in feed allowance during the last week of lactation reduced embryo weight by 9% and crown-rump length by 3% on d 30 of the subsequent gestation (Vinsky et al., 2006). In the current experiment, the LLStd and HLStd sows were not different in feed intake or litter weight gain over the summer lactation, implying that fetal development may only be compromised when a severe negative energy balance is experienced. The farrowing rate was similar between LLStd and HLStd sows in the current experiment, but an earlier study showed that farrowing rate was negatively affected when lactation weight loss was >10% in sows (Thaker and Bilkei, 2005). The disparity between the published studies and our results indicates that the high weight loss group created for our current experiment might not have been affected severely enough to influence the subsequent farrowing rate. The amount of feed intake during a summer lactation in the current experiment was 18% lower than that reported at the same research facility during a cool season (autumn) (Liu et al., 2019), and this magnitude of reduction in lactational feed intake agrees with other observations that Australian summer conditions usually reduces voluntary feed intake of lactating sows by 17% (Lewis and Bunter, 2011). Another possible reason for the lack of change in the subsequent reproductive performance between the HLStd and LLStd sows is the increasing resilience to lactational catabolism of prolific sows due to genetic selection. For example, a retrospective data analysis showed that the effect of lactational weight loss of sows on subsequent litter birth weight is genotype-dependent (Wientjes et al., 2013). It is speculated that other factors, such as heat stress during mating and early gestation, might play a critical role in contributing to summer infertility in sows. A recent climatically controlled study has demonstrated that exposing pregnant gilts to hot conditions during early-mid gestation can down-regulate the placental amino acid transporter, reduce placental efficiency, and reduce muscle fiber proliferation of fetuses (Zhao et al., 2020; Zhao et al., 2021).

In a conclusion, for the sows that lost 7% of their weight during a summer lactation, increasing the feed allowance from 2.6 kg to 3.5 kg during the first 30 d of gestation increased average piglet birth weight and reduced the proportion of born-light piglets in the subsequent litter, but reduced litter size. The lower proportion of born-light piglets should contribute to overall better growth performance, leaner carcasses, and less variation in carcass weight and backfat thickness in the resultant progeny born to the sows with high weight loss during a summer lactation.

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Disclosures

The authors have no conflicts of interest to declare.

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Tables and Figure Legends

Table 1. Lactation performance of experimental sows during summer for each treatment group depending on their summer lactational weight loss and compensatory feeding in early gestation (retrospective data analysis).

Variables	LLStd[1] (n=75 litters)	HLStd[2] (n=78 litters)	HLComp[3] (n=81 litters)	*P*-values		
				All groups	LLStd vs HLStd	HLStd vs HLComp
Parity of sows	3.0 ± 0.20	3.0 ± 0.19	3.1 ± 0.20	0.93	0.99	0.73
Lactation length, d	26.7 ± 0.33	26.6 ± 0.25	26.4 ± 0.24	0.79	0.90	0.52
Sow body weight, d 3 of lactation, kg	278.9 ± 0.37	284.0 ± 2.90	281.4 ± 2.73	0.53	0.27	0.50
Sow body weight, weaning, kg	275.8 ± 3.97[a]	265.1 ± 3.08[b]	261.9 ± 2.87[b]	0.016	0.030	0.45
Weight change during summer lactation, kg	-3.1 ± 1.54[a]	-18.9 ± 1.20[b]	-19.4 ± 1.15[b]	<0.001	<0.001	0.77
Backfat of sow, d 3 of lactation, mm	20.5 ± 0.87	22.3 ± 0.67	21.7 ± 0.63	0.26	0.10	0.50
Backfat of sow, weaning, mm	17.6 ± 0.60	18.4 ± 0.47	17.8 ± 0.44	0.49	0.28	0.36
Backfat change during summer lactation, mm	-3.0 ± 0.58	-3.9 ± 0.45	-4.0 ± 0.43	0.31	0.20	0.88
BA[4] before summer lactation	13.6 ± 0.48[a]	12.5 ± 0.38[ab]	12.1 ± 0.36[c]	0.055	0.010	0.39
SB[5] before summer lactation	1.5 ± 0.25	0.9 ± 0.20	1.2 ± 0.18	0.20	0.077	0.31
MUM[6] before summer lactation	0.3 ± 0.12	0.2 ± 0.10	0.4 ± 0.09	0.28	0.65	0.12
TB[7] before summer lactation	15.4 ± 0.60[a]	13.7 ± 0.47[b]	13.7 ± 0.45[b]	0.050	0.030	0.96
Number of piglets, post-foster	12.0 ± 0.22	12.1 ± 0.17	12.0 ± 0.16	0.75	0.52	0.51
Number of piglets, weaned	10.0 ± 0.34	9.9 ± 0.26	10.0 ± 0.25	0.93	0.81	0.70
ADFI[8] of sows (d 3-weaning), kg	6.57 ± 0.228	6.37 ± 0.176	6.32 ± 0.169	0.66	0.49	0.82
Litter weight gain (d 3-weaning), kg	48.1 ± 2.94	50.4 ± 2.26	52.5 ± 2.14	0.52	0.54	0.56

[1]LLStd: sows had low lactational weight loss (average 1%) and received a standard gestational feeding regime (2.6 kg during d 0-30) in the following gestation.

[2]HLStd: sows had high lactational weight loss (average 7%) and received a standard gestational feeding regime (2.6 kg during d 0-30) in the following gestation.

[3]HLComp: sows had high lactational weight loss (average 7%) and received a compensatory gestational feeding regime (3.5 kg during d 0-30) in the following gestation.

[4]Number of piglets born alive

[5]Number of stillborn piglets

[6]Number of mummified fetuses

[7]Number of total born piglets

[8]Average daily feed intake

[a, b, c] Values with different superscripts differ ($P < 0.05$).

Table 2. Change of bodyweight and backfat of gestating sows with low vs high lactational weight loss and receiving a standard vs compensatory gestation feeding regime.

Variables	LLStd[1] (n=75 litters)	HLStd[2] (n=78 litters)	HLComp[3] (n=81 litters)	*P*-values		
				All groups	LLStd vs HLStd	HLStd vs HLComp
Body weight, weaned, kg	275.8 ± 3.97[a]	265.1 ± 3.08[b]	260.8 ± 2.91[b]	0.011	0.034	0.31
Weaning to remating interval, d	4.2 ± 0.08	4.3 ± 0.09	4.3 ± 0.09	0.91	0.85	0.80
Body weight, d 0, kg	263.7 ± 3.98	259.5 ± 3.08	252.8 ± 2.92	0.068	0.91	0.12
Body weight, d 30, kg	265.7 ± 3.64	266.4 ± 2.82	267.1 ± 2.66	0.95	0.55	0.86
Body weight, d 108 kg	288.5 ± 3.56	288.2 ± 2.76	287.4 ± 2.61	0.96	0.80	0.84
Body weight change, weaned- d 0, kg	-12.1 ± 1.46[a]	-5.6 ± 1.13[b]	-8.1 ± 1.07[b]	0.002	<0.001	0.11
Body weight change, d 0- d 30, kg	2.0 ± 1.82[a]	6.9 ± 1.41[a]	14.3 ± 1.33[b]	<0.001	0.34	<0.001
Body weight change, d 30- d 108, kg	22.9 ± 1.93	21.8 ± 1.49	20.3 ± 1.41	0.54	0.50	0.47
Body weight change, d 0- d 108, kg	24.9 ± 2.37[a]	28.7 ± 1.83[a]	34.6 ± 1.74[b]	0.003	0.85	0.021
Backfat, weaned, mm	17.6 ± 0.61	17.6 ± 0.48	17.6 ± 0.49	1.00	0.28	0.35
Backfat, d 0, mm	18.3 ± 0.65	18.8 ± 0.50	18.5 ± 0.48	0.79	0.66	0.58
Backfat, d 30, mm	18.3 ± 0.61	19.0 ± 0.47	19.2 ± 0.45	0.52	0.90	0.76
Backfat, d 108, mm	19.1 ± 0.71	19.4 ± 0.55	20.5 ± 0.52	0.17	0.59	0.12
Backfat change, weaned- d 0, mm	0.8 ± 0.43	0.4 ± 0.33	0.7 ± 0.31	0.81	0.27	0.63
Backfat change, d 0- d 30, mm	0.0 ± 0.43	0.1 ± 0.33	0.7 ± 0.31	0.29	0.39	0.21
Backfat change, d 30- d 108, mm	0.8 ± 0.44	0.4 ± 0.35	1.4 ± 0.33	0.13	0.39	0.042
Backfat change, d 0- d 108, mm	0.8 ± 0.60[a]	0.3 ± 0.46[a]	2.1 ± 0.44[b]	0.020	0.65	0.007

[1]LLStd: sows had low lactational weight loss (average 1%) and received a standard gestational feeding regime (2.6 kg during d 0-30).

[2]HLStd: sows had high lactational weight loss (average 7%) and received a standard gestational feeding regime (2.6 kg during d 0-30).

[3]HLComp: sows had high lactational weight loss (average 7%) and received a compensatory gestational feeding regime (3.5 kg during d 0-30).

[a, b, c] Values with different superscripts differ ($P < 0.05$).

Table 3. Farrowing outcomes of sows with low vs high lactational weight loss and receiving a standard vs compensatory gestation feeding.

Variables	LLStd[1] (n=75 litters)	HLStd[2] (n=78 litters)	HLComp[3] (n=81 litters)	*P*-values		
				All groups	LLStd vs HLStd	HLStd vs HLComp
Farrowing rate, %	83.1	81.4	82.1	0.96	0.76	0.91
Gestational length, d	115.9 ± 0.17	115.9 ± 0.19	116.4 ± 0.18	0.075	0.94	0.046
Number of total born	15.9 ± 0.53[a]	14.4 ±0.41[b]	13.0 ± 0.39[c]	<0.001	0.032	0.015
Number of born alive	13.2 ± 0.47[a]	12.5 ± 0.36[ab]	11.7 ± 0.35[b]	0.012	0.28	0.16
Number of stillborn	2.4 ± 0.24[a]	1.6 ± 0.18[b]	0.9 ± 0.18[c]	<0.001	0.010	0.009
Number of mummies	0.3 ± 0.11	0.3 ± 0.09	0.3 ± 0.08	0.94	0.84	0.86
Litter birth weight[4], kg	20.0 ± 0.68	19.3 ± 0.53	18.2 ± 0.50	0.10	0.41	0.16
Average birth weight, kg	1.31 ± 0.043[a]	1.37 ± 0.034[ab]	1.49 ± 0.032[c]	0.002	0.28	0.009
Within-litter CV of birth weight, %	24.5 ± 1.21	23.4 ± 0.97	22.0 ± 0.88	0.25	0.49	0.30
Within-litter CV of birth weight[5], %	23.4 ± 0.77	23.2 ± 0.74	22.9 ± 0.73	0.90	0.89	0.75
Percentage of piglet ≤ 1.1 kg, %	29.2 ± 3.15[a]	23.5 ± 2.40[bc]	17.1 ± 2.31[c]	0.007	0.002	0.054
Percentage of piglet ≤ 1.1 kg[6], %	25.0 ± 2.77	23.4 ± 2.08	21.2 ± 2.06	0.54	0.64	0.46

[1]LLStd: sows had low lactational weight loss (average 1%) and received a standard gestational feeding regime (2.6 kg during d 0-30).

[2]HLStd: sows had high lactational weight loss (average 7%) and received a standard gestational feeding regime (2.6 kg during d 0-30).

[3]HLComp: sows had high lactational weight loss (average 7%) and received a compensatory gestational feeding regime (3.5 kg during d 0-30).

[4]Born-alive and stillborn piglets were weighed.

[5]The sum number of born alive and stillborn (14.1) was used as a covariate.

[6]The sum number of born alive and stillborn (14.1) was used as a covariate.

[a, b, c] Values with different superscripts differ ($P < 0.05$).

Table 4. Growth performance of focal progeny pigs (4-10 weeks age) born to the sows with low vs high lactational weight loss and receiving a standard vs compensatory gestation feeding.

Variables	Progeny birth weight class	Sow treatment			*P*-values				
		LLStd[1]	HLStd[2]	HLComp[3]	Sow treatment	Birth weight	Interaction	LLStd vs HLStd	HLStd vs HLComp
Birth weight, kg	born-light	1.02 ± 0.019	1.01± 0.019	1.02 ± 0.019	0.88	<0.001	0.32	0.56	0.73
	born-normal	1.56 ± 0.020	1.55 ± 0.020	1.54 ± 0.019					
Body weight, weaned, kg	born-light	6.20 ± 0.33	5.80 ± 0.29	5.44 ± 0.29	0.72	<0.001	0.16	0.74	0.61
	born-normal	7.60 ± 0.30	7.99 ± 0.30	7.98 ± 0.29					
ADFI[4], kg	born-light	640 ± 32.1	621 ± 28.9	586 ± 28.9	0.88	<0.001	0.23	0.94	0.65
	born-normal	730 ± 29.8	772 ± 29.9	780 ± 28.9					
ADG[5], g	born-light	469 ± 18.8	434 ± 17.0	433 ± 17.0	0.58	<0.001	0.24	0.33	0.52
	born-normal	509 ± 17.8	508 ± 17.6	534 ± 17.0					
Gain: Feed, kg:kg	born-light	0.72 ± 0.018	0.71 ± 0.016	0.74 ± 0.017	0.21	0.009	0.64	0.24	0.11
	born-normal	0.70 ± 0.035	0.67 ± 0.035	0.70 ± 0.034					
Body weight (10 wk), kg	born-light	26.9 ± 1.01	24.9 ± 0.91	24.5 ± 0.91	0.68	<0.001	0.14	0.27	0.88
	born-normal	30.0 ± 0.94	30.3 ± 0.94	31.4 ± 0.91					

[1]LLStd: sows had low lactational weight loss (average 1%) and received a standard gestational feeding regime (2.6 kg during d 0-30). N=15 born-light and 15 born-normal pens of progeny pigs were selected from LLStd sows (two pigs/pen).

[2]HLStd: sows had high lactational weight loss (average 7%) and received a standard gestational feeding regime (2.6 kg during d 0-30). N=16 born-light and 16 born-normal pens of progeny pigs were selected from HLStd sows (two pigs/pen).

[3]HLComp: sows had high lactational weight loss (average 7%) and received a compensatory gestational feeding regime (3.5 kg during d 0-30). N=16 born-light and 16 born-normal pens of progeny pigs were selected from HLComp sows (two pigs/pen).

[4]Average daily feed intake

[5]Average daily gain

Table 5. Growth performance of focal progeny pigs (from 10 weeks to slaughter at 100 kg) born to the sows with low vs high lactational weight loss and receiving a standard vs compensatory gestation feeding.

Variables	Progeny birth weight class	Sow treatment			*P*-values				
		LLStd[1]	HLStd[2]	HLComp[3]	Sow treatment	Birth weight	Interaction	LLStd vs HLStd	HLStd vs HLComp
Birth weight, kg	born-light	1.01 ± 0.021	1.05 ±0.023	1.03 ±0.022	0.72	<0.001	0.32	0.84	0.58
	born-normal	1.55 ± 0.021	1.53 ± 0.021	1.57 ± 0.021					
Body weight, 10 wk, kg	born-light	27.6 ± 1.10	25.6 ± 1.14	25.9 ± 1.04	0.99	<0.001	0.11	0.94	0.92
	born-normal	29.5 ± 1.07	31.7 ± 1.07	31.4 ± 1.07					
ADFI[4], kg	born-light	2.06 ± 0.079	2.04 ± 0.081	2.16 ± 0.074	0.74	<0.001	0.086	0.77	0.64
	born-normal	2.50 ± 0.076	2.45 ± 0.076	2.29 ± 0.076					
ADG[5], g	born-light	928 ± 23.8	932 ± 24.5	959 ± 22.4	0.67	<0.001	0.13	0.84	0.4
	born-normal	1067 ± 23.1	1023 ± 23.1	1004 ± 23.1					
Gain: Feed, kg:kg	born-light	0.46 ± 0.011	0.46 ± 0.012	0.46 ± 0.012	0.75	0.005	0.48	0.37	0.84
	born-normal	0.44 ± 0.011	0.42 ± 0.011	0.43 ± 0.011					
Days to reach 100 kg, d	born-light	147 ± 1.8	149 ± 1.9	147 ± 1.7	0.29	<0.001	0.33	0.71	0.37
	born-normal	135 ± 1.8	138 ± 1.8	140 ± 1.8					
Body weight slaughter, kg	born-light	99.2 ± 1.02	99.9 ± 1.05	100.4 ± 0.96	0.94	0.15	0.60	0.88	0.74
	born-normal	101.2 ± 0.98	101.3 ± 0.98	100.4 ± 0.98					

[1]LLStd: sows had low lactational weight loss (average 1%) and received a standard gestational feeding regime (2.6 kg during d 0-30). N=18 born-light and 17 born-normal progeny pigs were selected from LLStd sows.

[2]HLStd: sows had high lactational weight loss (average 7%) and received a standard gestational feeding regime (2.6 kg during d 0-30). N=15 born-light and 17 born-normal progeny pigs were selected from HLStd sows.

[3]HLComp: sows had high lactational weight loss (average 7%) and received a compensatory gestational feeding regime (3.5 kg during d 0-30). N=16 born-light and 17 born-normal progeny pigs were selected from HLComp sows.

[4]Average daily feed intake

[5]Average daily gain

Table 6. Carcass traits of progeny born to the sows with low vs high lactational weight loss and receiving a standard vs compensatory gestation feeding.

		Sow treatment			*P*-values				
Variables	Progeny birth weight class	LLStd[1]	HLStd[2]	HLComp[3]	Sow treatment	Birth weight	Interaction	LLStd vs HLStd	HLStd vs HLComp
Dressing, %	born-light	77.4 ± 0.60	77.3 ± 0.63	76.7 ± 0.64	0.76	0.77	0.87	0.98	0.54
	born-normal	77.3 ± 0.70	77.3 ± 0.59	77.2 ± 0.58					
Carcass weight, kg	born-light	77.4 ± 0.85	77.4 ± 0.85	78.2 ± 0.79	0.96	0.50	0.64	0.94	0.88
	born-normal	78.2 ± 0.77	78.5 ± 0.79	77.8 ± 0.79					
Backfat[4], mm	born-light	14.4 ± 0.58	15.4 ± 0.63	14.9 ± 0.62	0.14	0.049	0.96	0.15	0.73
	born-normal	13.4 ± 0.57	14.7 ± 0.59	13.8 ± 0.59					
Loin depth, mm	born-light	54.3 ± 1.28	53.0 ± 1.41	52.6 ± 1.40	0.95	0.25	0.52	0.98	0.78
	born-normal	53.8 ± 1.37	55.1 ± 1.33	54.8 ± 1.33					

[1]LLStd: sows had low lactational weight loss (average 1%) and received a standard gestational feeding regime (2.6 kg during d 0-30). N=18 born-light and 17 born-normal progeny pigs were selected from LLStd sows.

[2]HLStd: sows had high lactational weight loss (average 7%) and received a standard gestational feeding regime (2.6 kg during d 0-30). N=15 born-light and 17 born-normal progeny pigs were selected from HLStd sows.

[3]HLComp: sows had high lactational weight loss (average 7%) and received a compensatory gestational feeding regime (3.5 kg during d 0-30). N=16 born-light and 17 born-normal progeny pigs were selected from HLComp sows.

[4]Carcass weight (78.0 kg) was used as a covariate.

Table 7. Fasting glucose and insulin concentrations at 18 weeks of age of progeny born to the sows with low vs high lactational weight loss and receiving a standard vs compensatory gestation feeding.

Variables	Progeny birth weight class	Sow treatment: LLStd[1]	Sow treatment: HLStd[2]	Sow treatment: HLComp[3]	P-values: Sow treatment	P-values: Birth weight	P-values: Interaction	P-values: LLStd vs HLStd	P-values: HLStd vs HLComp
Glucose, mmol/L	born-light	5.57 ± 0.184	5.46 ± 0.184	5.70 ± 0.184	0.39	0.70	0.95	0.70	0.18
	born-normal	5.44 ± 0.184	5.41 ± 0.184	5.70 ± 0.206					
Insulin, mU/L	born-light	3.31 ± 0.797	4.31 ± 0.797	3.23 ± 0.797	0.97	0.65	0.34	0.93	0.82
	born-normal	3.78 ± 0.797	2.64 ± 0.797	3.50 ± 0.891					
HOMA-IR[4]	born-light	0.84 ± 0.208	1.10 ± 0.208	0.83 ± 0.208	0.98	0.52	0.38	0.98	0.88
	born-normal	0.92 ± 0.208	0.65 ± 0.208	0.85 ± 0.232					

[1]LLStd: sows had low lactational weight loss (average 1%) and received a standard gestational feeding regime (2.6 kg during d 0-30). N=10 born-light and 10 born-normal progeny pigs were selected from LLStd sows.

[2]HLStd: sows had high lactational weight loss (average 7%) and received a standard gestational feeding regime (2.6 kg during d 0-30). N=10 born-light and 10 born-normal progeny pigs were selected from HLStd sows.

[3]HLComp: sows had high lactational weight loss (average 7%) and received a compensatory gestational feeding regime (3.5 kg during d 0-30). N=10 born-light and 9 born-normal progeny pigs were selected from HLComp sows.

[4]Homeostatic model assessment for insulin resistance; HOMA-IR equals glucose concentration (mmol per liter) /22.5×insulin concentration (microunits per liter).

Fig. 1. Flowchart of the experimental design.

The experiment consisted of two parts. Part 1 of the experiment compared the birth weight of piglets born to the sows that were allocated to three treatment groups- low lactational weight loss (average 1%) plus standard gestation feeding (2.6 kg feed from d 0-30 gestation; abbreviated as LLStd; n=75 sows farrowed in the subsequent parity), high lactational weight loss (average 7%) plus standard gestation feeding (2.6 kg feed from d 0-30 gestation; abbreviated as HLStd, n=78 sows farrowed in the subsequent parity), and high lactational weight loss (average 7%) plus compensatory gestation feeding (3.5 kg feed from d 0-30 gestation; abbreviated as HLComp; n=81 sows farrowed in the subsequent parity). All the experimental sows lactated and weaned in summer (February-March 2019; Corowa, NSW, Australia) then allocated to the above treatments. Data on birth weight were analyzed using ANOVA with two planned comparisons (LLStd vs HLStd and HLStd vs HLComp). In Part 2 of the experiment, the focal progeny pigs from each sow treatment group were stratified as born-light (0.8-1.1 kg range) and born-normal (1.3-1.7 kg range) and grown to 100 kg live weight. Growth performance (from weaning to 100 kg live weight) and carcass backfat thickness of the progeny pigs were analyzed using two-way ANOVA for the effect of sow treatments, birthweight class of progeny and their interactions.

Fig. 2. Plasma progesterone concentrations (mean ± standard error) of gestating sows with low vs high lactational weight loss and receiving a standard vs compensatory gestation feeding.

LLStd: sows had low lactational weight loss (average 1%) and received a standard gestational feeding regime (2.6 kg during d 0-30); HLStd: sows had high lactational weight loss (average 7%) and received a standard gestational feeding regime (2.6 kg during d 0-30); HLComp: sows had high lactational weight loss (average 7%) and received a compensatory gestational feeding regime (3.5 kg during d 0-30). N=15 sows per treatment.

Fig. 3. Blood IGF-1 concentrations (mean ± standard error) of 1-d age progeny pigs born to the sows with low vs high lactational weight loss and receiving a standard vs compensatory gestation feeding.

LLStd: sows had low lactational weight loss (average 1%) and received a standard gestational feeding regime (2.6 kg from d 0-30); HLStd: sows had high lactational weight loss (average 7%) and received a standard gestational feeding regime (2.6 kg from d 0-30); HLComp: sows had high lactational weight loss (average 7%) and received a compensatory gestational feeding regime (3.5 kg from d 0-30). Blood samples were taken from newborn piglets via jugular venipuncture at 24 h after birth (n= 20 born-light (0.8-1.1 kg) and 20 born-normal (1.3-1.7 kg) piglets from each sow treatment group; half male and half female pigs).

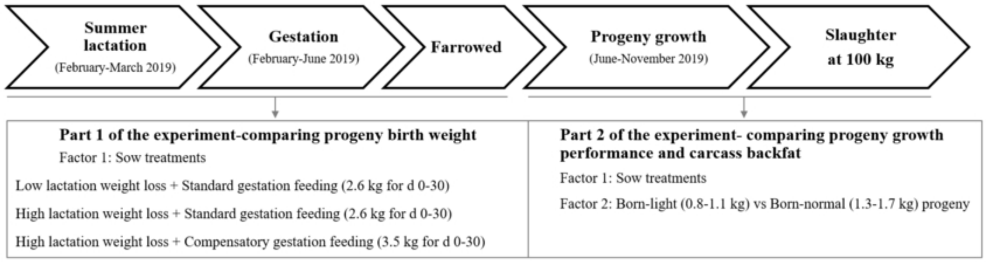

Fig. 1. Flowchart of the experimental design.

The experiment consisted of two parts. Part 1 of the experiment compared the birth weight of piglets born to the sows that were allocated to three treatment groups- low lactational weight loss (average 1%) plus standard gestation feeding (2.6 kg feed from d 0-30 gestation; abbreviated as LLStd; n=75 sows farrowed in the subsequent parity), high lactational weight loss (average 7%) plus standard gestation feeding (2.6 kg feed from d 0-30 gestation; abbreviated as HLStd, n=78 sows farrowed in the subsequent parity), and high lactational weight loss (average 7%) plus compensatory gestation feeding (3.5 kg feed from d 0-30 gestation; abbreviated as HLComp; n=81 sows farrowed in the subsequent parity). All the experimental sows lactated and weaned in summer (February-March 2019; Corowa, NSW, Australia) then allocated to the above treatments. Data on birth weight were analyzed using ANOVA with two planned comparisons (LLStd vs HLStd and HLStd vs HLComp). In Part 2 of the experiment, the focal progeny pigs from each sow treatment group were stratified as born-light (0.8-1.1 kg range) and born-normal (1.3-1.7 kg range) and grown to 100 kg live weight. Growth performance (from weaning to 100 kg live weight) and carcass backfat thickness of the progeny pigs were analyzed using two-way ANOVA for the effect of sow treatments, birthweight class of progeny and their interactions.

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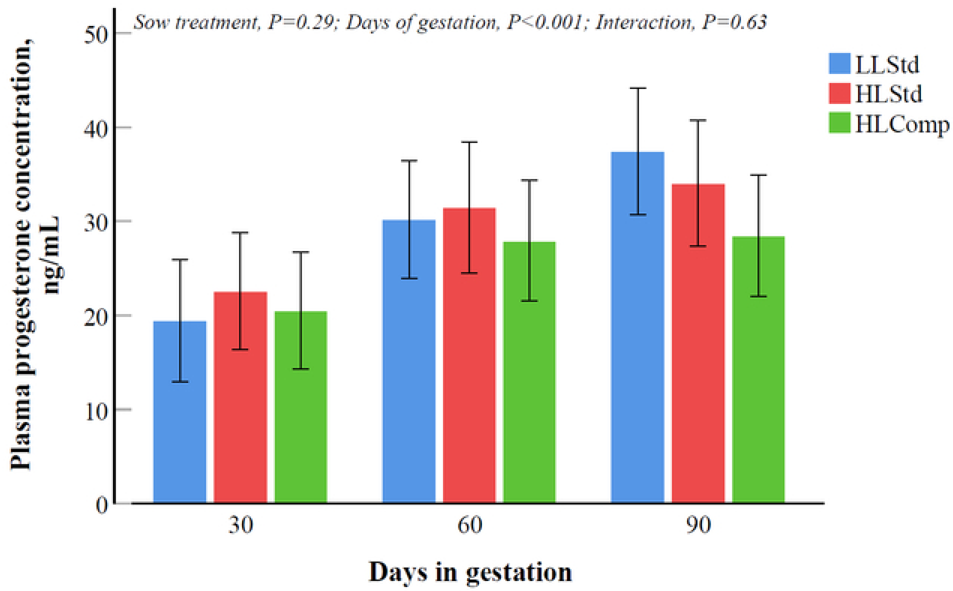

Fig. 2. Plasma progesterone concentrations (mean ± standard error) of gestating sows with low vs high lactational weight loss and receiving a standard vs compensatory gestation feeding.
LLStd: sows had low lactational weight loss (average 1%) and received a standard gestational feeding regime (2.6 kg during d 0-30); HLStd: sows had high lactational weight loss (average 7%) and received a standard gestational feeding regime (2.6 kg during d 0-30); HLComp: sows had high lactational weight loss (average 7%) and received a compensatory gestational feeding regime (3.5 kg during d 0-30). N=15 sows per treatment.

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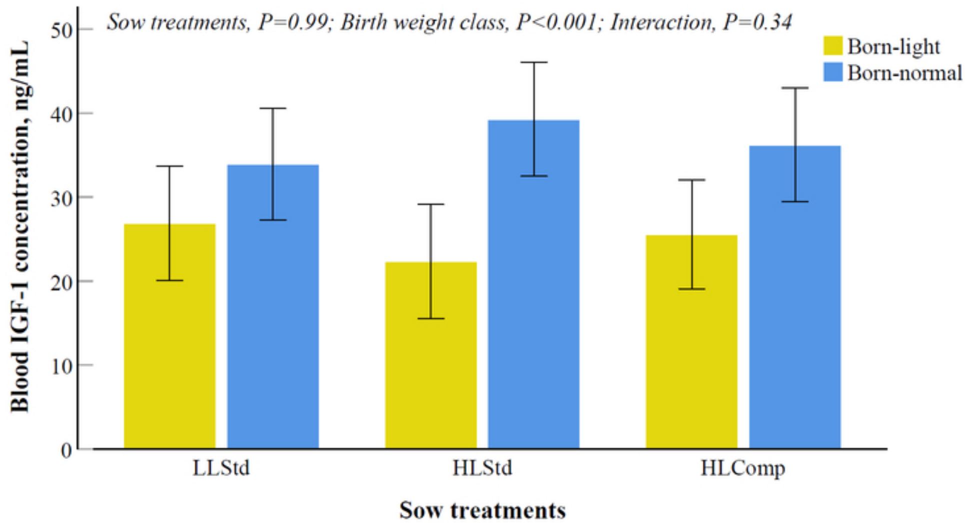


Fig. 3. Blood IGF-1 concentrations (mean ± standard error) of 1-d age progeny pigs born to the sows with low vs high lactational weight loss and receiving a standard vs compensatory gestation feeding. LLStd: sows had low lactational weight loss (average 1%) and received a standard gestational feeding regime (2.6 kg from d 0-30); HLStd: sows had high lactational weight loss (average 7%) and received a standard gestational feeding regime (2.6 kg from d 0-30); HLComp: sows had high lactational weight loss (average 7%) and received a compensatory gestational feeding regime (3.5 kg from d 0-30). Blood samples were taken from newborn piglets via jugular venipuncture at 24 h after birth (n= 20 born-light (0.8-1.1 kg) and 20 born-normal (1.3-1.7 kg) piglets from each sow treatment group; half male and half female pigs).

64x36mm (300 x 300 DPI)

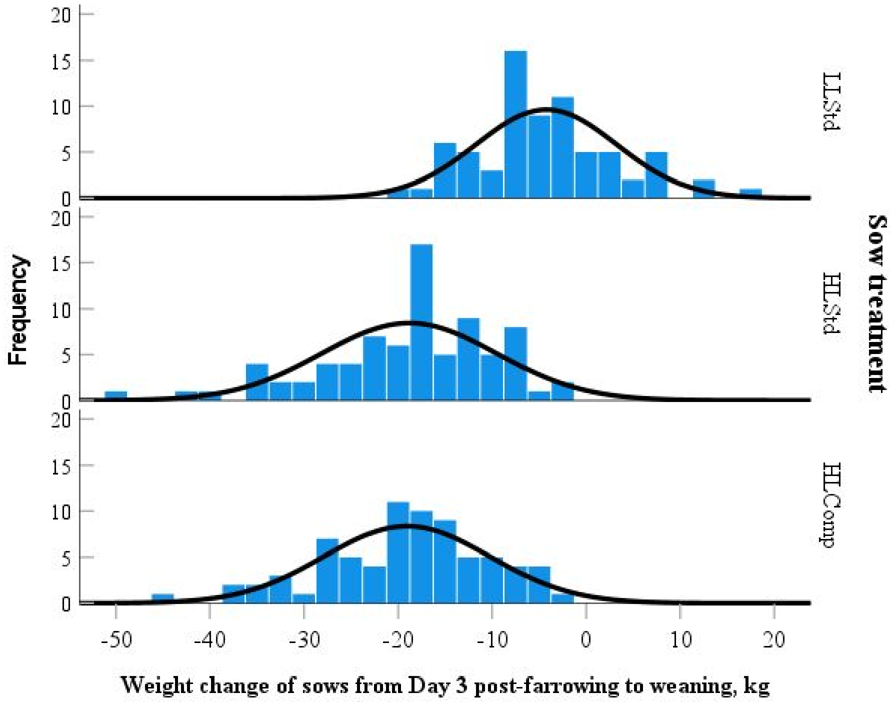
Supplementary Materials

Supplementary Table 1. Composition of experimental diet

Ingredient	Composition as fed-basis
Wheat, %	44
Barley, %	26
Oats, %	9.5
Flour byproduct, %	10
Canola meal (37%), %	5
Meat meal (60%), %	2
Fish oil, %	0.2
Tallow, %	1.0
Liquid betaine, %	0.4
Limestone, %	1.43
Salt, %	0.3
Dicalcium Phosphorus, %	0.57
Lysine-HCl, %	0.17
Threonine, %	0.025
Vitamin blend premix[1], %	0.13
Mineral blend premix[2], %	0.16
Phytase, %	0.01
Calculated nutrients	
Dry Matter, %	89.1
DE, MJ/kg	13.1
Fat, %	3.2
Crude protein, %	13.0
Fiber, %	4.8
Calcium, %	0.99
Available Phosphorous, %	0.45
SID lysine, %	0.52

[1] Supplied per kg of diet: vitamin A, 15000 IU; vitamin D_3, 3125 IU; vitamin E 75 IU; vitamin K, 1.0 mg; vitamin C, 50 mg; vitamin B-1, 1.5 mg; vitamin B-2, 5.0 mg; vitamin B-6 3.0 mg; vitamin B-12 70.0 mg; niacin, 20.0 mg; pantothenic acid, 15.0 mg; folic acid, 10.0 mg,

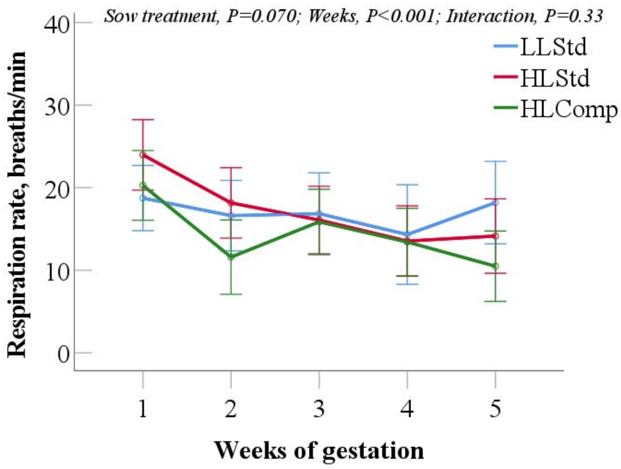
[2] Supplied per kg of diet: copper, 8.0 mg; manganese, 26.7 mg; zinc, 53.3 mg; iron, 71.1 mg; iodine, 1.80 mg; selenium; 0.27 mg; chromium, 0.36 mg



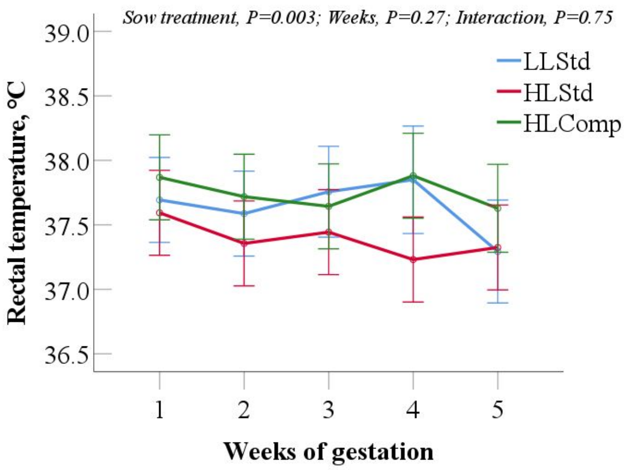
Supplementary Figure 1. Frequency chart of body weight change of sows over summer lactation by the retrospective allocations.

Sows were retrospectively allocated to three treatments based on the weight loss over summer lactation and the early gestational feeding level. LLStd: sows had low lactational weight loss (average 1% body weight loss) and received a standard gestational feeding regime (2.6 kg from d 0-30) (n=75 sows farrowed in the subsequent parity); HLStd: sows had high lactational weight loss (average 7% body weight loss) and received a standard gestational feeding regime (2.6 kg from d 0-30) (n=78 sows farrowed in the subsequent parity); HLComp: sows had high lactational weight loss (average 7% body weight loss) and received a compensatory gestational feeding regime (3.5 kg from d 0-30) (n=81 sows farrowed in the subsequent parity).

A



B



Supplementary Figure 2. Respiration rate (A) and rectal temperature (B) of gestating sows with low vs high lactation weight loss and received standard vs compensatory gestation feeding.

LLStd: sows had low lactational weight loss (av. 1%) and received a standard gestational feeding regime (2.6 kg from 0-30 d); HLStd: sows had high lactational weight loss (av. 7%) and received a standard gestational feeding regime (2.6 kg from 0-30 d); HLComp: sows had high lactational weight loss (av. 7%) and received a compensatory gestational feeding regime (3.5 kg from 0-30 d). N=8 sows per treatment