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Effects of timing of grouping and split-weaning on growth performance and behaviour of piglets in a multi-suckling system

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A R T I C L E I N F O

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A B S T R A C T

Variation in body weight (**BW**) of piglets at weaning is a drawback for successful implementation of multi-suckling (**MS**) systems. The current study investigated the combination of two intervention strategies, i.e. the timing of grouping and split-weaning, aiming to improve the BW gain of low birthweight piglets in an MS system and thereby reduce the BW variation at weaning on day 48 postpartum (**p.p.**). Eight batches of 5 sows with their litters were divided into 4 control (**CTRL**) and 4 treatment (**TREAT**) batches. In each litter, the second lowest (**LBW**) and highest (**HBW**) birthweight piglets from both sexes were selected as focal piglets. CTRL piglets were grouped on day 8 p.p. and no split-weaning was applied; TREAT piglets were grouped on day 13 p.p. and the three heaviest non-focal piglets per litter were split-weaned on day 35 p.p. Behaviour and feed intake were measured in focal piglets, and BW and mortality were measured in all piglets. Results showed that: (1) Throughout lactation there were no differences in BW or BW gain between CTRL and TREAT, nor were birthweight × treatment interactions found. (2) After grouping, there were no obvious differences between CTRL and TREAT in feeding and suckling behaviours on day 18, damage scores on snout, ear or tail and skin lesions on day 27, nor were birthweight × treatment interactions found. (3) After split-weaning, in week 6, piglets in TREAT tended to consume less feed than CTRL ($P = 0.072$). Low birthweight piglets in TREAT consumed numerically less feed and spent numerically less time contacting feed during the day than CTRL piglets. In week 6, there was a significant birthweight × treatment interaction in dry matter milk intake ($P = 0.030$), caused by a higher milk intake of TREAT-LBW piglets compared with CTRL-LBW piglets. In week 6, TREAT piglets tended to be present more at front and middle teats ($P = 0.052$) and tended to have lower snout damage scores ($P = 0.084$) than CTRL piglets. (4) Piglet crushing of all piglets in TREAT tended to be higher during the period when TREAT piglets were not yet grouped i.e. during days 9–14 than CTRL ($P = 0.087$). To conclude, split-weaning of the heavy piglets increased milk intake particularly of low birthweight piglets but this did not lead to a reduction in BW variation at weaning, as the increased milk intake was largely compensated for by a simultaneous decrease in feed intake.

1. Introduction

Multi-suckling (**MS**) systems for sows and piglets have been developed as an alternative for conventional single litter housing systems to improve animal welfare. However, in such systems, BW variation of piglets at weaning was observed to be large (Thomsson et al., 2016; Van Nieuwamerongen, 2017a). Our recent study in an MS system found that variation in BW gain in week 2–4 was mainly explained by birthweight and in week 4–8 by piglet feed intake (Tang et al., 2022b). The early stage of pigs' lives is crucial as it can influence pigs' lifetime

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performance (Zeng et al., 2019). As low birthweight piglets have the potential to compensate during their lifetime growth (Douglas et al., 2013), specific interventions might support these piglets to catch up. The current study aimed to improve piglet homogeneity through improving performance of low birthweight piglets in an MS system, by using a combination of two intervention strategies, one applied in early lactation during days 13–14 postpartum (**p.p.**) and one in late lactation on day 35 p.p.

The first intervention strategy applied in early lactation, is to delay the age at which piglets are allowed to enter the communal area, i.e. the grouping of litters, from days 6–8 p.p. applied in earlier studies (Van Nieuwamerongen et al., 2017b; Tang et al., 2022b) to days 13–14 p.p. Early grouping of non-littermates during lactation, i.e. on day 5 p.p. helped piglets to stimulate social skills and reduce fighting in the post-weaning period (Bohnenkamp et al., 2013). In addition, unacquainted piglets that were shortly placed together at a younger age (day 5 vs. day 12) fight shorter and had fewer injuries (Pitts et al., 2000). Also, the teat order of the majority of piglets is stable at 2 weeks of age (Hemsworth et al., 1976). Therefore, grouping at a younger age might lead to a higher occurrence of cross-suckling (Vanheukelom et al., 2012; Downing, 2015), which can cause stress and can result in a negative effect on piglet BW gain in MS systems (Olsen et al., 1998). Cross-suckling might have a more negative effect on smaller piglets, as they are at a disadvantage in settling new dominance hierarchies and competing for milk.

It was reported that sow recognition of the litter (Nowak et al., 2000) was well-established after day 7 p.p. The increased grouping age, i.e. later grouping, might help sows to recognize their own litter better which benefits especially young litters and smaller piglets in the MS system. The increased grouping age may also reduce the rate of crushing in MS systems (Verdon et al., 2020), and the reason could be that the reduced cross-suckling and reduced interrupted nursing lead to less crushing. The increased grouping age was even reported to have the potential for improving piglet homogeneity shortly after grouping (Verdon et al., 2020). In their study, piglets grouped on day 14 p.p. had less variation in BW on day 26 p.p. compared with piglets grouped on day 10 p.p. In contrast, Thomsson et al. (2016) did not find differences in BW variation at weaning at week 6 when piglets were housed in a group lactation system from 7,14 or 21 days of age. In the current study, we hypothesized that the increased grouping age, i.e., later grouping will increase growth performance of especially low birthweight (**LBW**) piglets, by strengthening the stability of the teat order and reducing cross suckling, and will also reduce mortality during lactation. In addition, LBW piglets would stay closer to their mother, also during sow feeding times, and as a result spend more time contacting feed during sow feeding times.

The second intervention, applied in late lactation on day 35 p.p., is split-weaning, i.e. the removal of several heavy piglets per litter from the MS system two weeks before the weaning of all remaining piglets at 48 days of age. Split-weaning, i.e. the earlier removal of about half of the piglets per litter from sows is thought to increase milk intake and pre-weaning performance for the remaining piglets (Pluske and Williams, 1996; Vesseur et al., 1997). We expected that in our MS system, split-weaning could reduce fights at the udder, and thereby enable especially LBW piglets to have an increased milk consumption and thus increased growth rate. We also expected that split-weaning can reduce the competition between piglets in the feeding area and thereby increase the feed intake of LBW piglets. Thus, the current study investigated the combination of two intervention strategies, i.e. the timing of grouping and split-weaning, aiming to improve the body weight (**BW**) gain of low birthweight piglets in an MS system and thereby reduce the BW variation at weaning on day 48 p.p.

2. Materials and methods

2.1. Animals, management and experimental design

The experiment was conducted at the facilities of Swine Innovation Centre Sterksel in the Netherlands from January 23rd until November 4th, 2020 and was approved by the Animal Care and Use Committee of Wageningen University & Research (Wageningen, the Netherlands). Eight consecutive batches of five multiparous sows (Topigs 20) and their litters (Tempo × Topigs 20) were kept per batch in an MS system (Fig. 1a–f) during a 7 week-lactation, with four control (**CTRL**) (batch 1, 4, 5, and 8) and four treatment (**TREAT**) (batch 2, 3, 6, and 7) batches. In total, eight batches of five sows with 160 focal piglets were studied (parity of all sows: 3.6 ± 0.2 (mean ± standard error); parity of sows in CTRL: 3.5 ± 0.3; parity of sows in TREAT: 3.7 ± 0.3). In each litter, two boars and two gilts with the second lowest and highest birthweight within sex were selected as focal piglets on day 14 postpartum (**p.p.**). Sows within a batch were distinguished by different colours of marker sprays.

The MS system was previously described by Tang et al. (2022b). The MS system consisted of two MS units and one Intermittent Suckling (IS) area (Fig. 1a). In each batch of the experiment, only one MS unit was used. Each MS unit contained five farrowing pens, and a communal MS area including a lying area, a feeding area and a dunging area. The feeding area contained five feeding places for the sows and a surrounding area which was accessible only to the piglets. In the feeding area, piglets had access to piglet feed at all times and to sow feed from day 28 p.p. onwards.

One week before farrowing (Fig. 2), five sows were moved to the MS system, balanced for parity and expected farrowing date. Sows were only locked up in a crate in the farrowing pen in the first 3 days p.p. during the whole day to prevent piglet crushing. Within 24–48 h p.p., litter sizes were standardized to 14 or 15 piglets per litter (average: 14.3 ± 0.1 piglets), based on the number of functional teats per sow. Piglets were ear-tagged within 24 h p.p. Piglets received an iron injection within 3 days p.p. and were vaccinated on day 19 p.p., but were not castrated nor tail-docked. Sows were able to access the communal area again from day 4 p.p. while piglets could not pass a piglet barrier. During days 8–9 p.p. (average: 8.2 ± 0.1) in CTRL batches and during days 13–14 p.p. (average: 13.4 ± 0.1) in TREAT batches, piglets could access to the communal area. During days 28–34 p.p., forced IS was conducted by transferring sows to the IS area for 10 h/day (07:00 – 17:00 h), to stimulate lactational oestrus and inseminate the sows. During days 35–49 p.p., voluntary IS was applied, during which sows could freely choose to access the IS area by a flexible partition which only sows could step over. This combination of forced and gradual IS results in a gradual weaning process for the piglets (Van Nieuwamerongen et al., 2017b). On day 35 p.p. in TREAT batches, the three heaviest non-focal piglets in each litter with a total number of 15 piglets/batch were split-weaned and transferred to a rearing department (4.1 x 2.6 m) until 7 weeks of age (Fig. 1g). One sow in TREAT was seriously wounded and the sow and her piglets were removed from the system and the experiment. One litter in TREAT only had 5 piglets on day 35 p.p., therefore no piglets from this litter were split-weaned on day 35 p.p. Piglets in CTRL and piglets remaining in the MS system in TREAT were weaned on day 48 p.p.

Provision of enrichment materials, temperature settings and the lighting schedule were as described in Tang et al. (2022b). In the rearing department, two hessian sacks and four ropes were provided attached to the wall and two handfuls of straw were provided on the floor twice/-day; the temperature was set at 28 °C on day 35 and 24 °C during days 36–48; artificial lighting was on at 07:00–18:00 h.

2.2. Feeding regime

The ingredient and calculated nutrient composition of sow and piglet diets are described in Tang et al. (2022b). Sows were fed twice daily at

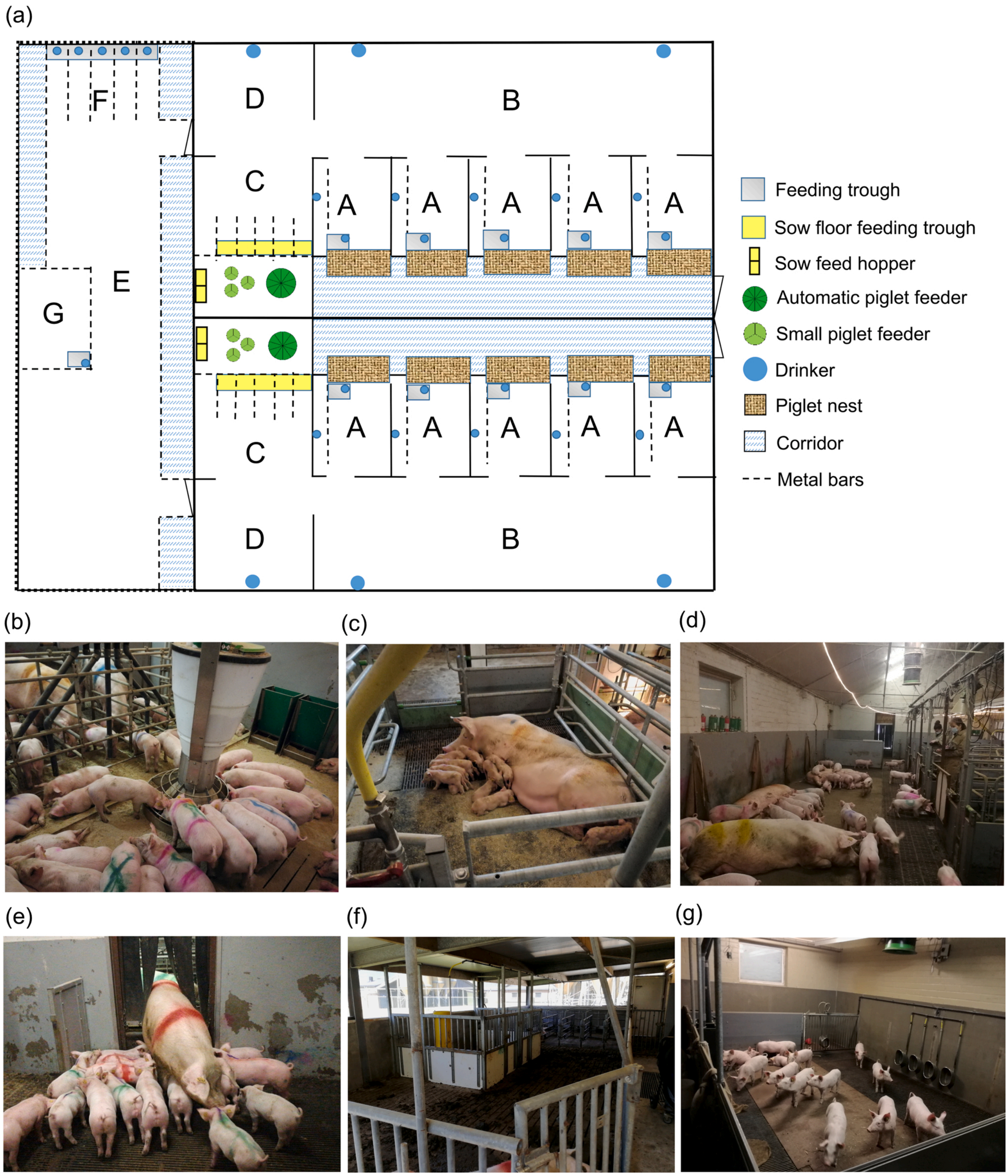

Fig. 1. (a) Layout of the multi-suckling (MS) system for sows and piglets consisting of two MS units and an intermittent suckling (IS) area. Each MS unit contained 5 farrowing pens with piglet nests (A), a communal MS area which included a lying area (B), a feeding area (C) and a dunging area (D). In each farrowing pen, there were a heated nest for the piglets, a feeding trough with a drinking nipple for the sows, and a water nipple for the piglets. Two extra drinking bowls in the lying area and one drinking bowl in the dunging area were available for the sows and piglets. The feeding area contained five feeding places for the sows and a surrounding area which was accessible only to the piglets. In the five feeding places there was a stainless steel feeding trough on the floor with five feeding places, separated by horizontal metal bars, which was accessible to both sows and piglets. In the surrounding area, there were three small round feeders (diameter: 28 cm) (used until day 35 p.p.), a sensor-controlled automatic piglet feeder containing ten feeding places (Rondomat, Fancom B.V., the Netherlands) (used from day 28 p.p.) and two feed hoppers with sow feed (used from day 28 p.p.) to enable piglets access to sow feed during the whole day. Connected to the MS unit was the IS area (E), which included feeding stalls for sows (F) and a boar pen (G). (b) Communal feeding area. (c) Farrowing pen. (d) Communal MS area. (e) The area between MS area and IS area. (f) IS area. (g) Rearing department.

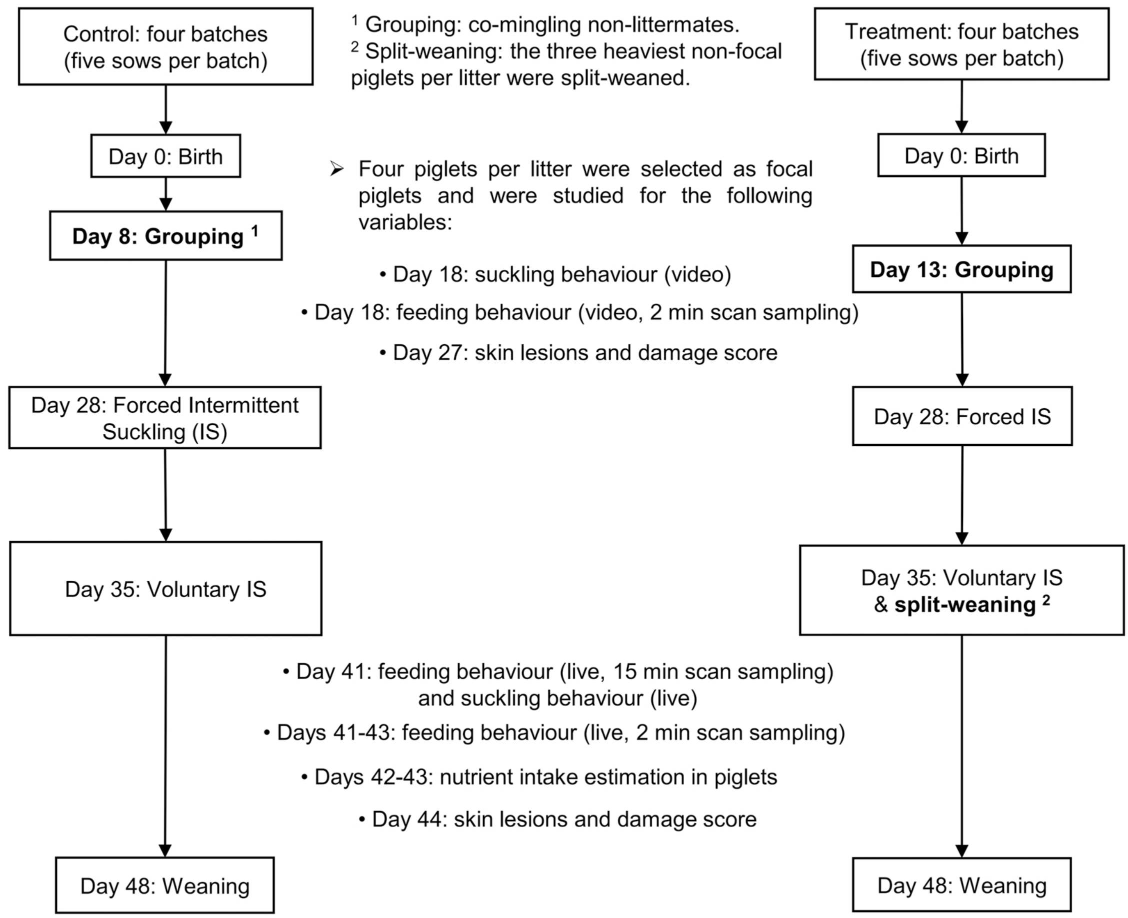

Fig. 2. Time schedule of experiment setup of sows and piglets in control (CTRL) and treatment (TREAT) batches during a 7-week lactation in the multi-suckling system.

08:00 and 16:00 h, with 3.0 kg/day of sow diet before farrowing and the amount gradually increased up to 8.5 kg/day on day 15 p.p. Before farrowing, sows were fed in the MS feeding area in the morning and in the farrowing pen in the afternoon. In the first 3 days p.p., sows were fed in the farrowing pen due to the confinement. During days 4–27, sows were fed in the MS feeding area. During days 28–34 during forced IS, sows were fed in the IS area at 07:30 h and in the MS feeding area at 17:30 h. During days 35–48, sows were fed in the MS feeding area at 08:00 and 16:00 h. Sows had ad libitum access to water via drinking bowls and nipples.

From 2 days p.p. until grouping, large feed pellets (8 mm diameter) for piglets were spread on the floor of the farrowing pen twice/day, which were out of reach for the sow. During days 9–14 p.p., piglets in TREAT had two round feeders in the farrowing pen, one with sow feed and one with weaner diet. For 3 days after grouping, the large feed pellets were provided to the piglets in the piglet feeding area. Additionally, a weaner diet was provided during days 9–21 p.p., a pre-starter diet during days 20–38 p.p. and a starter diet during days 37–48 p.p. The feed was provided in small round feeders after grouping until day 35 p.p. and during days 28–48 p.p. in an automatic piglet feeder. Piglets could also access sow feed in the MS feeding area from the feeding trough during sow feeding times from grouping until weaning at day 48 p.p. and from two sow feed hoppers during days 21–48 p.p. Piglets had ad libitum access to water via drinking bowls and nipples.

During days 35–48 p.p., the split-weaned TREAT piglets in the rearing department received sow and piglet feed via a feed hopper. For piglet feed, the pre-starter diet was provided during days 35–38 p.p. and the starter diet during days 37–48 p.p. The sow feed was provided during days 35–48 p.p. Four drinking nipples were provided.

2.3. Measurements

2.3.1. BW of all piglets

All piglets were weighed on day 0, 6, 27, 35 and 48 p.p. Within-batch standard error, standard deviation and coefficient of variation in BW and BW gain of all piglets in the MS system were calculated.

2.3.2. Video and live observations of feeding and suckling behaviours of focal piglets

Focal piglets within each batch were marked with stock marker spray for recognition of low and high birthweight class one day before the day for behavioural observation from video, and were marked for individual recognition before live observations.

2.3.2.1. Feeding behaviour during sow feeding times and during the day. Feeding behaviour of the piglets during sow feeding times was scored from video on day 18 p.p., and live during days 41–43 p.p. using 2-min instantaneous scan sampling at 08:00–08:30 h and 16:00–16:30 h. Feeding behaviour during the day was scored live on day 41 p.p. using 15-min instantaneous scan sampling at 08:30 h–16:00 h. During these times, every 2 min (during sow feeding times) or 15 min (during the day) it was observed whether a piglet was in the feeding area, contacting (i.e. sniffing or eating) sow feed or contacting (i.e. sniffing or eating) piglet feed. For live observations, the percentage of time spent on contacting sow feed and piglet feed was calculated per piglet; for video observations, it was calculated per high or low birthweight piglet.

2.3.2.2. Suckling behaviour. Suckling behaviour was scored from video at 08:30–16:00 h on day 18 p.p., and live at 08:30–16:00 h on day 41 p.

p. A nursing bout was scored as 'unsuccessful' and excluded from analysis when a new nursing bout began within 20 min after a previous nursing bout (Weary et al., 2002), and no milk let-down was noted. The frequency of presence at the front pair (first two pairs), middle pair or rear pair (last two pairs) of teats were recorded. For live observations, the frequency of presence at teats at both their own mother and cross-suckling sows was calculated per piglet during the 7.5 h; the frequency of presence at alien teats i.e. the teats of cross-suckling sows was calculated per piglet during the 7.5 h as well. For video observations, the frequency of presence at teats at both their own mother and cross-suckling sows was calculated per high or low birthweight piglet during the 7.5 h. For video observations, focal piglets can only be recognized as high or low birthweight piglet without individual recognition, therefore the specific recognition of presence at alien teats was not available. The frequency of presence at front and middle teats were summed into one variable for further analysis.

Suckling behaviour could not be observed from video for batch 3 due to technical problems, therefore batch 3 was not taken into account for further video analysis. In addition, the number of successful suckling bouts per sow during 7.5 h (no.) was calculated. Besides, the cross-suckling related variables were calculated, including percentage of piglets involved in cross-suckling at least once per litter (%), percentage of non-permanent cross-sucklers per litter (i.e. focal piglets that were present both at their own mother and alien sows during suckling bouts) (%), and percentage of permanent cross-sucklers per litter (i.e. focal piglets that were present only at alien sows during suckling bouts and never present at their own sows) (%).

2.3.3. Skin lesions and damage score of focal piglets and mortality of all piglets

During days 27 and 44 p.p., the number of skin lesions of focal piglets was counted per piglet by visual assessment as the number of fresh lesions on the whole body, except for ears and tails. These skin lesions are regarded as a proxy for aggressive behaviour given and received (Turner et al., 2006). The damage on snout, ears, and tail of focal piglets were scored from 0 to 3, from no damage to the presence of a wound or erosion (adapted from (Van Nieuwamerongen et al., 2015)) (Supplementary Table 1). Snout damage can be regarded as a reflection of head knocking (Van Nieuwamerongen et al., 2015) and fighting for teats during suckling bouts. The damage on ears and tails can be regarded as a measure of oral manipulation from other pigs (Van Nieuwamerongen et al., 2015). The averaged ear and snout damage score for left and right were used for further analysis.

Piglet mortality of all piglets in the MS system were calculated after litter standardisation i.e. 24–48 h p.p. until weaning. In order to test the effect of interventions on mortality, stillborn piglets and piglets that died before cross-fostering were excluded from the data set. Piglet mortality was calculated as the percentage of piglet mortality per litter (%) and the percentage of crushed piglets per litter (%).

2.3.4. Estimation of individual feed and milk intake of focal piglets

Individual dry matter intake of the focal piglets of sow feed and piglet feed during days 42–43 p.p. was measured using the dual alkane method (Tang et al., 2022a). Dotriacontane (**C32**) was considered as a reference marker and was administered to the piglets for three times/day during days 42–43 (60 mg/d). The alkane C32 was melted on a small amount of feed in a forced air oven and was mixed with lemonade syrup to make ~2.0 g/bolus containing 20 mg of C32. Piglets had a habituation period during days 36, 37 and 40, during which piglets were given boluses without marker twice a day. The number of boluses eaten by the piglets was recorded. Hentriacontane (**C31**) and hexatriacontane (**C36**) were considered as in-feed markers for the sow and piglet diets, respectively. The alkane C31 was provided via the inclusion of 15 % alfalfa in the sow feed, and C36 was melted on soybean meal in a forced air oven followed by mixing it into the piglet feed. This provided around 40 mg/kg of C31 in sow feed and 160 mg/kg of C36 in piglet feed. On day 44, two spot faecal samples were collected from each focal piglet at 08:30 and 12:30 h. N-alkanes in faecal and feed samples were measured by gas chromatography (Smit et al., 2005).

Dry matter intake of the sow feed and piglet feed in each piglet were calculated for days 42–43 using eq. [1]:

$$\text{Estimated intakeof piglet or sow feed }(\text{g}/\text{day}) = \frac{\left(\frac{\text{concentration of in-feed marker in faeces (mg/kg)}}{\text{concentration of reference marker C32in faeces (mg/kg)}} \times \text{ daily intake of reference marker C32 }(\text{mg}/\text{day})\right)}{\text{concentration of in} - \text{feed marker in diet(mg/kg)}} \times 1000 \quad (1)$$

Milk intake was calculated using eq. [2], assuming fixed feed conversion ratios (**FCR**) of converting dry matter feed intake into BW gain of 1.5 g/g, and assuming a fixed efficiency of converting fresh milk into BW gain of 4.89 g/g (Theil et al., 2002). Resulting negative estimates were replaced by 0, assuming these piglets did not consume sow milk anymore (CTRL: 13, TREAT: 7 piglets; therein, in CTRL 2 high birthweight (**HBW**) piglets and 11 low birthweight (**LBW**) piglets; in TREAT 3 HBW piglets and 4 LBW piglets).

$$\text{Estimated intake of milk (g/day)(BW gain (g/day) – intake of total feed (g/day) / FCR (g/g))} \times 4.89 \quad (2)$$

Dry matter intake of milk was then calculated assuming a dry matter content of 19 % (Hurley, 2015). The complete procedures for the calculation of nutrients intake can be found in Supplementary Text 1.

2.4. Statistics

Statistical analyses were conducted with SAS 9.4. The effects of treatment (i.e. grouping day plus split-weaning vs. control), birthweight class (HBW vs. LBW) and their interaction on multiple response variables based on piglet level were analysed by analysis of variance. For response variables based on piglet level, (1) For response variables piglet BW, BW gain, dry matter intake of feed and milk, live feeding behaviour, live suckling behaviour, damage scores on snout, ear and tail and skin lesions, fixed effects included treatment, birthweight class and their interaction; the random effect was sow nested within batch. (2) For video feeding behaviour and video suckling behaviour where piglets could only be distinguished into high and low birthweight class within batch, fixed effects included treatment, birthweight class and their interaction; the random effect included batch only. When the interaction between treatment and birthweight class was significant, it was further investigated with post hoc pairwise comparisons using the differences of the least square means among four types of focal piglets (CTRL-HBW, CTRL-LBW, TREAT-HBW, TREAT-LBW).

For response variables based on sow or batch level, (1) For suckling related variables, number of successful suckling bouts per sow during 7.5 h, percentage of piglets involved in cross-suckling at least once per litter, percentage of non-permanent cross-sucklers per litter, percentage of permanent cross-sucklers per litter, percentage of piglet mortality per litter and percentage of crushed piglets per litter, the fixed effect was treatment; the random effect included batch only. (2) For homogeneity related variables, within-batch standard error and standard deviation included treatment as fixed effect, and within-batch coefficient of variation included treatment as fixed effect as well as batch as random effect.

(1) For continuous variables (i.e. BW, BW gain, dry matter intake of feed and milk, damage score on snout and ear, and within-batch standard error and standard deviation in BW and BW gain), the normality of model residuals was checked using PROC UNIVARIATE. The distribution of residuals in the models with dry matter intake of milk as response variables was not normal, therefore these variables was converted using log (1 +N) before analysis in PROC MIXED. For the other continuous variables, the distribution of residuals was normal, therefore PROC MIXED was used. (2) For proportions, i.e. proportion of time spent on contacting sow feed and piglet feed during sow feeding times and during the day, percentage of piglets involved in cross-suckling at least once per litter, percentage of non-permanent cross-sucklers per litter, percentage of permanent cross-sucklers per litter, percentage of piglet mortality per litter, percentage of crushed piglets per litter, within-batch coefficient of variation in BW and BW gain which were in the range of 0–1, PROC GLIMMIX with a beta distribution and logit link function was used; when the proportion was equal to 0 and 1, it was converted to 0.0000001 and 0.9999999 before analysis, respectively, to accommodate a beta distribution. (3) For count data, i.e. the frequency of presence at teats, skin lesions and number of successful suckling bouts per sow during 7.5 h, PROC GLIMMIX with Laplace approximation, Poisson distribution and log link function were initially used. In models where no evidence of overdispersion was present, i.e. the values of Pearson Chi-Square / DF were smaller than one (Stroup et al., 2018), Poisson distribution was used; when overdispersion was detected, a negative binomial distribution was used as an alternative for the Poisson distribution. (4) For categorial data, i.e. damage score on tail, PROC GLIMMIX with a multinomial distribution and cumulative logit link function was used. Statistical significance was set at $P < 0.05$ and data are presented as mean ± SEM.

3. Results

3.1. *The effect of two intervention strategies on piglet and sow traits*

3.1.1. *After grouping*

During the 7 weeks of lactation, as piglets grew older, variation in BW increased in both CTRL and TREAT for both focal piglets (Fig. 3) and all piglets (Supplementary Fig.1). The BW of the focal piglets showed a similar pattern as that of all piglets illustrating that the performance of the focal piglets was representative for the entire litters in the MS system. There was no significant difference in within-batch standard error, within-batch standard deviation or within-batch coefficient of variation in BW, or BW gain between CTRL and TREAT in either focal piglets or all piglets during lactation (Supplementary Table 2).

As shown in Table 1, in early lactation, no significant differences were found between CTRL and TREAT in the variables measured up to day 35, i.e. BW, BW gain, percentage of time spent on contacting feed during sow feeding times and the frequency of presence at teats on day 18, or damage scores and skin lesions on day 27.

3.1.2. *After split-weaning*

As shown in Table 1, after split-weaning on day 35, no significant interaction between treatment and birthweight class was found, except for dry matter intake of milk during days 42–43 (Treatment × birthweight class interaction: $P = 0.030$, Fig. 4a). The results of the pairwise comparisons among the four types of focal piglets (CTRL-HBW, CTRL-LBW, TREAT-HBW, TREAT-LBW) showed that TREAT-LBW piglets drank more milk than CTRL-LBW piglets (182 ± 16 g/day vs. 103 ± 14 g/day, $P = 0.004$), but there was no difference between TREAT-HBW and CTRL-HBW piglets (197 ± 23 g/day vs. 169 ± 18 g/day, $P = 0.828$). In addition, although there was no significant interaction between treatment and birthweight class, it was noted that the effect of treatment on total feed intake during days 42–43 was more pronounced for LBW piglets (CTRL: 493 ± 29 g/day, TREAT: 401 ± 27 g/day) than for HBW piglets (CTRL: 512 ± 29 g/day, TREAT: 476 ± 33 g/day);

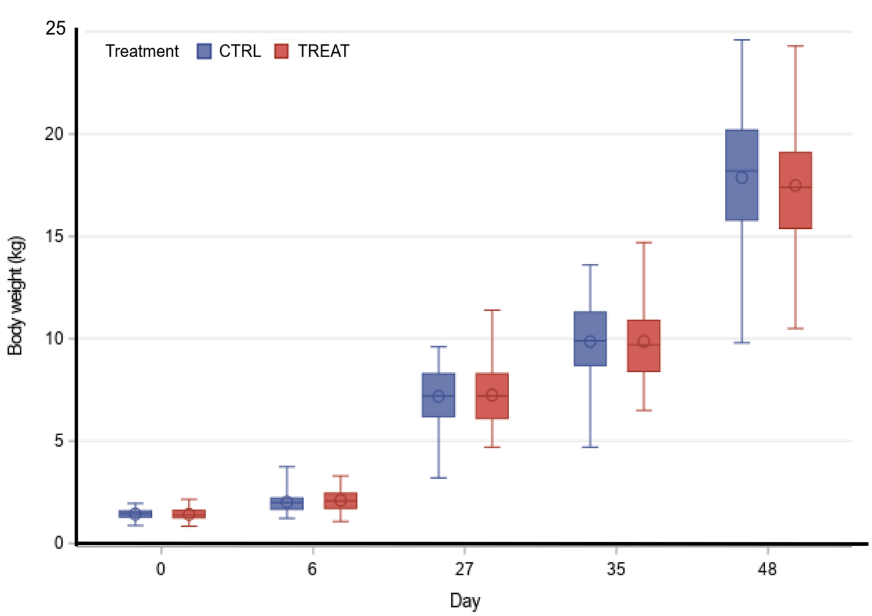

Fig. 3. Boxplot showing the body weight (BW) of focal piglets during a 7-week lactation in the multi-suckling system at five weighing times, with indicating minimum, 25th percentile values of BW, median, 75th percentile values of BW, maximum of BW of piglets. The hollow circle in each box indicates mean values of BW of piglets. CTRL: piglets were grouped during days 8–9 p.p. and no split-weaning was applied; TREAT: piglets were grouped during days 13–14 p.p. and the three heaviest non-focal piglets per litter were split-weaned on day 35 p.p.

Table 1
The body weight (BW), BW gain, dry matter intake, feeding behaviours, suckling behaviours, and damage scores of snout, ears and tails, and skin lesions of focal piglets (n = 160) in control (CTRL) and treatment (TREAT) batches, and in two birthweight classes of piglets, i.e. high birthweight (HBW) and low birthweight (LBW) piglets during a 7-week lactation in the multi-suckling system. CTRL: piglets were grouped during days 8–9 p.p. and no split-weaning was applied; TREAT: piglets were grouped during days 13–14 p.p. and the three heaviest non-focal piglets per litter were split-weaned on day 35 p.p.

Variables[a]		Mean ± SEM				*P*		
		Treatment		Birthweight class[b]				
		CTRL	TREAT	HBW	LBW	Treatment	Birthweight class	Interaction
BW (kg)								
	Day 0	1.4 ± 0.0	1.4 ± 0.0	1.6 ± 0.0	1.3 ± 0.0	0.774	**< 0.001**	0.653
	Day 48	17.9 ± 0.3	17.5 ± 0.3	18.7 ± 0.3	16.7 ± 0.4	0.479	**< 0.001**	0.746
BW gain (g/day)								
	Days 35–48	618 ± 14	586 ± 18	641 ± 14	563 ± 17	0.230	**< 0.001**	0.742
	Days 0–35	241 ± 5	242 ± 6	251 ± 5	232 ± 5	0.906	**0.004**	0.767
	Days 0–48	343 ± 7	335 ± 7	357 ± 6	321 ± 7	0.495	**< 0.001**	0.753
Dry matter intake (g/day) on days 42–43								
	Piglet feed	329 ± 21	261 ± 21	313 ± 22	278 ± 20	0.120	0.173	0.594
	Sow feed	173 ± 8	178 ± 10	180 ± 9	170 ± 9	0.773	0.331	0.131
	Total feed	502 ± 20	439 ± 21	494 ± 22	449 ± 20	**0.072**	0.103	0.296
	Milk	135 ± 12	190 ± 14	183 ± 15	141 ± 11	**0.039**	**0.027**	**0.030**
Feeding behaviour during sow feeding times (%)								
Day 18	Contacting piglet feed	9.2 ± 2.4	10.5 ± 4.2	10.9 ± 4.1	8.8 ± 2.5	0.855	0.412	0.732
	Contacting sow feed	9.4 ± 2.2	7.4 ± 1.6	11.1 ± 2.1	5.7 ± 1.2	0.582	**0.050**	0.923
	Contacting total feed	18.6 ± 2.8	18.0 ± 4.2	22.1 ± 3.5	14.5 ± 2.9	0.858	**0.059**	0.914
Days 41–43	Contacting piglet feed	8.5 ± 0.9	5.3 ± 0.8	6.7 ± 0.9	7.1 ± 0.9	**0.072**	0.304	0.254
	Contacting sow feed	10.0 ± 0.8	9.4 ± 0.8	10.1 ± 0.9	9.3 ± 0.7	0.613	0.412	0.271
	Contacting total feed	18.4 ± 1.2	14.7 ± 1.2	16.8 ± 1.2	16.4 ± 1.2	0.169	0.829	0.660
Feeding behaviour during the day (%)								
Day 41	Contacting piglet feed	5.6 ± 0.5	3.2 ± 0.5	4.4 ± 0.5	4.5 ± 0.5	**0.005**	0.792	0.537
	Contacting sow feed	4.9 ± 0.6	5.6 ± 0.5	4.8 ± 0.5	5.7 ± 0.6	0.303	0.192	0.591
	Contacting total feed	10.5 ± 0.8	8.9 ± 0.6	9.2 ± 0.7	10.2 ± 0.8	0.298	0.266	0.910
Suckling behaviour: the presence at teats (no./7.5 h)								
Day 18	Front and middle teats	3.5 ± 0.4	3.5 ± 0.5	4.3 ± 0.5	2.7 ± 0.4	0.843	**0.021**	0.347
	Total teats	5.0 ± 0.5	4.8 ± 0.6	5.7 ± 0.6	4.0 ± 0.5	0.960	**0.036**	0.944
Day 41	Front and middle teats	3.9 ± 0.3	5.0 ± 0.4	4.5 ± 0.3	4.4 ± 0.4	**0.052**	0.731	0.693
	Total teats	6.0 ± 0.2	6.4 ± 0.3	6.2 ± 0.3	6.2 ± 0.3	0.471	0.964	0.871
	Alien teats	1.4 ± 0.3	2.0 ± 0.3	1.7 ± 0.3	1.8 ± 0.3	0.177	0.793	0.447
Damage score								
Day 27	Snout	0.4 ± 0.1	0.6 ± 0.1	0.6 ± 0.1	0.4 ± 0.1	0.146	0.172	0.678
	Ear	0.4 ± 0.0	0.4 ± 0.1	0.4 ± 0.1	0.4 ± 0.1	0.868	0.516	0.784
	Tail	0.3 ± 0.1	0.4 ± 0.1	0.3 ± 0.1	0.4 ± 0.1	0.221	0.283	0.697
Day 44	Snout	0.4 ± 0.1	0.3 ± 0.0	0.4 ± 0.1	0.3 ± 0.0	**0.084**	0.612	0.439
	Ear	0.4 ± 0.1	0.4 ± 0.1	0.4 ± 0.0	0.5 ± 0.1	0.913	0.521	0.545
	Tail	0.5 ± 0.1	0.5 ± 0.1	0.4 ± 0.1	0.5 ± 0.1	0.934	0.509	0.400
Skin lesions								
Day 27	Total lesions	3.5 ± 0.4	4.9 ± 0.6	4.8 ± 0.6	3.6 ± 0.5	0.216	**0.080**	0.226
Day 44	Total lesions	8.4 ± 0.8	8.0 ± 0.7	8.9 ± 0.9	7.6 ± 0.6	0.932	0.161	0.472

[a] Variables: (1) Contacting feed during sow feeding times (% of observations): contacting (i.e. sniffing or eating) sow feed or piglet feed during sow feeding times on day 18 (video observation), during days 41–43 (live observation) using 2-min instantaneous scan sampling at 08:00–08:30 h and 16:00–16:30 h. For live observations, the percentage of time spent on contacting feed was calculated per piglet; for video observations, it was calculated per high or low birthweight piglet. (2) Contacting feed during the day (% of observations): contacting (i.e. sniffing or eating) sow feed or piglet feed during the day on day 41 (live observation) using 15-min instantaneous scan sampling at 08:30 h–16:00 h; it was calculated per piglet. (3) Suckling behaviour on day 18 (video observation) at 08:30 h– 16:00 h: the frequency of presence at teats per (high or low birthweight) piglet during 7.5 h; suckling behaviour on day 41 (live observation) at 08:30–16:00 h: the frequency of presence at teats per piglet during 7.5 h. Front and middle teats: front (first two pairs) and middle pairs of teats at both their own mother and cross-suckling sows; Total teats: the sum of front, middle and rear teats at both their own mother and cross-suckling sows. Alien teats on day 41: teats of cross-suckling sows. (4) The damage scores on ear and snout were averaged from left and right sides. (5) Skin lesions were counted as the number of fresh lesions on the whole body, except for ears and tails.

[b] Birthweight class: HBW and LBW focal piglets. In each litter, two boars and two gilts with the second lowest and highest birthweight within sex were selected as focal piglets on day 14 postpartum (p.p.).

similarly, the effect of treatment on the frequency of presence at front and middle teats during 7.5 h on day 41 was more pronounced for LBW piglets (CTRL: 3.8 ± 0.5, TREAT: 5.0 ± 0.5) than for HBW piglets (CTRL: 4.1 ± 0.4, TREAT: 5.0 ± 0.5). The detailed description of dry matter intake of nutrients and BW gain, and BW in four types of focal piglets (CTRL-HBW, CTRL-LBW, TREAT-HBW, TREAT-LBW) are shown in Fig. 4a and b, respectively. The detailed description of all measured variables in four types of focal piglets are shown in Supplementary Table 3.

During sow feeding times during days 41–43, TREAT piglets tended to spend less time on contacting piglet feed than CTRL piglets (5.3 ± 0.8 % vs. 8.5 ± 0.9 %) ($P = 0.072$). On day 41 during the day, TREAT piglets spent less time on contacting piglet feed than CTRL piglets (3.2 ± 0.5 % vs. 5.6 ± 0.5 %) ($P = 0.005$). Correspondingly, TREAT piglets tended to consume less feed than CTRL piglets (439 ± 21 g/day vs. 502 ± 20 g/day) during days 42–43 ($P = 0.072$). On day 41, TREAT piglets tended to present more often at front and middle teats per 7.5 h during suckling bouts than CTRL piglets (5.0 ± 0.4 vs. 3.9 ± 0.3) ($P = 0.052$). In addition, during days 42–43, 9.3 % of piglets in TREAT (HBW: 4 %, LBW: 5.3 %) and 16.9 % of piglets in CTRL (HBW: 2.6 %, LBW: 14.3 %) did not consume milk. On day 44, TREAT piglets tended to have lower damage scores on snout than CTRL piglets (0.3 ± 0.0 vs. 0.4 ± 0.1) ($P = 0.084$). No other significant differences were found between CTRL and TREAT (Table 1).

As shown in Supplementary Table 4, there were no differences between CTRL and TREAT in the number of successful suckling bouts per

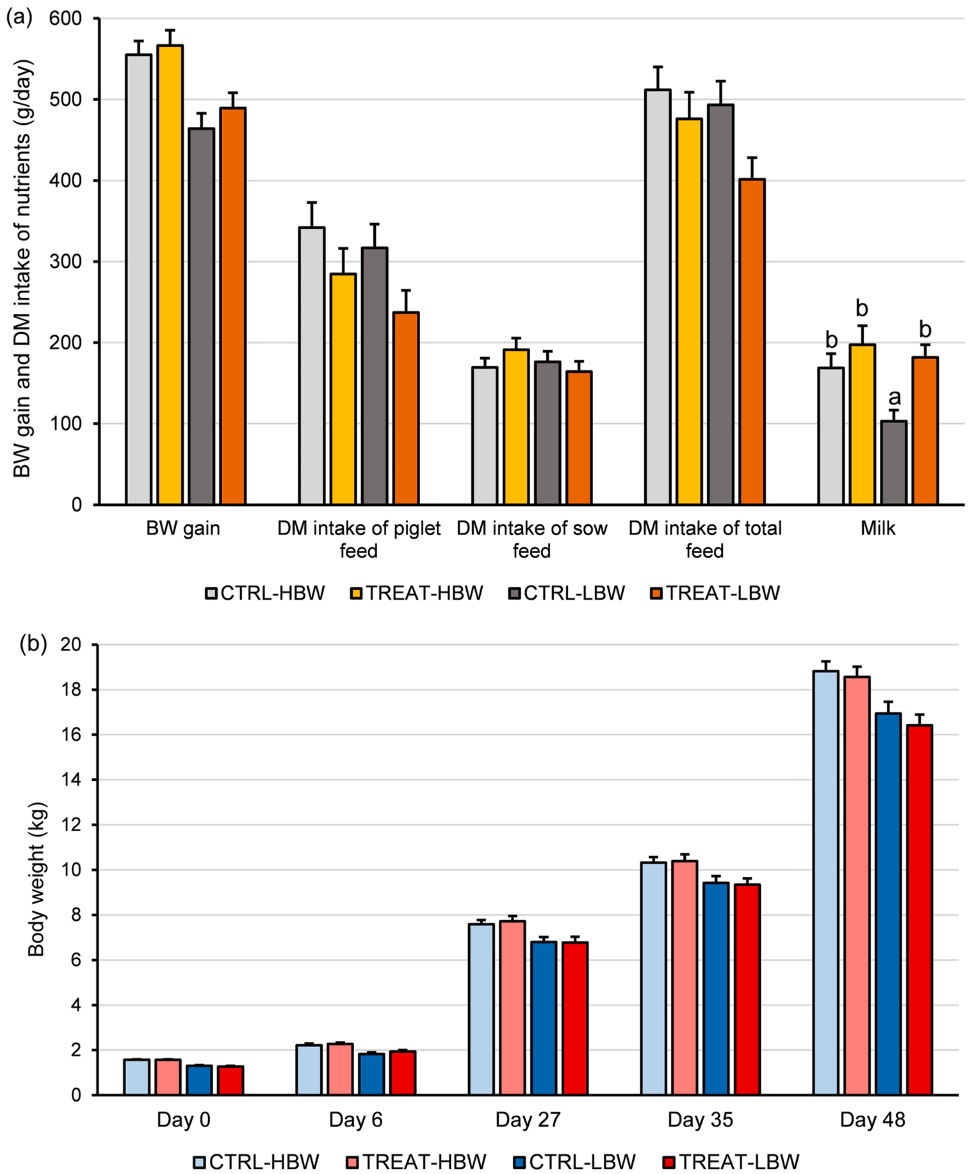

Fig. 4. (a) Bar chart showing BW gain during days 35–48 (g/day), dry matter intake of nutrients (g/day) during days 42–43 in four types of focal piglets during a 7-week lactation in the multi-suckling system. [a,b] values with different letters differ significantly within nutrient intake or BW gain among four types of focal piglets ($P < 0.05$). (b) Bar chart showing the body weight (BW) in four types of focal piglets, i.e. high birthweight piglets in control (CTRL-HBW), high birthweight piglets in treatment (TREAT-HBW), low birthweight piglets in control (CTRL-LBW) and low birthweight piglets in treatment (TREAT-LBW) during a 7-week lactation in the multi-suckling system at five weighing times. CTRL: piglets were grouped during days 8–9 p.p. and no split-weaning was applied; TREAT: piglets were grouped during days 13–14 p.p. and the three heaviest non-focal piglets per litter were split-weaned on day 35 p.p.

sow during 7.5 h either on day 18 (mean: 8.8 ± 0.4) or day 41 (mean: 5.5 ± 0.3). The percentage of piglets involved in cross-suckling at least once per litter was higher in TREAT than that in CTRL (68.0 ± 5.3 % vs. 37.1 ± 6.6 %, $P = 0.020$). The percentage of non-permanent cross-sucklers per litter (i.e. piglets which were present both at their own mother and alien sows during sucking bouts) was higher in TREAT than that in CTRL (62.7 ± 5.5 % vs. 27.1 ± 5.8 %, $P = 0.008$). The percentage of permanent cross-sucklers per litter (i.e. piglets which were only present at alien sows and never present at their own mother during suckling bouts) did not differ between the two groups (mean: 7.7 ± 2.3 %).

3.1.3. Mortality of all piglets during lactation

As shown in Supplementary Table 4, no difference in percentage of piglet mortality per litter was found between CTRL and TREAT during the entire lactation. In total, 68.4 % and 80.6 % of deaths in CTRL and TREAT were due to crushing. The percentage of crushed piglets per litter tended to be higher in TREAT than in CTRL groups during days 9–14 (7.3 ± 1.7 % vs. 2.9 ± 1.1 %; $P = 0.087$), i.e. during the period in which the TREAT piglets were not yet grouped; but over the complete period during days 0–48, neither the 5 % higher crushing, nor the 3 % higher piglet mortality in TREAT was statistically different from CTRL.

3.2. Comparison between low and high birthweight piglets

As shown in Table 1, there was a significant effect of birthweight class on BW and BW gain during all periods examined, with HBW piglets performing better, except for the period during days 27–35 in which the difference in BW gain was not significant.

The difference in BW gain during days 0–27 (difference: 21 g/day, $P = 0.001$) and during days 0–35 (difference: 19 g/day, $P = 0.004$) was in line with the observed percentage of time spent on contacting total feed (difference: 7.6 %, $P = 0.059$) and sow feed (difference: 5.4 %, $P = 0.050$) during sow feeding times on day 18. Moreover, it was in line with the observed teat presence of piglets on day 18, where HBW piglets suckled more often from front and middle teats during 7.5 h (difference: 1.6, $P = 0.021$) and from total teats (difference: 1.7, $P = 0.036$) than LBW piglets. Skin lesions on day 27 were higher in HBW than in LBW piglets (difference: 1.2, $P = 0.080$), while damage scores on snout, ear and tail on day 27 were similar in HBW and LBW piglets.

After split-weaning on day 35, HBW piglets had a higher BW gain during days 35–48 than LBW piglets (difference: 78 g/day, $P < 0.001$) likely because of both a numerical increase in total feed intake (difference: 45 g/day, $P = 0.103$) and an increase in milk intake (difference: 42 g/day, $P = 0.027$) during days 42–43. No other significant differences were found between HBW and LBW piglets.

4. Discussion

The aim of the present study was to investigate if performance and behaviours of HBW and LBW piglets during a 48 day lactation in an MS system differed in view of the two interventions, i.e. later grouping of litters at day 13 p.p. instead of day 8 p.p. and split-weaning of three heavy piglets from each litter at day 35 p.p. These interventions aimed to improve the BW gain of LBW piglets and thereby reduce the BW variation at weaning.

4.1. Later grouping

In our study, grouping at either day 8 p.p. or day 13 p.p. did not affect BW, BW gain or within-batch variation in BW or BW gain in either focal piglets or all piglets after grouping, nor was there an interaction between treatment and high vs. low birthweight focal piglets. Consistently, in MS systems, Thomsson et al. (2016) found no differences between piglets co-mingled at day 7 and 14 p.p. in their BW and within-litter variation in BW at weaning on day 44 p.p. However, one study with MS systems found that piglets grouped on day 7 p.p. had a lower BW gain during days 6–26 p.p. than those grouped on day 14 p.p. (Verdon et al., 2020). In the current study, no differences were found in growth performance of LBW focal piglets before day 35 between early and later grouping batches, possibly indicating later grouping does not improve the growth performance of LBW piglets.

In early lactation, piglets are mainly reliant on sow milk for their development. The occurrence of cross-suckling after grouping can have detrimental consequences for milk intake and performance of piglets (Dybjaer et al., 2001) owing to increased competition at the udder (Olsen et al., 1998) and missing of milk injection when fighting for teats (Wattanakul et al., 1997). This might be especially harmful for LBW piglets, as they have less ability to fight for teats compared with HBW piglets. We expected that later grouping would reduce cross-suckling, snout damage scores and increase the presence at teats of especially LBW focal piglets. However, in the current study, no effect of grouping age was observed on snout damage scores at day 27 and teat presence at day 18. The reason could be that grouping has been applied 10 and 4 days before day 18 in early and late grouping batches respectively, and the effects of later grouping on these indicators might have disappeared.

It was found that piglets during 16–20 days of age can learn feeding behaviours from sows by observation and participation, which is called 'vertical social learning' (Oostindjer et al., 2011). We expected that later grouped piglets, especially LBW piglets in later grouping batches would have a higher teat presence due to reduced cross-suckling, stay closer to their mother, and thereby spend more time contacting feed during sow feeding times by observing and learning from sows to eat. However, in the current study, later grouping did not affect the percentage of time spent on contacting solid feed during sow feeding times on day 18, nor was there an interaction between treatment and birthweight class. It might be that TREAT piglets stay close to their mother waiting for suckling bouts during sow feeding times rather than contacting feed.

Reciprocal fighting commonly occurs after grouping of litters for establishing a new hierarchy (Turner et al., 2006; Van Kerschaver et al., 2021). Unacquainted piglets that were shortly placed together were reported to fight shorter and had fewer injuries at younger age (day 5 vs. day 12) (Pitts et al., 2000). We expected that later grouping piglets have more skin lesions than early grouping piglets. However, in the present study, no differences in fresh skin lesions on the focal piglets' body were found between treatment groups on day 27 p.p. It was found that piglets performed frequent aggressive behaviours resulting in skin lesions within 1 day after grouping on day 10 p.p. (D'Eath, 2005). As grouping had been applied 14 and 19 days earlier respectively in CTRL and TREAT, it might be that aggressive behaviours have disappeared on day 27 p.p. On the other hand, in semi-natural conditions, when encountering unfamiliar piglets, the majority of interactions was peaceful nose-to-nose contacts while the frequency of aggressive behaviour was low (Petersen et al., 1989). It could also be that MS systems are closer to the semi natural conditions than conventional housing. Piglets may have shown minimal aggressive behaviour after grouping which thus led to minimal skin lesions and no difference between the groups at day 27 p.p.

In the current study, for all piglets in the MS system, the proportion of crushing tended to be higher in TREAT than CTRL during the period when TREAT piglets were not yet grouped during days 9–14 p.p. This higher crushing might be that in TREAT batches, sows have to nurse their piglets in the loose farrowing pens during days 9–14 when these piglets did not have access to communal MS area. These piglets have less free moving space compared to early grouping piglets, which probably increased the difficulty for escaping from nursing sows in the process of lying down. But over the entire lactation, piglet mortality, due to crushing or other causes, did not differ between early and later grouping batches.

To summarise, later grouping had little effect on most parameters measured in our study. Later grouping does appear to increase crushing shortly after grouping, even though piglet mortality during the entire lactation during days 0–48 was not statistically different between early and later grouping batches. We could not confirm our hypothesis that later grouping helps to improve the growth performance of LBW piglets post grouping.

4.2. Split-weaning

In the TREAT group on day 35 p.p., the three heaviest non-focal piglets per litter were removed from the MS system. The remaining piglets in TREAT and all piglets in CTRL were weaned on day 48 p.p. We expected that split-weaning could reduce the competition at the udder and in the feeding area, thereby enabling especially LBW piglets to have an increased milk consumption and solid feed intake, and thus accelerated growth. However, during week 6 and 7 after split-weaning, there was no difference in BW, BW gain and within-batch variation in BW or BW gain in either focal piglets or all piglets between CTRL and TREAT. But as expected, we observed a significant higher milk intake and a tendency of decreased snout damage in TREAT focal piglets during days 42–44, compared with CTRL focal piglets. Moreover, during days 42–43, TREAT piglets tended to be present more often at the front and middle teats, while numerically present less often at rear teats than CTRL piglets, possibly due to their moving from teats with a lower milk yield to teats with a higher milk yield after split-weaning. Similarly, Pluske and Williams (1996) found that following split-weaning, the remaining piglets used the anterior teats previously occupied by the split-weaned piglets. The front and middle part of the udder is known to have a higher milk production than the rear part of the udder (Skok et al., 2007).

We expected that split-weaning could reduce the competition at the feeder and increase feed intake of piglets due to a lower number of piglets in the MS area. Unexpectedly, no difference in skin lesions of focal piglets on day 44 was found between CTRL and TREAT. The TREAT piglets did not have an increased feed intake during days 42–43; inversely, TREAT piglets had a tendency of reduced feed intake and a numerically lower percentage of time contacting feed both during the day and during sow feeding times after split weaning. This may suggest that TREAT piglets seem to transfer their interest from feed to milk when more productive teats are available. The unchanged BW gain in TREAT piglets compared to CTRL piglets was probably a result of the increased milk intake being compensated for by the reduced feed intake. Moreover, no differences were found in BW and BW gain during days 35–48 in LBW piglets between CTRL and TREAT groups after split-weaning. But interestingly, we found that after split-weaning, the increased amount of milk intake, the increased presence at front and middle teats and the reduced amount of feed intake was more obvious for LBW piglets than for HBW piglets. Likewise, the increased milk intake in LBW piglets was seemingly compensated for by a reduced feed intake, resulting in no treatment effects on BW gain of LBW piglets. Some previous studies indicated that piglets mainly rely on milk in week 0–3 (Barber et al., 1955) (Abraham and Chhabra, 2004) and on solid feed for growth from week 4 onwards (Tang et al., 2022b). Therefore, an earlier split-weaning age for HBW piglets before day 35 may be more helpful to increase milk intake and thus the growth rate of LBW piglets. However, the welfare of HBW piglets should be also taken into consideration.

On day 41, cross-suckling seems to occur more often in TREAT focal piglets, as the percentage of piglets involved in cross-suckling at least once per litter was higher in TREAT focal piglets than in CTRL focal piglets (68.0 % vs. 37.1 %). In addition, on day 41, the proportion of non-permanent cross sucklers per litter (i.e. piglets which were present both at their own mother and alien sows) was higher in TREAT than in CTRL (62.7 % vs. 27.1 %). It could be that, after split-weaning, more teats were available for piglets, which results in a higher number of non-permanent cross-sucklers trying to attain milk from foreign mothers, especially when their own mother was in the IS area, or when their own mother has a low milk production (Olsen et al., 1998). This could also explain the increased milk intake in TREAT compared with CTRL. According to Algers and Jensen (1991), milk production is influenced by intensity of teat stimulation. If so, TREAT sows might have had lower milk production as fewer piglets remained in the MS system to stimulate teats after split-weaning. However, TREAT piglets still achieved a higher milk intake, which could be that they transferred to more productive teats or became cross-sucklers. It is interesting to see that on day 41 the permanent cross-sucklers per litter (i.e. cross-sucklers which were never present at their own mother) (5.3 % vs. 10.0 %) in TREAT was numerically lower than that in CTRL. There might be an interaction between later grouping and split-weaning on cross-suckling, as later grouping seems to help to reduce cross-suckling, while split-weaning seems to stimulate cross-suckling. The two intervention strategies might also have interaction effects on other measured variables and cannot be separated, as these two interventions were imposed on the same group of piglets.

5. Conclusion

The aim of current study was to investigate the effect of later grouping of litters and split-weaning on performance, nutrient intake, suckling and feeding behaviour of focal piglets during a 7-week lactation in a multi-suckling system to improve the BW gain of LBW piglets and thereby reduce the BW variation at weaning. We found that grouping litters during days 13 –14 instead of days 8 – 9 did not affect their BW gain, within batch variation in BW gain, suckling and feeding behaviours after grouping. Piglet crushing was higher during days 9–14 in later grouping piglets when piglets were not yet grouped, compared to early grouping piglets; but no difference in piglet mortality was found between the two treatments during the entire lactation. We could not confirm our hypothesis that later grouping helps to improve the growth performance of LBW piglets after grouping. After split-weaning of three heaviest non-focal piglets on day 35, no differences were found in growth performance or piglet homogeneity between the two groups. But split-weaning did appear to reduce the competition at the udder, as snout damages were reduced, and milk intake and presence at front and middle teats increased. The treatment did not favour the LBW piglets, with the exception of milk intake. The milk intake and presence at front and middle teats in TREAT piglets was increased in particular in LBW piglets, but this was seemingly compensated for by a reduction in feed intake and therefore likely not reflected in an increased BW gain and reduced BW variation. Further research is needed for example changing the age of split-weaning in order to reduce BW variation in MS systems.

Ethics approval

All experimental procedures were approved by the Dutch Central Committee of Animal Experiments in the Netherlands (IVD number 2016. W-0096.001).

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CRediT authorship contribution statement

Tianyue Tang: Methodology, Investigation, Software, Formal analysis, Data curation, Writing – original draft, Visualization. **Walter J.J. Gerrits:** Conceptualization, Methodology, Formal analysis, Writing – review & editing, Supervision, Project administration, Funding acquisition. **Nicoline M. Soede:** Methodology, Formal analysis, Writing – review & editing, Supervision, Project administration, Funding acquisition. **Carola M.C. van der Peet-Schwering:** Conceptualization, Methodology, Resources, Writing – review & editing, Supervision, Project administration, Funding acquisition. **Inonge Reimert:** Conceptualization, Methodology, Formal analysis, Writing – review & editing, Supervision.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

The datasets generated and analysed during the current study are available from the corresponding author on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.applanim.2023.105835.

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