Animal 16 (2022) 100651

Contents lists available at ScienceDirect

Animal
The international journal of animal biosciences

Variation in piglet body weight gain and feed intake during a 9-week lactation in a multi-suckling system

T. Tang [a,b], W. J. J. Gerrits [a], I. Reimert [b], C. M. C. van der Peet-Schwering [c], N.M. Soede [b,*]

[a] Animal Nutrition Group, Department of Animal Sciences, Wageningen University & Research, Wageningen, the Netherlands
[b] Adaptation Physiology Group, Department of Animal Sciences, Wageningen University & Research, Wageningen, the Netherlands
[c] Wageningen Livestock Research, Wageningen University & Research, Wageningen, the Netherlands

ARTICLE INFO

Article history:
Received 26 March 2022
Revised 6 September 2022
Accepted 8 September 2022

Keywords:
Behaviour
Group lactation
Individual feed intake
Individual growth variation
N-alkanes

ABSTRACT

A multi-suckling (**MS**) system for sows and piglets has been developed aiming to improve animal welfare. In this system, large variation in BW gain exists between piglets up to weaning at 9 weeks of age. We aimed to study the causes of variation in BW gain and DM intake of solid feed (**DFI**) (piglet + sow feed) of piglets during lactation in the MS system. A total of 15 sows and 60 focal piglets across three batches were studied. Individual intake of piglet and sow feed was measured by the dual marker method, and multiple variables were recorded. Multiple linear regression analysis with forward selection was conducted on BW gain and DFI after correcting for piglet sex and batch, using multiple explanatory variables including genetic background, birthweight (**BiW**), DM feed intake, behaviours and number of skin lesions. These factors jointly explained less than 45 % and 21 % of the variation in BW gain and DFI, respectively. In weeks 2–4, variation in BW gain was mainly explained by BiW (12.0 %) and play and nosing behaviours (7.6 %). In weeks 4–6 and 6–8, it was largely explained by DM intake of piglet feed with 15.1 % and 25.9 %, respectively. Individual variation in DFI in weeks 2–4 was explained by the presence at front and middle teats during suckling bouts (2.9 %), in weeks 4–6 by BiW (9.6 %), and in weeks 6–8 by the number of skin lesions (5.1 %). The unexplained variation in BW gain and DFI warrants further investigation.

Implications

In this study, we investigated the causes of variation in BW gain and feed intake of piglets during lactation in multi-suckling systems. Our findings revealed that variation in BW gain of piglets was mainly explained by piglet's birthweight and positive behaviour in weeks 2–4, and by its solid feed intake in weeks 4–8; variation in feed intake was explained by piglet's teat presence in weeks 2–4, by its birthweight in weeks 4–6, and by its number of skin lesions in weeks 6–8. These findings give direction to future investigations to reduce variation in the performance of piglets in multi-suckling systems.

Introduction

Multi-suckling (**MS**) systems for sows and piglets have been developed to improve animal welfare (Thomsson et al., 2016; Van Nieuwamerongen et al., 2017; Verdon et al., 2020). Such systems accommodate groups of lactating sows and their litters, allowing pigs more freedom of movement and social interactions (Weary et al., 2002; Van Nieuwamerongen et al., 2014; Grimberg-Henrici et al., 2018), as well as expression of play, explorative and other natural behaviours compared to conventional housing systems (Van Nieuwamerongen et al., 2015; van Nieuwamerongen, 2017; Schrey et al., 2019). In the study of Van Nieuwamerongen et al. (2017), the gradual weaning during a lactation period of 9 weeks helps to ease the weaning transition and improved the performance of piglets. In this system, piglets can access multiple food sources. They can access sow milk and piglet feed and can join sows to eat sow feed (Van Nieuwamerongen et al., 2015). Such settings resemble the semi-natural conditions, in which piglets are gradually weaned at 17 weeks of age (Jensen and Recén, 1989). During the long lactation period, sows spend an increasing amount of time away from piglets and piglets make a gradual transition from drinking milk to solid feed sources, and ultimately achieve nutritional independency from the sow (Newberry and Wood-Gush, 1986; Petersen et al., 1989).

Body weight homogeneity of piglets during lactation is important for successfully incorporating MS systems in all-in-all-out

* Corresponding author at: Adaptation Physiology Group, Department of Animal Sciences, Wageningen University & Research, P.O. Box 338, 6700 AH Wageningen, the Netherlands.
E-mail address: nicoline.soede@wur.nl (N.M. Soede).

https://doi.org/10.1016/j.animal.2022.100651
1751-7311/

pig production systems. However, substantial variation in BW gain was observed in MS systems at weaning during week 6 (Thomsson et al., 2016) and week 9 (Van Nieuwamerongen et al., 2017), and a better understanding of the factors affecting piglet BW gain variation is needed. As DM feed intake (**DFI**) also varies in piglets (Van Nieuwamerongen et al., 2017), it is of interest to study factors affecting piglet DFI in the MS system as well.

Therefore, the objective of the current study was to investigate how different variables including genetic background, birthweight (**BiW**), feed intake, piglet behaviours and skin lesions explain variation in BW gain and DFI of piglets in three periods (weeks 2–4, weeks 4–6, weeks 6–8) during a 9-week lactation in an MS system.

Material and methods

Animals, housing and experimental design

Fifteen multiparous sows (parity: 3.9 ± 0.4) (Topigs 20) (Topigs Norsvin, Beuningen, the Netherlands) and their litters (Tempo × Topigs 20) across three consecutive batches were studied at the animal facilities of Swine Innovation Centre Sterksel, the Netherlands. On day 14 postpartum (**p.p.**), in each litter, the surviving second lowest and highest BiW piglets from both sexes were selected as focal piglets (total: n = 60) and were intensively followed up to weaning at 64 days of age. Focal piglets were selected from original litters and were never cross-fostered piglets. Sows and piglets received a mark with stock marker spray to distinguish sows and piglets at individual level.

Per batch, five sows and their litters were housed in a MS housing system, which contained two MS units and an intermittent suckling (**IS**) area (Fig. 1a). Each MS unit contained five adjacent farrowing pens (2.2 × 3.2 m) (A), a communal MS area including a partially slatted lying area (11.1 × 2.8 m) (B), a solid concrete feeding area (3.2 × 3.3 m) (C) and a fully slatted dunging area (2.8 × 3.3 m) (D). Each farrowing pen consisted of a solid concrete floor (2.2 × 2.2 m) and a cast iron slatted floor (2.2 × 1.0 m) contained a heated nest for the piglets (0.65 × 1.6 m), a feeding trough with a water nipple for the sows, and a drinking nipple for the piglets. There were two extra drinking bowls for the sows in the lying area and in the dunging area which were also accessible to the piglets. The feeding area contained five feeding places for sows with a stainless steel feeding trough on the floor separated by horizontal metal bars, which was accessible to both sows and piglets (Fig. 1b). The feeding area also contained a surrounding area, which was accessible only to the piglets, with three small round feeders (diameter: 28 cm) (remained in use until day 35p.p.) and a sensor-controlled automatic piglet feeder containing ten feeding places (Rondomat, Fancom B.V., the Netherlands) (used from day 28 p.p.). The IS area was located beside both MS units. It was semi-outdoors and roofed, with three sides of 1.5 m high walls, and it consisted of a communal area, five feeding stalls for sows and a boar pen.

One week before expected farrowing, five sows from the same gestation pen were moved to one MS unit, balanced for expected farrowing date. Sows could access all areas in the MS unit, but were restrained between bars in a temporary crate constructed within the farrowing pens from one night before the expected farrowing date until day 3 p.p. to prevent piglet crushing. The piglets were ear tagged, and litter sizes were standardised (13.8 ± 0.3 piglets/litter) between 24 and 48 h p.p. based on the number of functional teats per sow. Within day 4p.p., piglets received an iron injection,

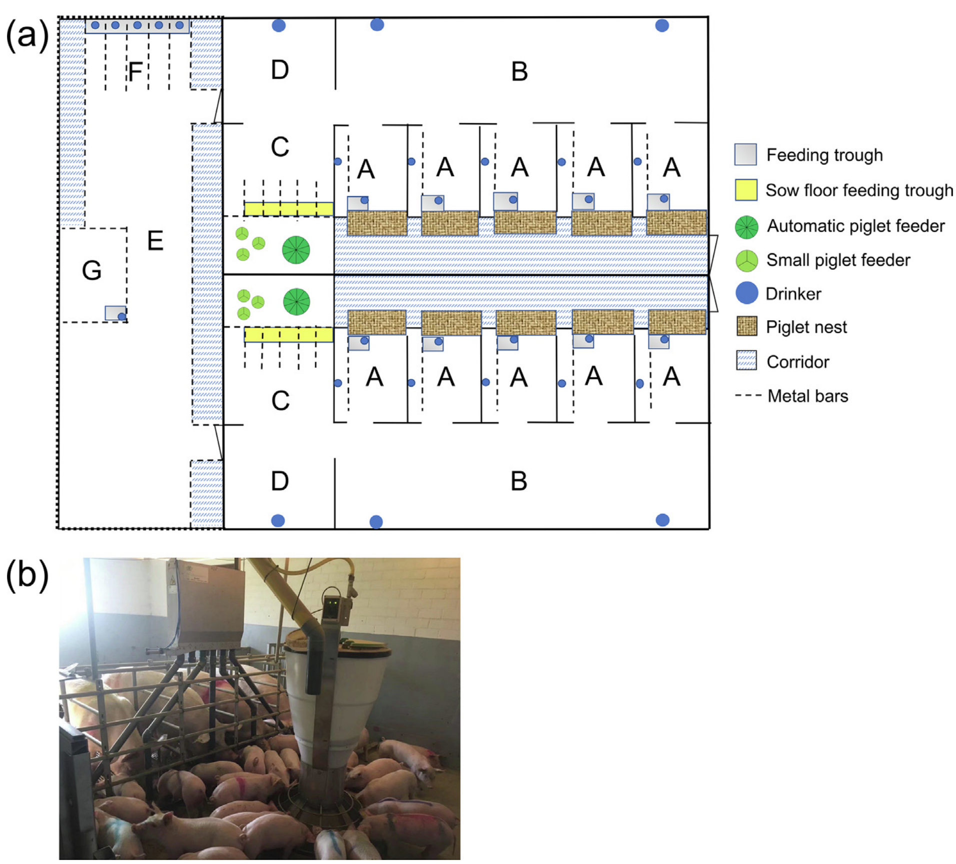


Fig. 1. (a) Layout of the multi-suckling (MS) system for sows and piglets consisting of two MS units and an intermittent suckling (IS) area. Each MS unit contained 5 farrowing pens with piglet nests (A), a communal MS area which included a lying area (B), a feeding area (C) and a dunging area (D). Connected to the MS unit was the IS area (E), feeding stalls for sows (F) and a boar pen (G). (b) Communal feeding area.

but were not tail docked, teeth resected or castrated. From day 4 onwards, the bars were opened to create loose housing and the sows were given access to the communal area. A 31 cm high piglet barrier was put in place to prevent piglets from leaving the farrowing pen until grouping (9.1 ± 0.1 days of age). On day 19, piglets were vaccinated (circovirus-mycoplasma /PRRS vaccine, Boehringer Ingelheim). From day 28 to 34, forced IS was applied by bringing the sows to the IS area for 10 h/day (from 0700 h to 1700 h), during which a sexually mature boar was kept in a boar pen in the IS area to stimulate oestrus. From day 35 until weaning at 64 days of age, sows could voluntarily access the IS and MS area by stepping over a flexible metal partition (height: 30–40 cm) between the two areas but the piglets could not. After the week of forced IS until weaning, no boar was present in the IS area. This IS procedure results in a gradual weaning process for the piglets (Van Nieuwamerongen et al., 2017). The time schedule of the experiment set-up per batch is shown in Fig. 2.

Enrichment materials were provided throughout lactation. During farrowing, two hessian sacks (110 cm × 60 cm) were provided on the solid concrete floor (2.2 × 2.2 m) for sows as nesting materials. From day 2p.p., about 200 g of long straw was provided on the solid floor daily in each farrowing pen. During the entire lactation period, five sisal ropes (length: 1.2 m, 10 mm diameter) and five hessian sacks were hung on the wall in the MS lying area; in the IS area, five metal chains (length: 1.2 m, 11 mm diameter), one rope and two hessian sacks were available to the sows, and one metal chain and one rope were available to the boar.

The sows and their piglets were exposed to natural daylight and supplementary artificial lighting from 0700 to 1800 h. Ambient temperature in the MS unit was maintained around 18 °C with warmwater pipe heating. In the piglet nests, the temperature was set at 33–35 °C (day 1p.p.), 29–31 °C (day 7p.p.) and 23–26 °C (from day 25p.p.) with warmwater floor heating. The IS area had natural light and temperature. Manure and dirty straw were removed daily from the farrowing pens. The MS and IS area were also cleaned daily when necessary. Sawdust and dry powder were scattered when it was wet in the system. The MS system was disinfected and dried after the end of each batch.

Feeding regime

Sows were fed twice daily at around 0800 h and 1600 h, with 2.8 kg/day of sow diet before farrowing and gradually increased up to 8.5 kg/day p.p. (net energy: 9.4 MJ/kg, CP: 146.3 g/kg) (Aveve Biochem BV, Belgium). Before farrowing, sows were fed in floor troughs in the MS feeding area in the morning and in the farrowing pen in the afternoon. On days 0–3, sows were fed in the farrowing pens. On days 4–27, sows were floor fed in the MS feeding area. During forced IS on days 29–34, sows were fed in the IS area at 0700 h and in the MS feeding area at 1730 h. During voluntary IS on days 35–64, sows were fed in the IS area at 0800 h and were floor fed in the MS feeding area at 1600 h. Sows had *ad libitum* access to water via drinking bowls and nipples.

From day 2 p.p. until grouping on day 9, piglets were provided with a commercial diet of large creep feed pellets (8 mm diameter) (Research Diet Services BV, the Netherlands) which was spread over the floor of the farrowing pen which sows could not access. On days 9–11, the large creep feed pellets were provided in the three small

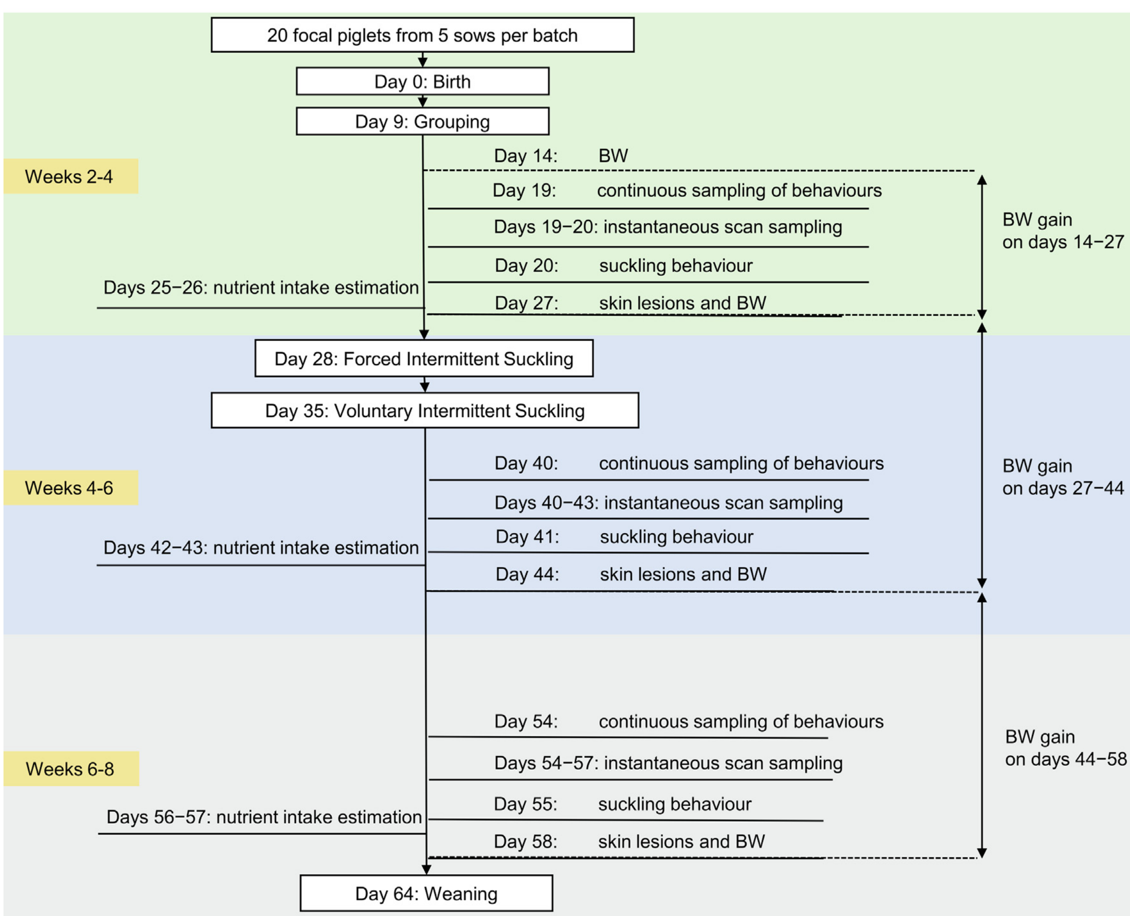


Fig. 2. Time schedule of experiment set-up of sows and piglets in each batch during a 9-week lactation in the multi-suckling system.

round feeders in the MS feeding area together with a commercial weaner diet (Research Diet Services BV, the Netherlands), after which only the weaner diet was provided in small round feeders. Only piglets could access the small round feeders while sows could not. On days 20–21, the weaner diet was mixed with a pre-starter diet (net energy: 10.38 MJ/kg, CP: 164.4 g/kg), after which only the pre-starter diet was provided. On days 37–38, the pre-starter diet was mixed with a starter diet (net energy: 10.09 MJ/kg, CP: 173.5 g/kg), after which only starter diet was provided until weaning on day 64. The pellet size of all diets was 4 mm.

On days 9–28, feed was provided in the small round feeders in the feeding area, which were re-filled twice a day. On days 28–31, feed was also given in the trough of the automatic piglet feeder to make piglets get familiar with the trough. On days 32–64, the storage container of the automatic piglet feeder was filled with feed so that piglets could eat feed *ad libitum*. The piglets had *ad libitum* access to water via the drinking nipples and bowls in the MS system. The ingredient and calculated nutrient composition of sow, piglet pre-starter and starter diets are provided in Supplementary Tables S1, S2 and S3.

Measurements

Body weight

Piglets were weighed on days 0, 14, 27, 44, 58 and 64.

Estimated breeding value of BW gain

The estimated breeding value (**EBV**) of BW gain from birth to slaughter (g/day) of a piglet was calculated as the relative difference between the expected individual BW gain and the population average, based on the performance of the relatives and the genomic relationship matrix. Therefore, an EBV is an estimate of the genetic potential of the piglet. An ear tissue sample was collected from each piglet at the moment of ear tagging within 24 h after birth. DNA extraction and genotyping were performed by Topigs Norsvin (Beuningen, the Netherlands), thus providing BLUPs of the genetic potential of the piglets for the life time daily gain.

Feeding behaviour during sow feeding times and suckling behaviour

Feeding behaviour of the piglets was scored using 2-min instantaneous scan sampling during sow feeding times on days 19–20 (week 3) at 0800–0830 h and 1600–1630 h, and on days 40–43 (week 6) and days 54–57 at 1600–1630 h (week 8) (Fig. 2). During the forced and voluntary IS period, the sows were fed in the IS area in the morning, and therefore, feeding behaviour of piglets in week 6 and week 8 was only observed in the afternoon. During these sow feeding times, every 2 min for each focal piglet, it was noted whether it was in the feeding area, contacting (i.e. sniffing or eating) sow feed or contacting (i.e. sniffing or eating) piglet feed. From these observations, the percentage of time spent on contacting sow feed and piglet feed was calculated per week.

On days 20 (week 3), 41 (week 6) and 55 (week 8), suckling behaviour was observed at 0900–1600 h (Fig. 2). A nursing bout was scored as'unsuccessful' and excluded from analysis when the nursing began within 20 min after a previous nursing (Weary et al., 2002), and no milk let-down was noted. Unsuccessful nursings comprised less than 3 % of total nursings. The frequency of presence at teats of each focal piglet in all suckling bouts (at biological mother and other sows) was scored, on either the front (the first two pairs of teats), the rear (the last two pairs of teats) or the middle teats (the remaining teats). The frequency of presence at front and middle teats (**FM teats**) was summed into one variable for further analysis.

Other behavioural observations and lesions

On days 19 (week 3), 40 (week 6) and 54 (week 8) at 0900–1600 h (Fig. 2), continuous behaviour sampling was performed to determine the frequency of play, nosing, manipulation, aggression, exploration, and ingestion using the ethogram in Table 1. Continuous behavioural sampling was done during five observational

Table 1
Ethogram used for behavioural observations of play, nosing, exploration, manipulation, aggression, and ingestion of piglets in the multi-suckling system.

Category	Behaviour	Description
Play	Individual play	Scampering (forward hops in rapid succession), turning (rapid turn on the spot), head tossing, flopping (rapid drop from an upright position to lying), rolling on back, sliding, or running individually
	Social play (2 pigs or more)	Nudging (play invitation: gentle pushing of another piglet), gambolling (running together), play fighting, or scampering together
	Substrate play	Shaking of head while holding material (e.g. straw, rope) that protrudes from mouth (not scored when only chewing on material)
Nosing	Nosing head or body - piglets	Touching or sniffing any part of another piglet except nose contact, without manipulative behaviours
	Nose contact - piglets	Mutual nose contact between piglets, without manipulative behaviours
	Nosing head or body - sow	Touching or sniffing any part of a sow except nose contact, without manipulative behaviours or massaging the udder
	Nose contact - sow	Mutual nose contact between piglet and sow, without manipulative behaviours
Manipulation	Manipulating piglet	Nibbling, sucking, or chewing part of the body (ears, tail, or other parts) of a piglet, not scored when a piglet clearly only bites an ear tag
	Manipulating sow	Nibbling, sucking, or chewing part of the body (ears, tail, or other parts) of a sow, not scored when a piglet clearly only bites an ear tag
	Belly nosing	Rubbing belly of another pig with up and down snout movements ($\geq$3 up and down movements)
Aggression	Individual or mutual fighting	Horizontal or vertical knocking with the head or forward thrusting with the snout towards another piglet (single event or short series of events) / Biting another piglet (single event or short series of events) / Intense mutual ramming or pushing (parallel or antiparallel), with or without biting, in rapid succession
	Aggression at feeder	Feed-related aggression: pushes, head knocks or bites given at feeder (not scored when e.g. pig gives a head knock at the feeder resulting from manipulative behaviour
Exploration	Exploring system	Nibbling, sucking or chewing on parts of the multi-suckling system such as iron bars, walls, door, floor, ropes, hessian sacks and straw
Ingestion	Sniffing/nosing sow feed	Sniffing/nosing sow feed
	Eating sow feed	Chewing on sow feed (jaw moves up and down)
	Sniffing/nosing piglet feed	Sniffing/nosing piglet feed
	Eating piglet feed	Chewing on piglet feed (jaw moves up and down)
	Drinking	Drinking from water nipple

blocks. The four focal piglets of each litter were observed for 10 min in each block, resulting in a total observation period per piglet of 50 min per day. Play is regarded as an indicator for good welfare (Brown et al., 2015), and nosing is regarded as a positive social interaction (Camerlink and Turner, 2013); therefore, they were summed as positive behaviour. Manipulative and aggressive behaviour towards pigs (Schouten, 1985) are regarded as negative social interactions; therefore, they were summed as negative behaviour. Explorative behaviour belongs to inherent behavioural needs which is a biologically important behaviour to gain information about the surrounding environment and available food resources (Docking et al., 2008). Ingestion behaviour is related with the pigs' requirement of energy. Explorative and ingestion behaviour were analysed separately.

On days 27 (week 4), 44 (week 6) and 58 (week 8) (Fig. 2), the number of skin lesions was counted per piglet by visual assessment as the number of fresh superficial and deep lesions on the whole body, except for ears and tails. Scoring was performed according to the procedure of Turner et al. (2006). The length or diameter per lesion was not taken into account. Lesions were deemed to be deep when haemorrhage was present, otherwise, lesions were noted as being superficial. Skin lesions can be regarded as a proxy for aggressive behaviour given and received (Turner et al., 2006).

Estimation of individual feed and milk intake

Administration of alkanes

Individual daily DM intake of sow feed and piglet feed was measured for each focal piglet on days 25–26 (week 4), days 42–43 (week 6) and days 56–57 (week 8) using the dual alkane marker technique, according to Tang et al. (2022). Two pairs of dual markers were used: C32 and C31 for the estimation of DM intake of sow feed, C32 and C36 for the estimation of DM intake of piglet feed. C32 (42 mg/d, 60 mg/d and 78 mg/d in weeks 4, 6 and 8, respectively) was considered as a reference marker and was melted on a small amount of feed in a forced air oven (melting temperature: 69 °C). Reference marker C32 boluses were prepared freshly before oral administration in an amount of ~ 1.4 g/bolus in week 4, ~ 2.0 g/bolus in week 6, ~ 2.6 g/bolus in week 8, kneaded to a firm bolus using a few drops of sucrose-based lemonade syrup (Karvan Cévitam, the Netherlands). C31 and C36 were considered as in-feed markers, therein 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 (melting temperature: 72 °C) followed with the mixing into the pre-starter and starter diet, providing around 50 mg/kg of C31 in sow feed and 170 mg/kg of C36 in piglet feed, respectively.

On days 22–23, focal piglets were habituated with placebo boluses without reference marker by hand twice per day. On days 25–26 in week 4, days 42–43 in week 6 and days 56–57 in week 8, focal piglets were orally administered one C32 bolus by hand for three times/day at 0830, 1430 and 2030 h, with a total dosing frequency of six times /week per piglet. The number of marker bolus consumed by the piglets was recorded. On days 27, 44 and 58, spot faecal samples of around 20 ~ 70 g were taken from the rectum with a cotton swab from each piglet at 0830 and 1230 h. Sow feed and piglet feed samples were collected for weeks 4, 6 and 8 separately. All feed and faecal samples were stored at − 20 ℃ for further laboratory analysis.

Laboratory analysis

Faecal samples were pooled per piglet per day, and oven-dried at 65 °C and ground to pass a 1 mm screen. The concentrations of n-alkanes in faeces and feed were analysed using gas chromatography as described by Smit et al. (2005).

Dry matter intake of the sow feed and piglet feed in each batch were calculated for days 25–26, 42–43 and 56–57 separately, using eq. [1]:

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

Milk intake was calculated from BW gain, assuming a fixed efficiency of converting fresh milk into BW gain of 4.2 g/g for week 4 (Everts et al., 1995). For weeks 6 and 8, milk intake was calculated using eq. [2], by subtracting DM feed intake from BW gain, assuming fixed feed conversion ratios (**FCRs**) of converting DM feed intake into BW gain of 1.5 g/g (week 6) and 1.7 g/g (week 8), 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.

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

Dry matter intake of milk was then calculated assuming a DM content of 19 % (Hurley, 2015). The complete procedures for the calculation of nutrients intake can be found in Supplementary Material S1.

Statistics

SAS (SAS 9.4, SAS Institute Inc.) was used for all statistical analyses. Observations of individual focal piglets were used for all analyses. $P < 0.05$ was regarded as significant.

A multiple linear regression analysis per period (weeks 2–4, weeks 4–6, weeks 6–8) was performed to explain variation in BW gain and DFI by multiple variables. Before the regression analysis, the observed BW gains and DFIs were corrected for sex and batch as fixed effect. The model residuals of BW gain and DFI were subsequently used as response variables.

In the initial model in which BW gain was the response variable, 12 variables were selected as explanatory variables based on biological plausibility, or single relationships between the explanatory variables and the response variable (Supplementary Table S4). In the initial model in which DFI was the response variable, 10 explanatory variables which were the same variables as in the BW gain model were included, except for 'DM intake of sow feed' and 'DM intake of piglet feed'.

Regression functions were analysed using PROC REG. For the initial multiple regression models, forward selection with alpha = 0.999999 was used to determine the significance of all 12 and 10 explanatory variables per period in the model of BW gain and DFI, respectively. The initial models were also performed using backward selection with alpha = 0.000001, and the results were similar with forward selection. For the final regression models, forward selection with alpha = 0.25 was used to select the variables with $P < 0.25$. The final models were also performed using stepwise selection with alpha = 0.25, and using backward selection with alpha = 0.25, of which the results were similar with using forward selection. Therefore, the results of the forward selection are presented for both of the initial and the final models. The criteria for selection were based on the recommendations in the REG procedure in SAS user's guide ($P < 0.10–0.25$) (SAS®, 2018), as well as considering the relevant biology of candidate variables.

Assumptions of the multiple regression analysis were checked. The normality of model residuals was checked with Skewness-Kurtosis test, Shapiro-Wilk test and quantile–quantile plot using PROC UNIVARIATE. Collinearity between the 12 explanatory variables was tested by checking the variable inflation factor and correlation analyses among the 12 variables (Supplementary Table S5). The variable inflation factors were less than 10 in all multiple linear regression models showing that there was no collinearity between the 12 explanatory variables, according to Kleinbaum et al. (2013).

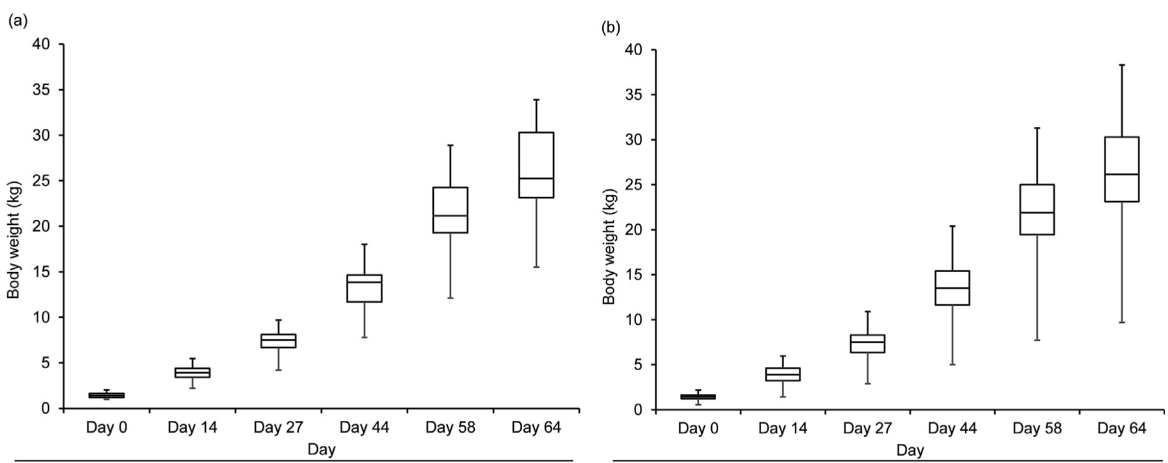
Results

Descriptive statistics of performance and nutrient intake

During the 9 weeks of lactation, the BW of the focal piglets (Fig. 3a) showed a similar pattern as that of all piglets (Fig. 3b) thus being representative of all piglets in the system. As piglets grew older, DM intake of both sow feed and piglet feed increased over time, while DM intake of milk decreased over time (Fig. 4). The percentage of focal piglets with zero milk intake increased over time and was 0 %, 26.3 % and 43.1 % in weeks 2–4, 4–6 and 6–8, respectively (data not shown). As piglets grew older, the variability in BW and BW gain, and the variability in DM intake of nutrients including sow feed, piglet feed, total feed and milk numerically increased (Table 2; Supplementary Fig. S1).

Exploring variation in BW gain by multiple linear regression

In initial models containing all 12 variables (Supplementary Table S6), these variables jointly explained less than 45 % of the



(a)

	Day 0	Day 14	Day 27	Day 44	Day 58	Day 64
Max	2.0	5.5	9.7	18.0	28.9	33.9
Min	1.0	2.2	4.2	7.8	12.1	15.5
Mean	1.4	3.9	7.3	13.4	21.7	26.1
Median	1.4	3.9	7.5	13.9	21.2	25.3
N	60	60	60	60	58	58

(b)

	Day 0	Day 14	Day 27	Day 44	Day 58	Day 64
Max	2.2	6.0	10.9	20.4	31.3	38.3
Min	0.6	1.4	2.9	5.0	7.7	9.7
Mean	1.4	3.9	7.3	13.4	21.8	26.1
Median	1.4	3.9	7.5	13.5	21.9	26.2
N	207	189	188	187	186	186

Fig. 3. Boxplots showing the BW of (a) focal piglets (n = 58 on day 64) and (b) all piglets (n = 186 on day 64) during a 9-week lactation in the multi-suckling system at six weighing times, with indicating minimum, 25th percentile values of BW, median, 75 % percentile values of BW, maximum of BW of piglets.

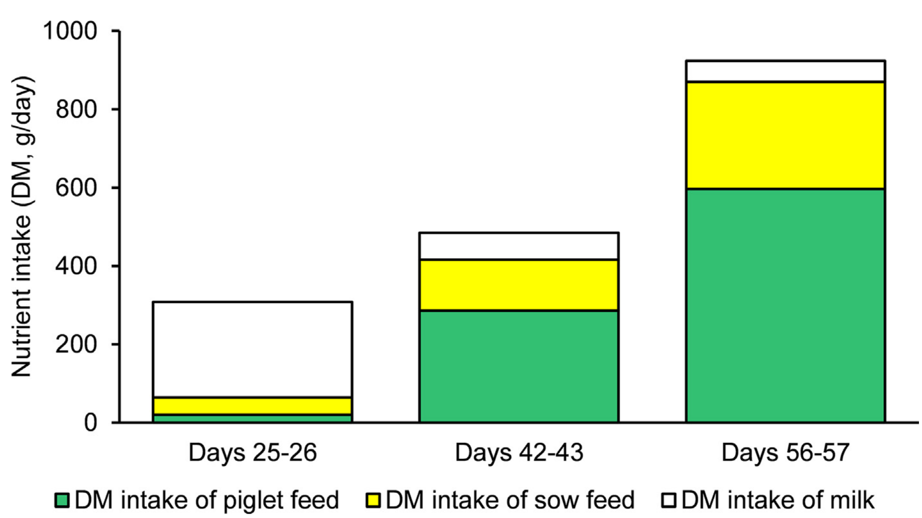


Fig. 4. Stacked bar plot showing the average values of DM intake of piglet feed, sow feed and milk of focal piglets during a 9-week lactation in the multi-suckling system on days 25–26 (feed: n = 52, milk: n = 60), days 42–43 (n = 57) and days 56–57 (n = 58).

Table 2
Descriptive values for performance, genetics, nutrient intake, behaviours, and body lesions of focal piglets (n = 60) in each of the three periods during a 9-week lactation in the multi-suckling system.

Item	Variables[1]	Mean ± SE of individual means			Within-batch SD		
		Weeks 2–4	Weeks 4–6	Weeks 6–8	Weeks 2–4	Weeks 4–6	Weeks 6–8
Performance	Birthweight (kg)	1.4 ± 0.0	–	–	0.2	–	–
	BW (kg)	7.3 ± 0.2	13.4 ± 0.3	21.7 ± 0.5	1.1	2.0	3.4
	BW gain (g/day)	262.5 ± 6.4	359.5 ± 10.5	578.6 ± 17.4	40.7	72.0	132.9
Genetics	EBV (g/day)	20.3 ± 1.9	–	–	13.5	–	–
Nutrient Intake	DM intake of sow feed (g/day)	44.2 ± 6.1	130.0 ± 11.7	273.9 ± 24.8	35.5	72.4	130.2
	DM intake of piglet feed (g/day)	19.8 ± 2.8	286.2 ± 21.7	596.3 ± 36.5	16.7	163.8	249.3
	DM intake of total feed (g/day)	64.0 ± 8.3	416.2 ± 23.1	870.2 ± 30.5	48.0	171.5	235.8
	DM intake of milk (g/day)	243.9 ± 5.9	68.4 ± 7.8	53.4 ± 9.2	37.8	59.7	70.5
Feeding behaviour	Contacting feed during sow feeding times (% of observed time)	7.1 ± 0.9	24.9 ± 1.8	21.3 ± 1.8	5.6	14.0	13.7
Suckling behaviour	The presence at the front and middle teats (no. of times)	4.5 ± 0.4	3.8 ± 0.4	1.8 ± 0.3	2.8	2.9	1.7
	The presence at the rear teats (no. of times)	1.7 ± 0.3	1.6 ± 0.4	0.9 ± 0.2	2.6	2.7	1.6
Behaviours	Positive behaviour (no. of times /hour)	13.9 ± 1.1	13.6 ± 1.2	9.1 ± 1.0	8.9	9.1	6.9
	Negative behaviour (no. of times /hour)	4.8 ± 0.5	5.5 ± 0.7	3.7 ± 0.5	3.6	4.8	3.3
	Explorative behaviour (no. of times /hour)	7.9 ± 0.8	10.7 ± 1.2	9.5 ± 1.0	5.9	8.8	7.3
	Ingestion (no. of times /hour)	5.9 ± 1.1	14.2 ± 1.5	10.6 ± 1.3	6.9	11.3	9.4
Body lesions	Skin lesions (no.)	7.9 ± 1.1	8.4 ± 1.0	13.0 ± 1.1	6.2	5.3	7.9

Variables: (1) BW (kg): piglets were weighed on day 27 (weeks 2–4), 44 (weeks 4–6) and 58 (weeks 6–8); BW gain (g/day): the difference between BW on different days divided by numbers of days between both days, during days 14–27 (weeks 2–4), days 27–44 (weeks 4–6), days 44–58 (weeks 6–8); (2) Nutrient intake (g/day): Individual daily DM intake of sow feed and piglet feed was measured per focal piglet on days 25–26 (week 4), days 42–43 (week 6) and days 56–57 (week 8); (3) Contacting feed during sow feeding times (% of observations): contacting (i.e. sniffing or eating) sow feed or piglet feed during sow feed times on days 19–20 at 0800–0830 h and 1600–1630 h, and on days 40–43 and 54–57 at 1600–1630 h; (4) Suckling behaviour (on days 20, 41, 55 at 0900 h – 1600 h): The presence at the front and middle teats (no. of times): the frequency of presence at front (first 2 pairs) and middle pairs of teats of each focal piglet in all suckling bouts during the day; Rear teats (no. of times): the frequency of presence at rear (last 2 pairs) of teats of each focal piglet in all suckling bouts during the day; (5) Behaviours (on day 19, 40, 54): Positive behaviour (no. of times /hour): the frequency of play and nosing/nose contacting sows and piglets during the day; Negative behaviour (no. of times /hour): the frequency of manipulating sows and piglets, belly nosing, and aggressive behaviour during the day; Explorative behaviour (no. of times /hour): exploring the system, i.e. nibbling, sucking or chewing on parts of the multi-suckling system such as iron bars, walls, door, floor, ropes, hessian sacks and straw; Ingestion behaviour (no. of times /hour): sniffing/nosing/eating sow feed and piglet feed, drinking during the day; (6) Skin lesions (no.): the number of fresh superficial and deep lesions on the whole body, except for ears and tails on days 27, 44 and 58.

[1] Abbreviation: EBV: the estimated breeding value of BW gain from birth to slaughter.

variation in BW gain (weeks 2–4: 34.4 %, weeks 4–6: 42.4 %, weeks 6–8: 44.9 %). In final models, after forward selection, the 5–6 retained variables explained 31.4 %, 39.2 % and 42.6 % of the variation in BW gain in the consecutive periods (Fig. 5a, Table 3). In these models, BiW explained the highest percentage of variation (12.0 %) in BW gain in weeks 2–4 compared to other variables and more than in weeks 4–6 (2.0 %) and 6–8 (7.5 %). Birthweight was positively related with BW gain in weeks 2–4 (regression coefficient (**β**) = 0.1, $P = 0.001$) and tended to be positively related with BW gain in weeks 6–8 ($\beta = 0.1$, $P = 0.051$). DM intake of piglet feed explained the highest percentage of variation in BW gain in weeks 4–6 (15.1 %) and 6–8 (25.9 %) compared to other variables; it was positively related with BW gain in weeks 4–6 ($\beta = 0.1$, $P = 0.008$) and weeks 6–8 ($\beta = 0.2$, $P < 0.001$). Similarly with DM intake of piglet feed, ingestion behaviour also exceeded the impact of BiW in weeks 4–6 and it became the second important variable to explain variation in BW gain in that period (10.7 %), but it explained very little variation in weeks 6–8 (0.5 %); ingestion behaviour was positively related with BW gain in weeks 4–6 ($\beta = 1.5$, $P = 0.036$). DM intake of sow feed was only retained in weeks 2–4 after forward selection in which it accounted for 3.9 % of the variation in BW gain. It explained only little variation in weeks 4–6 (0.8 %) and 6–8 (0.5 %) and appeared unrelated with BW gain in each of the three periods. Presence at FM teats increasingly explained variation in BW gain with age, but explained less variation (2.4 % in weeks 4–6 and 2.6 % in weeks 6–8) than DM intake of piglet feed (15.1 % in weeks 4–6 and 25.9 % in weeks 6–8) and BiW in weeks 6–8 (7.5 %); presence at FM teats tended to be negatively related with BW gain in weeks 4–6 ($\beta = -6.0$, $P = 0.083$). Of the frequency of positive, explorative and negative behaviour, only positive behaviour was retained after forward selection in weeks 2–4 and accounted for 7.6 % of the variation in BW gain. It explained only little variation in weeks 4–6 (1.5 %) and 6–8 (0.5 %); Of the frequency of behaviours, only positive behaviour was positively related with BW gain in weeks 2–4 ($\beta = 1.7$, $P = 0.003$), and no relationship was found in the other two periods. Contacting feed during sow feeding times explained the highest variation in BW gain in weeks 2–4 (4.1 %) compared to weeks 4–6 (0.1 %) and weeks 6–8 (1.7 %), and it was positively related with BW gain in weeks 2–4 ($\beta = 1.8$, $P = 0.020$). The number of skin lesions explained little variation in BW gain in weeks 2–4 (1.0 %) but more in weeks 4–6 (4.2 %) and weeks 6–8 (2.5 %), and it tended to be positively related with BW gain in weeks 4–6 ($\beta = 1.8$, $P = 0.093$). The EBV of BW gain explained the highest variation in BW gain in weeks 2–4 (3.7 %) compared with weeks 4–6 (0.1 %) and weeks 6–8 (2.4 %); EBV of BW gain explained relatively less variation in BW gain compared to BiW in each of the three periods; it only tended to be positively related with BW gain in weeks 2–4 ($\beta = 0.6$, $P = 0.094$). The results of the single linear regression are presented in Supplementary Table S4, largely confirming results of the multiple linear regression.

Exploring variation in DM intake of total feed by multiple linear regression

In initial models (Supplementary Table S6), 10 variables jointly explained less than 21 % of the variation in DFI (weeks 2–4: 12.8 %, weeks 4–6: 21.0 %, weeks 6–8: 16.9 %). In final models, after forward selection, the 1–4 retained variables explained 8.1 %, 19.5 % and 5.1 % of the variation in DFI in the consecutive periods (Fig. 5b, Table 3). In these models, BiW explained the highest percentage (9.6 %) of variation in DFI in weeks 4–6 compared to the other variables; and more than in weeks 2–4 (2.8 %) and weeks 6–8 (2.8 %). Also, ingestion behaviour explained the highest variation in weeks 4–6 (2.2 %) compared to weeks 2–4 (0.2 %) and weeks

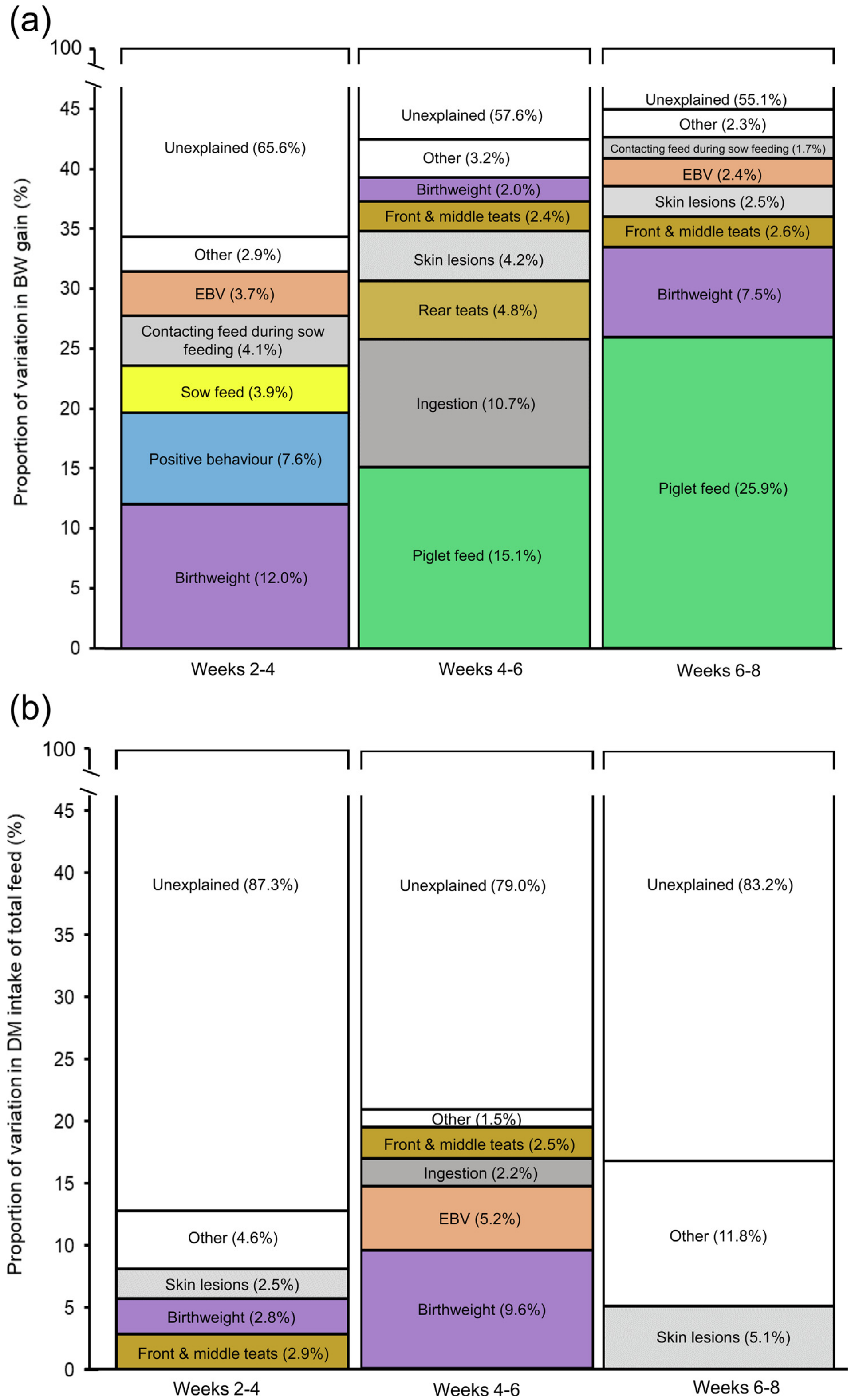


Fig. 5. Stacked bar plot showing the percentage of variation in (a) BW gain and (b) DM intake of total feed (DFI) of focal piglets (n = 60) explained by explanatory variables in weeks 2–4, 4–6 and 6–8 using multiple regression analysis. Variables with $P < 0.25$ were remained in the model after forward selection. 'Other' indicates variables that were not remained after forward selection. The response variables were the residuals of BW gain and DFI corrected for sex and batch. The explanation of the variables can be found in Table 2.

6–8 (0.4 %). The variation of DFI explained by the presence at FM teats gradually decreased over the three periods (weeks 2–4: 2.9 %, weeks 4–6: 2.5 %, weeks 6–8: 1.6 %) and explained more variation in weeks 2–4 compared to other variables. The frequency of positive, explorative and negative behaviour and the percentage of contacting feed during sow feeding times explained less than

Table 3
Multiple linear regression of BW gain and DM intake of total feed (DFI) of piglets on multiple explanatory variables in three periods during a 9-week lactation in the multi-suckling system after forward selection ($P < 0.25$).

Period	Response variables[1]													
	BW gain							DFI						
			Forward selection			Multiple regression				Forward selection			Multiple regression	
	Step	Explanatory Variables[2]	Partial R^2 (×100)[3]	Model R^2 (×100)[4]	*P*-value selection	Partial Regression coefficient (β)[5]	*P*-value of β	Step	Explanatory variables	Partial R^2 (×100)	Model R^2 (×100)	*P*-value selection	Partial Regression coefficient (β)	*P*-value of β
Weeks 2–4	1	Birthweight	12.0	12.0	0.007	0.1	0.001	1	FM teats	2.9	2.9	0.198	−3.9	0.095
	2	Positive behaviour	7.6	19.7	0.024	1.7	0.003	2	Birthweight	2.8	5.7	0.197	0.0	0.131
	3	DM intake of sow feed	3.9	23.6	0.096	−0.2	0.041	3	Skin lesions	2.5	8.1	0.226	−1.0	0.226
	4	Contacting feed during sow feeding	4.1	27.7	0.082	1.8	0.020							
	5	EBV	3.7	31.4	0.094	0.6	0.094							
Weeks 4–6	1	DM intake of piglet feed	15.1	15.1	0.002	0.1	0.008	1	Birthweight	9.6	9.6	0.017	0.2	0.076
	2	Ingestion	10.7	25.8	0.006	1.5	0.036	2	EBV	5.2	14.8	0.070	−2.2	0.128
	3	Rear teats	4.8	30.6	0.057	−10.9	0.004	3	Ingestion	2.2	17.0	0.229	2.4	0.185
	4	Skin lesions	4.2	34.8	0.068	1.8	0.093	4	FM teats	2.5	19.5	0.201	−9.0	0.201
	5	FM teats	2.4	37.2	0.160	−6.0	0.083							
	6	Birthweight	2.0	39.2	0.195	0.0	0.195							
Weeks 6–8	1	DM intake of piglet feed	25.9	25.9	<0.0001	0.2	<0.001	1	Skin lesions	5.1	5.1	0.086	6.2	0.086
	2	Birthweight	7.5	33.4	0.016	0.1	0.051							
	3	FM teats	2.6	35.9	0.149	10.5	0.133							
	4	Skin lesions	2.5	38.5	0.145	3.1	0.071							
	5	EBV	2.4	40.8	0.155	1.3	0.182							
	6	Contacting feed during sow feeding	1.7	42.6	0.220	1.2	0.220							

[1] The response variables were the residuals of BW gain and DFI corrected for sex and batch.
[2] The explanation of the variables can be found in Table 2. Abbreviation: EBV: the estimated breeding value of BW gain from birth to slaughter; FM teats: the presence at the front and middle teats; Rear teats: the presence at the rear teats.
[3] Partial R^2 (×100) is the partial squared correlation coefficient multiplied by 100, which represents the percentage of the variation in BW gain and DFI explained by the explanatory variables in the model.
[4] Model R^2 (×100) is the cumulative squared correlation coefficient multiplied by 100, which is the R^2 from the previous variable plus the partial R^2 of the current explanatory variable and it represents the percentages of the variation in BW gain and DFI explained by having the identified explanatory variables in the model.
[5] The partial regression coefficient represents the effect of one explanatory variable when others were held constant. *P*-values in bold are *P*-values for forward selection < 0.25 and *P*-values for partial regression coefficients < 0.10.

1.6 % of variation in DFI in the three periods. The number of skin lesions explained the highest variation in DFI in weeks 6–8 (5.1 %) compared to weeks 2–4 (2.5 %) and weeks 4–6 (0.2 %), and it explained the highest variation in DFI in weeks 6–8 compared to the other variables. The EBV of BW gain explained the highest variation in DFI in weeks 4–6 (5.2 %) compared to weeks 2–4 (2.0 %) and weeks 6–8 (1.7 %). In the multiple regression of DFI, in weeks 2–4, presence at FM teats tended to be negatively related with DFI ($\beta = -3.9$, $P = 0.095$); in weeks 4–6, BiW tended to be positively related with DFI ($\beta = 0.2$, $P = 0.076$); in weeks 6–8, the number of skin lesions ($\beta = 6.2$, $P = 0.086$) and BiW ($\beta = 0.3$, $P = 0.051$) tended to be positively related with DFI, and presence at FM teats ($\beta = -36.1$, $P = 0.097$) negatively. The results of the single linear regression are presented in Supplementary Table S4, mostly confirming the results of the multiple linear regression.

Discussion

In the current study, we attempted to explain variation in BW gain of piglets during a 9-week lactation in an MS system. Therefore, we measured nutrient intake, and several behavioural parameters in individual piglets of known genetic background and evaluated their contribution to BW gain. We also evaluated their contribution to a major contributor of BW gain, i.e. variation in feed intake. In initial models, these variables jointly explained 45 % and 21 % of the variation in BW gain and DFI, respectively.

Feed intake

Total DM intake of sow plus piglet feed, estimated using the dual marker approach (Tang et al., 2022), was 64, 416 and 870 g/day per piglet on days 25–26, 42–43, 56–57, respectively. To the best of our knowledge, it is the first quantitative estimation of feed intake obtained from individual piglets in an MS environment. These estimates are in range with earlier findings in week 4: 63 g/d (Pajor et al., 1991) and 66 g/d (Bøe and Jensen, 1995), on days 36–42: 439 g/d (Fraser et al., 1994), and on days 42–53: 851 g/d per pig (Fraser et al., 1994), and with earlier findings in an MS system: on days 28–33: 45 g/d and on days 63–68: 1 220 g/d (Van Nieuwamerongen et al., 2017). Milk intake decreased over time, while feed intake increased over time, which is similar with semi-natural and group lactation conditions in which sows progressively reduce the nursing frequency (Jensen and Recén, 1989; Van Nieuwamerongen et al., 2017) and piglets increasingly foraged for solid food (Newberry and Wood-Gush, 1986; Petersen et al., 1989).

Exploring variation in BW gain by multiple linear regression

Birthweight

Birthweight explained a relatively large portion of the variation in BW gain in weeks 2–4 (12.0 %), only 2.3 % in weeks 4–6 and 7.5 % in weeks 6–8. Also in other studies, BiW was found to explain variation in BW and BW gain of piglets at weeks 3–6p.p. (Lodge and McDonald, 1959; McBride et al., 1965; Fraser et al., 1979; Fraser et al., 1994). For instance, BiW explained 27.3 % of the within-litter variation in BW of piglets at week 3p.p. (Fraser et al., 1979) and explained around 6.5 % of the variation of BW gain in weeks 5–6p.p. (Fraser et al., 1994). A similar positive relationship between BiW and BW gain was found in piglets both before and after weaning (Pajor et al., 1991; Douglas et al., 2013; Huting et al., 2019; Van der Peet-Schwering et al., 2021). The physiological explanation of this effect includes a higher number of muscle fibres (Alvarenga et al., 2013) and a better developed digestive system (Pajor et al., 1991; Michiels et al., 2013) in high BiW piglets. This, in turn, could lead to an increase in the intake capacity of sow milk and dry feed. Moreover, higher BiW piglets have a greater ability to occupy and stimulate the best performing teats, thereby allowing them to ingest more milk (Scheel et al., 1977).

Dry matter intake of feed

Feed intake explained variation in BW gain in especially middle and late lactation: only 3.9 % of the variation in BW gain in weeks 2–4 was explained by DM intake of sow feed, while 15.1 % and 25.9 % of the variation was explained by DM intake of piglet feed in weeks 4–6 and weeks 6–8, respectively. In addition, DM intake of sow feed was negatively related with BW gain in weeks 2–4, while DM intake of piglet feed was positively related with BW gain in weeks 4–6 and weeks 6–8. It is a direct consequence of the increased DFI and reduced intake of milk, as the dependency of the piglets on solid feed increases with age, which probably was increased by the intermittent suckling strategy (Berkeveld et al., 2007) that started at 4 weeks of age. DM intake of sow feed was limited as piglets could only access sow feed during sow feeding times, which likely explains the absence of a relationship between DM intake of sow feed and BW gain in each of the three periods.

The negative regression coefficient of DM intake of sow feed with BW gain in weeks 2–4 indicates a higher consumption of sow feed for slow-growing piglets. This might be linked with a lower milk intake, as we found that the presence at FM teats which are normally considered to have good milk output tended to be negatively related with DFI in weeks 2–4. Thus, in early lactation, faster-growing piglets seem to consume more milk, than slower-growing piglets, who ingested more solid feed as compensation.

Interestingly, similar to DM intake of sow feed, contacting feed during sow feeding times explained more variation in BW gain in weeks 2–4 compared to weeks 4–6 and weeks 6–8 and the regression coefficient was positive. This might be linked with floor feeding of the sows, which is thought to enhance the feed intake of piglets by vertical social learning, especially in early lactation (Oostindjer et al., 2011). As piglet dependence from the sow decreases, this effect disappears.

Solid feed intake explained more variation in BW gain than BiW did in middle and late lactation. As this is the first study that quantitatively estimated the feed intake of individual piglets, previous studies have not reported such relationships at piglet level, but have reported a similar difference at litter level (Lodge and McDonald, 1959). As DM intake of piglet feed explained a relatively high portion of the variation in BW gain, especially in weeks 4–6 and 6–8, understanding which factors influence feed intake variation is helpful to design potential intervention strategies to reduce variation in BW gain.

Ingestion behaviour

In our study, ingestion behaviour was measured by recording the frequency of contacting feed during the day (from 0900 to 1600 h). This variable hardly explained variation in BW gain and was not related with BW gain in weeks 2–4, likely because piglets mainly rely on milk. In weeks 4–6, ingestion behaviour was the second most important variable to explain variation in BW gain (10.7 %) after DM intake of piglet feed (15.1 %); while in weeks 6–8, it hardly explained variation in BW gain and was not related with BW gain. This might be linked with changes in feeding patterns from weeks 4–6 to weeks 6–8. In a review of Bus et al. (2021), feeding frequency generally reduces over time, while intake per visit increases over time in growing pigs. For piglets in semi-natural conditions, ingestion of significant quantities of solid food begins at 4–5 weeks, and increases considerably between 6 and 8 weeks (Petersen et al., 1989; Jensen, 1995). In our study, we observed that the mean ingestion frequency decreased in weeks 6–8 compared to weeks 4–6, and the feed intake per ingestion event increased in weeks 6–8 compared to weeks 4–6, where 64.8 % of the piglets had a decreased ingestion frequency and 86.7 % of the piglets had an increased feed intake per ingestion event (data not shown). This indicates that there is individual variation in meal patterns over time, confirming the findings of van Erp (2019). It also indicates that ingestion frequency alone does not accurately reflect daily feed intake and BW gain in late lactation.

Teat presence

The frequency of piglets being present at teats during suckling bouts was scored. In weeks 2–4, only a small percentage of the variation in BW gain was explained by the presence at both the FM teats (0.1 %) and the rear teats (0.5 %). The presence at FM teats (4.0 %) and rear teats (1.2 %) explained more variation in BW gain in the single regression than in the multiple regression in weeks 2–4. Possibly, in the multiple regression, part of the variation was attributed to BiW, as the presence at FM teats was significantly correlated with BiW (r = 0.3, P = 0.026). In the multiple regression, the presence at FM teats explained less variation in BW gain in weeks 2–4 than variation explained by BiW (12 %). This is similar with previous findings (Fraser and Jones, 1975; Fraser et al., 1979). The presence at FM teats and at rear teats had positive and negative regression coefficients though not significant in weeks 2–4, respectively. Similarly, piglets suckling front and middle teats had higher BW gain than those suckling rear teats before weaning (Kim et al., 2000; Huting et al., 2019). This could be associated with the difference in milk yield among teats (Skok et al., 2007). The reason could be that high BiW piglets tend to win more teat disputes which allows them to occupy teats with more milk yield (Scheel et al., 1977). Indeed, in our study, in weeks 2–4, the correlation between BiW and FM teats was positive (r = 0.3, P = 0.026), while the correlation between BiW and rear teats was negative (r = − 0.1, P = 0.418). Therefore, split-weaning of heavy piglets may be a strategy that allows low BiW piglets access to productive teats, which might positively affect piglet homogeneity in later life.

In middle and late lactation, both of presence at FM and rear teats explained less variation in BW gain in weeks 4–6 (2.4 % and 4.8 %) and in weeks 6–8 (2.6 % and 0.1 %) compared to the DM intake of piglet feed in weeks 4–6 (15.1 %) and weeks 6–8 (25.9 %). Similarly, Lodge and McDonald (1959) found that 10 % and 77 % of the between-litter variation in BW of pigs at week 8p.p. were explained by milk consumption and creep feed consumption to 8 weeks, respectively (Lodge and McDonald, 1959). This logically follows from the reduced dependency of the piglets on milk.

Behaviours

The frequency of positive behaviours (the sum of play and nosing behaviour) was retained in the multiple regression model after forward selection in weeks 2–4 and accounted for 7.6 % of the variation in BW gain. Likely, play behaviour was the underlying cause of this effect, as it also showed a positive correlation with BW gain in the single regression in weeks 2–4. It corresponds to the finding by Brown et al. (2015) in piglets on days 0–27, and Šilerová et al. (2010), who found that the relationship persisted after weaning on day 39. Play can have both immediate and long-lasting benefits (Pellis et al., 2010). As play behaviour in early life benefits muscle and bone development (Fagen, 1976; Graham and Burghardt, 2010), stimulating play behaviour in early life for example by providing more enrichment materials (Yang et al., 2018) might have potential positive effects on BW gain that may be preserved in later life. Interestingly, positive (play) behaviour did not explain a sizeable portion of BW variation in later lactation. Relationships between negative and explorative behaviours and BW gain were not observed in this study.

Skin lesions

The number of skin lesions explained more variation in BW gain in weeks 4–6 (4.2 %) and 6–8 (2.5 %) compared to weeks 2–4 (1.0 %), and the number of skin lesions tended to be positively related with BW gain in weeks 4–6. Similarly, a positive correlation between BW and lesion scores was found in postweaned pigs after week 4 (Turner et al., 2006). Skin lesion score provides a more sensitive measure of the duration of aggression (Turner et al., 2006) and aggressive interactions (Yang et al., 2018) than observations on the frequency of aggressive behaviour. Indeed, it has been reported that heavier piglets are more involved in fighting, win more fights (D'Eath, 2002) and had more skin lesions (Yang et al., 2018).

In socially stable groups, the majority of aggressive behaviours occurs around the feeding area to obtain limited food resources (Hoy et al., 2012). In our study, the piglet: feeding place ratio was fixed (6:1) which may explain the stronger relationship between skin lesions and BW gain with progressing age.

Estimated breeding value of BW gain from birth to slaughter

The genetic background of piglets affects their growth performance (Van der Peet-Schwering et al., 2013). In our study, the EBV for BW gain from birth to slaughter was assessed in all piglets. This parameter, however, hardly explained variation in BW gain in multiple and single regression analyses (weeks 2–4: 3.7 %, 0.4 %, weeks 4–6: 0.1 %, 1.0 %, weeks 6–8: 2.4 %, 0.2 %) and only tended to be positively related with BW gain in weeks 2–4. It might be that a breeding value that estimates BW gain from birth to slaughter does not reflect BW gain in early life very well. In addition, genotype × environment interactions might play a role, as piglets were group housed and could interact with group mates. Also, in weeks 2–4, BiW explained 12.0 % of the variation in BW gain. This might indicate that the genetic contribution to early-life BW gain is relatively limited compared to birthweight.

Exploring variation in feed intake by multiple linear regression

Dry matter feed intake was explained for less than 21 % by all factors considered in the three periods.

Birthweight

Birthweight explained 2.8 %, 9.6 % and 2.8 % of the variation in DFI in weeks 2–4, 4–6 and 6–8, respectively. In a conventional housing system, 9 % of the explained variation was found in piglets on days 10–28p.p. (Pajor et al., 1991). Also, BiW tended to be positively related with DFI in weeks 4–6 and 6–8 and similar positive relationships between BiW and DFI were found in pigs before (Pajor et al., 1991; Huting et al., 2019) and after conventional weaning (Bérard et al., 2010; Huting et al., 2019), and in pigs which were kept with their mother in weeks 4–8p.p. (Bøe and Jensen, 1995). In our study, BiW had a limited effect on DFI in weeks 2–4 when milk intake dominates, and in this period, the influence of BiW on BW gain is likely mediated through milk intake.

Teat presence

The presence at FM teats explained the highest portion of variation in DFI in weeks 2–4 (but still only 2.9 %) compared to other variables. It tended to be negatively related with DFI in weeks 2–4 and weeks 6–8 and had a negative regression coefficient in weeks 4–6. It indicates that piglets which are present more at FM teats ate less solid feed. Similarly in conventional housing systems, it was found that during weeks 3–4 before weaning, piglets that suckled at FM teats were less likely to eat creep feed compared to piglets that suckled rear teats (Huting et al., 2019).

Piglets that suckled more at FM teats did so in consecutive periods: weeks 2–4 and 4–6 (r = 0.73, $P < 0.001$) and weeks 4–6 and 6–8 (r = 0.48, $P < 0.001$). Similarly, Barber et al. (1955) found that piglets with the highest milk intake during the first 3 weeks of lactation also had the highest milk intake during the following 5 weeks up to weaning at 8 weeks.

Behaviours

Similar to the multiple regression of BW gain, positive, negative and explorative behaviours explained little variation in DFI in the three periods. Previous studies showed that piglet feeding activity was associated with exploration around the trough (Delumeau and Meunier-Salaün, 1995) and stimulation of exploratory behaviour using specific feeders and feed sources increased creep feed intake of piglets (Kuller et al., 2010; Middelkoop et al., 2019). However, in those studies, exploratory behaviour included nosing, sniffing and rooting on the feed and feeders, while not in the current study.

Skin lesions

Skin lesions explained 5.1 % of the variation in DFI in weeks 6–8 and tended to be positively related with DFI in weeks 6–8. It might be that piglets with a greater need to utilise the feeders involve in more fighting for food sources (Algers et al., 1990) and thus have more skin lesions and higher feed intake.

Unexplained variation and future research

In each of the three periods, more than 55 % of the variation in BW gain and 79 % of the variation in DFI remained unexplained. It is possible that the inherent variability associated with some explanatory variables contributed to this unexplained variation. The accuracy of feed intake estimation, as described in Tang et al. (2022), was around 10–15 % of the deviation from measured feed intake, which could possibly have contributed to this high unexplained variation. Further research to improve the accuracy of feed intake estimation is required. The inherent variability in behaviours remains unknown, as we only observed each focal piglet for 50 min per day for one day in each period. More days of behavioural observations are required.

Further investigations of other potentially influential factors are also required. Additional variables potentially contributing to the variation in BW gain and DFI of piglets include sow-related variables including DFI and milk production of sows (Ramanau et al., 2004; Strathe et al., 2017); piglet-related variables, including colostrum intake (Devillers et al., 2004), social rank (McBride et al., 1964; Bus et al., 2021), personality (O'Malley et al., 2019), digestive efficiency (Douglas et al., 2014; Gaillard et al., 2020), health status (Pastorelli et al., 2012; Van der Meer et al., 2020; Bus et al., 2021) and group size (Turner et al., 2003).

Conclusion

To conclude, a multiple regression analysis revealed that 19.7 % of the individual variation in BW gain of piglets in a multi-suckling system during a 9-week lactation was explained by birthweight, play and nosing behaviour in weeks 2–4, and 15.1 % and 25.9 % by solid feed intake of piglets in weeks 4–6 and 6–8. It also revealed that 2.9 % of the individual variation in DFI in weeks 2–4 was explained by the presence at front and middle teats, 9.6 % by birthweight in weeks 4–6, and 5.1 % by the number of skin lesions in weeks 6–8. Further investigation of other potentially influential factors is required.

Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.animal.2022.100651.

Ethics approval

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

Data and model availability statement

The data were not deposited in an official repository. The datasets generated and analysed during the current study are available from the corresponding author upon request.

Author ORCIDs

Tianyue Tang: https://orcid.org/0000–0003-4509–9668.
Walter Gerrits: https://orcid.org/0000–0003-0494–9259.
Inonge Reimert: https://orcid.org/0000–0002-3610–5037.
Nicoline Soede: https://orcid.org/0000–0003-0296-886X.

Author contributions

Tianyue Tang: Investigation, Software, Formal analysis, Data Curation, Writing - Original Draft, Visualisation.

Walter Gerrits: Conceptualisation, Methodology, Formal analysis, Writing - Review and Editing, Supervision, Project administration, Funding acquisition.

Inonge Reimert: Conceptualisation, Methodology, Formal analysis, Writing - Review and Editing, Supervision.

Carola van der Peet-Schwering: Conceptualisation, Methodology, Resources, Writing - Review and Editing, Supervision, Project administration, Funding acquisition.

Nicoline Soede: Methodology, Formal analysis, Writing - Review and Editing, Supervision, Project administration, Funding acquisition.

Declaration of interest

The authors declare no conflicts of interest.

Acknowledgements

We would like to thank the staff, and particularly Anita Hoofs, of Swine Innovation Center Sterksel, the Netherlands for their assistance during the experiment. The authors would also like to thank the staff Bjorge Laurenssen, Manon van Marwijk, Tamme Zandstra, and the master students Ashley Paige Sijmonsbergen, Jet Huijser, Milou Wals, Kelly Peters, Iris van der Poorten, Dulce María Aguilar López from Wageningen University & Research for their help with the execution of the experiment. We thank Egbert Frank Knol and Roos Vogelzang in Topigs Norsvin Research Center, Erik Bruininx in Agrifirm Innovation Center for providing assistance with the genetics data analysis and advice. We thank Sofie van Nieuwamerongen-de Koning for her advice on the visualisation of the layout of the multi-suckling system. The authors thank J. Elizabeth Bolhuis for her advice on the set-up of behavioural observations in the experiment.

Financial support statement

The research was conducted as part of the PhD project: utilising the growth potential of piglets in a novel, integrated multi-litter housing system for sows and piglets. It was funded by Ministry of Agriculture, Nature and Food Quality. Research grant funding was received from Oversea Study Program of Guangzhou Elite Project (No. JY201830) for T. Tang.

References

Algers, B., Jensen, P., Steinwall, L., 1990. Behaviour and weight changes at weaning and regrouping of pigs in relation to teat quality. Applied Animal Behaviour Science 26, 143–155.
Alvarenga, A., Chiarini-Garcia, H., Cardeal, P., Moreira, L., Foxcroft, G., Fontes, D., Almeida, F., 2013. Intra-uterine growth retardation affects birthweight and postnatal development in pigs, impairing muscle accretion, duodenal mucosa morphology and carcass traits. Reproduction, Fertility and Development 25, 387–395.
Barber, R., Braude, R., Mitchell, K., 1955. Studies on milk production of Large White pigs. The Journal of Agricultural Science 46, 97–118.
Bérard, J., Kreuzer, M., Bee, G., 2010. In large litters birth weight and gender is decisive for growth performance but less for carcass and pork quality traits. Meat Science 86, 845–851.
Berkeveld, M., Langendijk, P., van Beers-Schreurs, H.M., Koets, A.P., Taverne, M.A., Verheijden, J.H., 2007. Postweaning growth check in pigs is markedly reduced by intermittent suckling and extended lactation. Journal of Animal Science 85, 258–266.
Bøe, K., Jensen, P., 1995. Individual differences in suckling and solid food intake by piglets. Applied Animal Behaviour Science 42, 183–192.
Brown, S.M., Klaffenböck, M., Nevison, I.M., Lawrence, A.B., 2015. Evidence for litter differences in play behaviour in pre-weaned pigs. Applied Animal Behaviour Science 172, 17–25.
Bus, J.D., Boumans, I.J., Webb, L.E., Bokkers, E.A., 2021. The potential of feeding patterns to assess generic welfare in growing-finishing pigs. Applied Animal Behaviour Science 241, 105383.
Camerlink, I., Turner, S.P., 2013. The pig's nose and its role in dominance relationships and harmful behaviour. Applied Animal Behaviour Science 145, 84–91.
D'Eath, R.B., 2002. Individual aggressiveness measured in a resident-intruder test predicts the persistence of aggressive behaviour and weight gain of young pigs after mixing. Applied Animal Behaviour Science 77, 267–283.
Delumeau, O., Meunier-Salaün, M., 1995. Effect of early trough familiarity on the creep feeding behaviour in suckling piglets and after weaning. Behavioural processes 34, 185–195.
Devillers, N., van Milgen, J., Prunier, A., Le Dividich, J., 2004. Estimation of colostrum intake in the neonatal pig. Animal Science 78, 305–313.
Docking, C.M., Van de Weerd, H.A., Day, J., Edwards, S.A., 2008. The influence of age on the use of potential enrichment objects and synchronisation of behaviour of pigs. Applied Animal Behaviour Science 110, 244–257.
Douglas, S., Edwards, S., Sutcliffe, E., Knap, P., Kyriazakis, I., 2013. Identification of risk factors associated with poor lifetime growth performance in pigs. Journal of Animal Science 91, 4123–4132.
Douglas, S., Edwards, S., Kyriazakis, I., 2014. Too late to catch up: a high nutrient specification diet in the grower phase does not improve the performance of low birth weight pigs. Journal of Animal Science 92, 4577–4584.
Everts, H., Blok, M., Kemp, B., van der Peet-Schwering, C., Smits, C., 1995. Normen voor lacterende zeugen. CVB-Documentation Report no. 13, Centraal Veevoederbureau, Lelystad, The Netherlands.
Fagen, R.M., 1976. Exercise, play, and physical training in animals. In: Bateson, P.P. G., Klopfer, P.H. (Eds.), Perspectives in ethology. Springer, Boston, MA, USA, pp. 189–219.
Fraser, D., Jones, R.M., 1975. The 'teat order' of suckling pigs: I. Relation to birth weight and subsequent growth. The Journal of Agricultural Science 84, 387–391.
Fraser, D., Thompson, B., Ferguson, D., Darroch, R., 1979. The 'teat order'of suckling pigs: 3. Relation to competition within litters. The Journal of Agricultural Science 92, 257–261.

Fraser, D., Pajor, E., Feddes, J., 1994. The relationship between creep feeding behavior of piglets and adaptation to weaning: effect of diet quality. Canadian Journal of Animal Science 74, 1–6.
Gaillard, C., Brossard, L., Dourmad, J.Y., 2020. Improvement of feed and nutrient efficiency in pig production through precision feeding. Animal Feed Science and Technology, 114611.
Graham, K.L., Burghardt, G.M., 2010. Current perspectives on the biological study of play: signs of progress. The Quarterly Review of Biology 85, 393–418.
Grimberg-Henrici, C., Büttner, K., Ladewig, R., Burfeind, O., Krieter, J., 2018. Cortisol levels and health indicators of sows and their piglets living in a group-housing and a single-housing system. Livestock Science 216, 51–60.
Hoy, S., Schamun, S., Weirich, C., 2012. Investigations on feed intake and social behaviour of fattening pigs fed at an electronic feeding station. Applied Animal Behaviour Science 139, 58–64.
Hurley, W., 2015. Composition of sow colostrum and milk. In: Farmer, C. (Ed.), The gestating and lactating sow. Wageningen Academic Publishers, Wageningen, The Netherlands, pp. 193–230.
Huting, A.M., Sakkas, P., Kyriazakis, I., 2019. Sows in mid parity are best foster mothers for the pre-and post-weaning performance of both light and heavy piglets. Journal of Animal Science 97, 1656–1670.
Jensen, P., 1995. The weaning process of free-ranging domestic pigs: Within-and between-litter variations. Ethology 100, 14–25.
Jensen, P., Recén, B., 1989. When to wean—observations from free-ranging domestic pigs. Applied Animal Behaviour Science 23, 49–60.
Kim, S., Hurley, W., Hant, I., Easter, R., 2000. Growth of nursing pigs related to the characteristics of nursed mammary glands. Journal of Animal Science 78, 1313–1318.
Kleinbaum, D.G., Kupper, L.L., Nizam, A., Rosenberg, E.S., 2013. Applied regression analysis and other multivariable methods. Cengage Learning, Boston, MA, USA.
Kuller, W., Tobias, T., Van Nes, A., 2010. Creep feed intake in unweaned piglets is increased by exploration stimulating feeder. Livestock Science 129, 228–231.
Lodge, G.A., McDonald, I., 1959. The relative influence of birth weight, milk consumption and supplementary food consumption upon the growth rates of suckling piglets. Animal Science 1, 139–144.
McBride, G., James, J., Hodgens, N., 1964. Social behaviour of domestic animals. IV. Growing pigs. Animal Science 6, 129–139.
McBride, G., James, J., Wyeth, G., 1965. Social behaviour of domestic animals VII. Variation in weaning weight in pigs. Animal Science 7, 67–74.
Michiels, J., De Vos, M., Missotten, J., Ovyn, A., De Smet, S., Van Ginneken, C., 2013. Maturation of digestive function is retarded and plasma antioxidant capacity lowered in fully weaned low birth weight piglets. British Journal of Nutrition 109, 65–75.
Middelkoop, A., van Marwijk, M.A., Kemp, B., Bolhuis, J.E., 2019. Pigs like it varied; feeding behavior and pre-and post-weaning performance of piglets exposed to dietary diversity and feed hidden in substrate during lactation. Frontiers in veterinary science 6, 408.
Newberry, R., Wood-Gush, D., 1986. Social relationships of piglets in a semi-natural environment. Animal behaviour 34, 1311–1318.
O'Malley, C.I., Turner, S.P., D'Eath, R.B., Steibel, J.P., Bates, R.O., Ernst, C.W., Siegford, J.M., 2019. Animal personality in the management and welfare of pigs. Applied Animal Behaviour Science 218, 104821.
Oostindjer, M., Bolhuis, J.E., Mendl, M., Held, S., van den Brand, H., Kemp, B., 2011. Learning how to eat like a pig: effectiveness of mechanisms for vertical social learning in piglets. Animal behaviour 82, 503–511.
Pajor, E.A., Fraser, D., Kramer, D.L., 1991. Consumption of solid food by suckling pigs: individual variation and relation to weight gain. Applied Animal Behaviour Science 32, 139–155.
Pastorelli, H., van Milgen, J., Lovatto, P., Montagne, L., 2012. Meta-analysis of feed intake and growth responses of growing pigs after a sanitary challenge. Animal 6, 952–961.
Pellis, S.M., Pellis, V.C., Bell, H.C., 2010. The function of play in the development of the social brain. American Journal of Play 2, 278–296.
Petersen, H., Vestergaard, K., Jensen, P., 1989. Integration of piglets into social groups of free-ranging domestic pigs. Applied Animal Behaviour Science 23, 223–236.
Ramanau, A., Kluge, H., Spilke, J., Eder, K., 2004. Supplementation of sows with L-carnitine during pregnancy and lactation improves growth of the piglets during the suckling period through increased milk production. The Journal of nutrition 134, 86–92.
SAS®, 2018. SAS/STAT® 15.1 User's Guide. SAS Institute Inc., Cary, NC, USA.
Scheel, D.E., Graves, H., Sherritt, G., 1977. Nursing order, social dominance and growth in swine. Journal of Animal Science 45, 219–229.
Schouten, W.G.P., 1985. Rearing conditions and behaviour in pigs. PhD thesis, Wageningen University, Wageningen, the Netherlands.
Schrey, L., Kemper, N., Fels, M., 2019. Behaviour and skin injuries of piglets originating from a novel group farrowing system before and after weaning. Agriculture 9, 93.
Šilerová, J., Špinka, M., Šárová, R., Algers, B., 2010. Playing and fighting by piglets around weaning on farms, employing individual or group housing of lactating sows. Applied Animal Behaviour Science 124, 83–89.
Skok, J., Brus, M., Škorjanc, D., 2007. Growth of piglets in relation to milk intake and anatomical location of mammary glands. Acta Agriculturae Scandinavica, Section A - Animal Science 57, 129–135.
Smit, H.J., Taweel, H.Z., Tas, B.M., Tamminga, S., Elgersma, A., 2005. Comparison of techniques for estimating herbage intake of grazing dairy cows. Journal of Dairy Science 88, 1827–1836.
Strathe, A., Bruun, T., Hansen, C., 2017. Sows with high milk production had both a high feed intake and high body mobilization. Animal 11, 1913–1921.
Tang, T., van der Peet-Schwering, C.M.C., Soede, N.M., Laurenssen, B.F.A., Bruininx, E. M.A.M., Bos, E.J., Gerrits, W.J.J., 2022. A dual marker technique to estimate individual feed intake in young pigs. Animal 16, 100451.
Theil, P.K., Nielsen, T.T., Kristensen, N.B., Labouriau, R., Danielsen, V., Lauridsen, C., Jakobsen, K., 2002. Estimation of milk production in lactating sows by determination of deuterated water turnover in three piglets per litter. Acta Agriculturae Scandinavica, Section A - Animal Science 52, 221–232.
Thomsson, O., Sjunnesson, Y., Magnusson, U., Eliasson-Selling, L., Wallenbeck, A., Bergqvist, A.S., 2016. Consequences for piglet performance of group housing lactating sows at one, two, or three weeks post-farrowing. PloS one 11, e0156581.
Turner, S., Allcroft, D., Edwards, S., 2003. Housing pigs in large social groups: a review of implications for performance and other economic traits. Livestock Production Science 82, 39–51.
Turner, S.P., Farnworth, M.J., White, I.M., Brotherstone, S., Mendl, M., Knap, P., Penny, P., Lawrence, A.B., 2006. The accumulation of skin lesions and their use as a predictor of individual aggressiveness in pigs. Applied Animal Behaviour Science 96, 245–259.
Van der Meer, Y., Jansman, A., Gerrits, W., 2020. Low sanitary conditions increase energy expenditure for maintenance and decrease incremental protein efficiency in growing pigs. Animal 14, 1811–1820.
Van der Peet-Schwering, C., Troquet, L., Binnendijk, G., Knol, E., 2013. Effect of genetic background and birth weight on performance of piglets and growing and finishing pigs. Wageningen Livestock Research, Wageningen, the Netherlands.
Van der Peet-Schwering, C.M., Verschuren, L.M., Bergsma, R., Hedemann, M.S., Binnendijk, G.P., Jansman, A.J., 2021. The effects of birth weight and estimated breeding value for protein deposition on nitrogen efficiency in growing pigs. Journal of Animal Science 99, skab101.
Van Erp, R.J., 2019. Nutrient yield from starch in pigs: Consequences for energy balance and meal patterns. PhD thesis, Wageningen University, Wageningen, The Netherlands.
Van Nieuwamerongen, S., Bolhuis, J., Van der Peet-Schwering, C., Soede, N., 2014. A review of sow and piglet behaviour and performance in group housing systems for lactating sows. Animal 8, 448–460.
Van Nieuwamerongen, S.E., Soede, N.M., Van der Peet-Schwering, C.M.C., Kemp, B., Bolhuis, J.E., 2015. Development of piglets raised in a new multi-litter housing system vs. conventional single-litter housing until 9 weeks of age. Journal of Animal Science 93, 5442–5454.
Van Nieuwamerongen, S., Soede, N., Van der Peet-Schwering, C., Kemp, B., Bolhuis, J., 2017. Gradual weaning during an extended lactation period improves performance and behavior of pigs raised in a multi-suckling system. Applied Animal Behaviour Science 194, 24–35.
Van Nieuwamerongen, S., 2017. Development of pigs raised in a group housing system for lactating sows and their litters. PhD thesis, Wageningen University, Wageningen, The Netherlands.
Verdon, M., Morrison, R.S., Rault, J.L., 2020. The welfare and productivity of sows and piglets in group lactation from 7, 10, or 14 d postpartum. Journal of Animal Science 98, skaa037.
Weary, D.M., Pajor, E.A., Bonenfant, M., Fraser, D., Kramer, D.L., 2002. Alternative housing for sows and litters.: Part 4. Effects of sow-controlled housing combined with a communal piglet area on pre-and post-weaning behaviour and performance. Applied Animal Behaviour Science 76, 279–290.
Yang, C.H., Ko, H.L., Salazar, L.C., Llonch, L., Manteca, X., Camerlink, I., Llonch, P., 2018. Pre-weaning environmental enrichment increases piglets' object play behaviour on a large scale commercial pig farm. Applied Animal Behaviour Science 202, 7–12.