Animal 19 (2025) 101460

Contents lists available at ScienceDirect

Animal

The international journal of animal biosciences

Influence of genotype and environment on piglet vitality and metabolic state during the suckling period of divergent birth weight classes

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ARTICLE INFO

Article history:
Received 14 July 2024
Revised 4 February 2025
Accepted 4 February 2025
Available online 10 February 2025

Keywords:
Early life
Farrowing
Neonate
Piglet survival
Traditional breeds

ABSTRACT

The high mortality rate of suckling piglets in commercial farms is a cause for concern and requires the adoption of innovative breeding and management approaches for effective mitigation. Piglets are particularly vulnerable during the first days of life, which concerns especially neonates with a low birth weight. In this study, neonatal adaptation was analysed regarding genotype and housing conditions following hormonally induced farrowing. A total of 96 piglets from 27 farrowings of German Landrace (**GL**; birth induction at day 115 of gestation) and German Saddleback sows (**GS**; birth induction at day 112 of gestation), kept either in crates (1.0 square metre) or pens (6.5 square metre) were studied. The piglets were assigned to birth weight categories (hypotrophic: 800–1 100 g; eutrophic: > 1 100–1 500 g; hypertrophic: > 1 500 g) and examined via repeated blood analyses on the following time period: 0–6 h, day 1, day 4, day 20 *postnatum*, and one–day *post*weaning. Analysed plasma metabolites included albumin, ammonia, chloride, cortisol, creatinine, fructose, glucose, haptoglobin, inositol, insulin, lactate, non-esterified fatty acids, sodium, total protein, triglycerides, triiodothyronine, urea, and uric acid. Eutrophic and hypertrophic piglets were grouped as controls due to metabolic similarities ($P = 0.272$), whereas hypotrophic piglets could be discriminated from heavier littermates ($P = 0.025$). The GS piglets appeared to have higher tissue maturity compared to GL piglets, as indicated by improved clearance of plasma ammonia and creatinine levels. This suggests that inducing birth in GS sows at gestation day 112 corresponds to the physiological gestation length of this breed. The housing environment during farrowing influenced plasma glucose and inositol levels during the neonatal adaptation period, which might be attributed to differences in physical activity in farrowing pens compared to crates. Results suggest a higher risk for hypotrophic neonates to exhibit a hypoglycaemia-hypothermia complex at birth, which can have significant implications for neonatal health and development but might be mitigated by the observed increased release of cortisol. These findings highlight that piglet vitality and plasma metabolite dynamics during the suckling period are shaped by genetic background, housing conditions, and birth weight, reflecting differences in tissue maturity, physical activity, and energy reserves.

Implications

Farrowing and neonatal adaptation periods are crucial moments in life and are influenced by various factors, e.g. genotype and environment. Piglets of a traditional and a conventional breed were born from sows in crates or pens. Repeated blood samples were taken from these piglets over the suckling period. A higher organ maturity was found in German Saddleback neonates, as well as an influence of the housing system on carbohydrate metabolism, implying higher physical activity in pens. Hypotrophic piglets seem to be more susceptible to a hypoglycaemia-hypothermia complex immediately after birth, which can affect the health and development of the neonate.

Introduction

Lower average birth weights are associated with large litters, which are common in modern pig breeds in conventional farming (Baxter et al., 2008; König et al., 2021). Low birth weight piglets, often defined as piglets with a birth weight less than 1 000 g (Quesnel et al., 2008), have a significantly higher mortality risk

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https://doi.org/10.1016/j.animal.2025.101460

compared to heavier littermates (Baxter et al., 2008; Panzardi et al., 2013; Schild et al., 2020). Irrespective of birth weight, the preweaning mortality has been reported to range between 15 and 20% on average (Kielland et al., 2018; Nuntapaitoon et al., 2018), which raises both economic and ethical concerns. Most losses occur during the early postnatal adaptation phase, i.e. within the first three to four days of life (Baxter et al., 2008; Baude et al., 2022; Gladbach, 2022). In this context, sufficient vitality is considered important for the survival of the piglets (Baxter et al., 2008). Vitality at birth is expressed by physical activity, early suckling, and skin colour (Panzardi et al., 2013; Schodl et al., 2019) and is influenced by various factors, e.g. birth weight (Tuchscherer et al., 2000; Baxter et al., 2008; Blim, 2020) and birth order (Tuchscherer et al., 2000; Baxter et al., 2008; Langendijk and Plush, 2019).

The animal-intrinsic responses in adapting to extra-uterine life consist of three phases as reviewed previously by Diehl et al. (2022). The first phase includes the onset of breathing and the adaptation of the cardiovascular system immediately after birth. With the shift from the intrauterine to the extrauterine environment, the neonatal piglet needs to adjust its body temperature and acid-base balance within the first 24 h of life. Neonates exhibit a poor status of endogenous energy reserves, i.e. protein and glycogen content of body stores (Herpin et al., 2002; Theil et al., 2011) and are therefore dependent on colostrum and transient milk, to obtain macromolecules for energy utilisation as well as immune components for the acquisition of passive immunity (Le Dividich et al., 2005; Pedersen et al., 2011). In the second phase of neonatal adaptation, homeostasis and organ maturation are established (up to 14 days *postnatum*). As development progresses, the liver becomes fully functional, enabling vital protein synthesis. Concurrently, the kidneys attain their full physiological capacity, allowing for the regulation of plasma molarity and volume, thus maintaining fluid homeostasis within the body. The final third phase (up to the 28th day of life) shapes neurological, immunological and muscular characteristics (Diehl et al., 2022).

Low birth weight piglets require more time to reach the udder (Baxter et al., 2008; Pedersen et al., 2011) and are disadvantaged when competing for teats with heavier littermates (Devillers et al., 2007). Furthermore, the amount of colostrum does not increase with the number of piglets and remains constant in quantity. Consequently, a smaller amount of colostrum is available for the individual piglet (Devillers et al., 2007). Due to the unfavourable surface-to-volume ratio, low birth weight piglets are particularly prone to rapid cooling and hypothermia compared to heavier littermates (Tuchscherer et al., 2000; Kammersgaard et al., 2011; Quesnel et al., 2023), and therefore require a high amount of energy metabolites for thermoregulation in relation to their BW (Noblet et al., 1987; Tucker et al., 2022). Genetics also appear to be relevant, as Meishan piglets with an average birth weight of 0.46 kg less than Large White piglets do not have a higher preweaning mortality rate (Lee and Haley, 1995). Management strategies discussed for successful neonatal adaptation that influence piglet vitality and survival include the sow's housing conditions during parturition and early lactation, i.e. conventional farrowing crates or farrowing pens without fixation. However, there are inconsistent reports on piglet mortality in relation to housing systems, with higher preweaning mortality reported for piglets kept in farrowing pens (Marchant et al., 2000; Nicolaisen et al., 2019), while others found no differences (Pedersen et al., 2011; Kilbride et al., 2012; Höbel, 2019).

This study investigates piglets from two pig breeds, which differ fundamentally in performance, body composition, and breeding history. The German Landrace (**GL**) represents a modern, commercial line with pronounced maternity traits, whereas the German Saddleback (**GS**) is a non-commercial, indigenous breed. The GS has been described to exhibit a lower lean meat content than GL animals (Nürnberg et al., 1997). The gestation length of GS is approximately 1.2 days shorter compared to GL sows (Gladbach, 2022). The breeds GL and GS differ in parturition characteristics, such as a shorter farrowing duration of the GS (GS: 173.0 ± 104.7 min; GL: 266.6 ± 126.1 min), as well as in performance traits like litter size (GL: 14.7 ± 3.61; GS: 11.4 ± 3.08 total born piglets) (Gladbach, 2022). We hypothesised that the interaction between genotype and housing environment is relevant for the neonatal adaptation of low birth weight piglets (< 1 100 g) and that this interaction is verifiable via the blood metabolite profile. The aim of the study was to quantify plasma markers for energy utilisation, organ maturation, and stress response in neonates and suckling piglets depending on (i) the genetic background, (ii) the housing system, and (iii) birth weight.

Material and methods

Experimental groups, housing conditions and management

In order to investigate the effects of (i) breed, (ii) housing and (iii) birth weight class on the metabolic parameters of the piglets, the statistical design aimed at recording at least 5 litters per experimental sow group (breed × housing) to obtain a total of 96 piglets representing the experimental groups (breed × housing × BW class). Four experimental sow groups were analysed, consisting of 10 GL and 17 GS multiparous sows of parities two to eight (GL rate: 4.0 ± 0.55; GL pen: 4.2 ± 0.92; GS rate: 5.4 ± 0.98; GS pen: 3.6 ± 0.63). Notably, 12 sows were included in the 'GS farrowing pen' group instead of the planned five due to homogeneity of birth weight in some litters, i.e., few numbers of hypotrophic piglets and missing samples during the suckling period due to piglet losses. Sows were synchronised and artificially inseminated and group-housed until moving to the farrowing-station at 105 **dpc** (days *postconception*). Sows of both breeds were housed in two different farrowing systems, i.e., crates and pens (Fig. 1). Both housing systems had a total floor space of 6.5 square metres containing a creep area. The crate housing was applied one day prior to the estimated parturition for a period of five days. The accessible area for sows in crates was limited to 180 × 60–70 cm. For the pen housing, the sows had access to the entire area of 6.5 square metres except the creep-area. To approximate commercial conditions, a heating plate (76 × 60 cm) and a heating lamp were offered to the offspring in the creep-area (temperature 30 °C). The temperature in all farrowing compartments was set to 22 °C and computer-controlled together with the ventilation. From 105 dpc, all sows were fed twice daily in a total of 3.2 kg/day of a commercial gestation diet containing 12.2 MJ metabolisable energy per kg DM (Supplementary Table S1). From 109 dpc, the sows were switched to a commercial lactation diet with a higher energy content of 13.2 MJ metabolisable energy per kg DM, and the daily feed amount remained at 3.2 kg/day (Supplementary Table S1). On 112 dpc, the amount of feed was reduced to 2 kg/day. Water was provided *ad libitum*. *Partus* induction was applied for all 27 sows in consideration of the specific gestation length of GS and GL sows, respectively. The farrowing process was induced with a standard regimen of prostaglandin $F_{2\alpha}$ (**$PGF_{2\alpha}$**) and carbetocin, where 0.175 mg cloprostenol (2 ml PGF Veyx forte®; Fa. Veyx, Schwarzenborn, Germany) was applied at 112 dpc in GS sows and at 114 dpc in GL sows. At 113 dpc (GS) or 115 dpc (GL), sows received 70 µg carbetocin (1 ml Depotocin®; Fa. Veyx). Both injections were given intramuscularly.

Monitoring of sows and parturition data

All sows were video-monitored throughout the entire peripartal period. The farrowing of all sows were supervised. The *partus* was

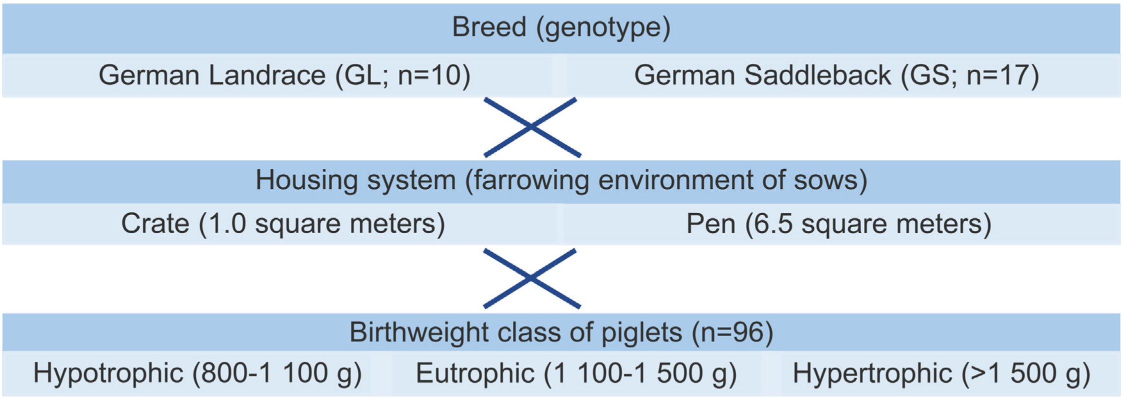

Fig. 1. Experimental groups to evaluate metabolic parameters of piglet vitality due to genotype, housing condition, and birth weight. German Landrace (GL) and German Saddleback (GS) sows were artificially inseminated and group-housed until 105 days *postconceptionem* (dpc). After entering the farrowing station, they farrowed in two different housing systems, i.e., crates and pens. The birth induction in the GS was done at 112/113 dpc and in the GL at 114/115 dpc with cloprostenol and carbetocin, respectively. Piglets from the four experimental sow groups were assigned according to birth weight as hypotrophic (800–1 100 g), eutrophic (>1 100–1 500 g), and hypertrophic (>1 500 g). Each experimental piglet group was represented by eight animals (n = 96) selected for repeated blood analyses during the whole suckling period.

defined as the time between the expulsions from the first to the last piglet. If there were inter-farrowing-intervals $\geq$ 60 min, manual obstetrics was performed. The farrowing length was recorded. Additionally, the time of birth was recorded for each individual piglet and inter-farrowing-intervals were calculated. Numbers of live-born piglets, stillborn piglets, and mummified piglets were recorded. Piglet mortality was recorded daily.

Piglet birth weight classification

After completion of the farrowing, the piglets were weighed and categorised by their birth weight. Applied birth weight classes were based on the stock percentiles of 135 GS-neonates and 13 620 GL-neonates retrieved from the herd data of the Research Institute for Farm Animal Biology (FBN) experimental station (unpublished results). Piglets with birth weights 800–1 100 g were defined as hypotrophic, from 1 100–1 500 g as eutrophic, and > 1 500 g as hypertrophic neonates. The cut-off at a birth weight < 800 g was set to minimise effects from intrauterine growth retardation (**IUGR**). For downstream data analyses, eutrophic and hypertrophic piglets were summarised as control piglets.

Clinical parameters

Body weight of all piglets was recorded after the first colostrum intake. In addition, the BW of those piglets (n = 96) that were assigned to the respective birth weight classes was recorded at 24 h (day 1), day 4, day 20 of life, and one day after weaning. Individual rectal temperature was measured after the first colostrum intake and on day 1. As shown in Table 1, the vitality from the piglets was quantified with a score based on Zaleski and Hacker (1993). Scores from 0 to 2 were assigned for each of the four parameters (breathing, skin-color, standing attempts, meconium staining) and summarised, resulting in vitality scores between 0 and 8. It was carried out by one veterinarian. The time from birth to first suckling was recorded.

Piglet management

Table 1
Vitality score applied to swine neonates. Source: Zaleski and Hacker (1993)

Parameter	Score		
	0	1	2
Breathing	Absent	First breath >15 s	First breath < 15 s
Skin-color	Pale	Cyanotic	Pink
Standing attempts	> 5 min	< 5 min	< 1 min
Meconium	Moderate to high amount	Low amount	Absent

Cross-fostering was not intended, except for three litters where the number of live-born piglets exceeded the number of functional teats on the sow, necessitating cross-fostering on day 1 of lactation. The piglets sampled during the suckling period always remained with their original litter. On the first day of life, the piglets received oral iron supplementation with additional vitamins (PUCORAL® FerroPlus, Pulte GmbH & Co. KG, Germany) and at day 14 of life an iron-injection (Ursoferran® 100 mg/ml, Serumwerk Bernburg, Germany). The piglets received a prestarter (Hakra-Immuno-G, 15.2 MJ/kg, 18.8% CP, Una Hakra) via an automatic feeder from day 14 of life. At the age of 21 days, the piglets were vaccinated against *Lawsonia intracellularis* (ENTERISOL® ILEITIS, Boehringer Ingelheim Vetmedica GmbH, Germany). The piglets were weaned at day 28 of life (GL piglets) and at day 30/31 of life (GS piglets), reflecting the differences in gestation length.

Blood sampling

Blood sample was taken from the *Vena jugularis* of all live–born piglets between 0.5 and 6 h of age, and the time of sampling was recorded (n = 329). At least one completed suckling event took place before sampling. Eight piglets were selected from each of the four experimental sow groups and the three birth weight classes (n = 96), which were monitored throughout the whole suckling period (Fig. 2). The eight piglets in each of the 12 experimental groups (2 breeds × 2 housing conditions × 3 birth weight classes) originate from > 3 litters to represent biological variation. To cover the neonatal adaptation period, blood samples were taken at 24 h (day 1) and day four of life (day 4). In addition, blood samples were obtained at day 20 and 1–day *post*weaning (GL: day 29; GS: day 31/32) to monitor changes elated to organ maturation, development, and weaning. Blood collection was performed using potassium-ethylenediaminetetraacetate (**K-EDTA**) tubes (Sarstedt, Nümbrecht, Germany). EDTA-samples were stored on ice and centrifuged (3 500 revolutions per minute; 4 °C; 15 min). Plasma was stored at –80 °C until analysis.

Plasma analyses of hormones and metabolites

Total protein, albumin, blood urea nitrogen, creatinine, ammonia, triglycerides, uric acid, sodium and chloride were quantified

Fig. 2. Sampling time points to evaluate metabolic parameters of piglet vitality due to genotype, housing condition, and birth weight class. At an age of 0–6 h, blood samples were taken from all live-born piglets (n = 329) of the supervised parturitions as indicated by the green dot. A subset of n = 96 piglets was selected according to birth weight class and subsequently longitudinal blood samples were taken at 24 h (day 1), day 4, day 20, and one–day *post*weaning as indicated by orange dots. GL = German Landrace; GS = German Saddleback.

in plasma via commercial kits (FUJI Dri-Chem 4000i, FujiFilm, Minato, Japan). Levels of plasma fructose, glucose, inositol, and lactate were quantified via HPLC (Agilent, Waldbronn, Germany) as described previously (Metges et al., 2014). Plasma levels of non-esterified fatty acids were quantified as single measurements with an automatic enzymatic analyser (ABX Pentra 400, HORIBA Medical, Montpellier, France) using kits (WAKO Chemicals GmbH, Neuss, Germany). Plasma haptoglobin (cat.-no. HAPT-9, Life Diagnostics, Inc., West Chester, Pennsylvania, USA) was determined in duplicate according to the manufacturer's protocol. Cortisol (cat.-no. EIA-1887, DRG Diagnostics GmbH, Marburg, Germany), insulin (cat.-no. EIA-4747, DRG Diagnostics GmbH, Marburg, Germany), and total triiodothyronine (cat.-no. EIA-4569, DRG Diagnostics GmbH, Marburg, Germany) were analysed in duplicate via commercial ELISAs. Not all parameters were measured at each of the time points. A corresponding overview is stated in Supplementary Table S2. Dynamic ranges and coefficients of variation (CV) for the applied methods are shown in Supplementary Table S3.

Statistical evaluation

Data on farrowing characteristics were analysed by a two-way ANOVA considering breed and housing system as main factors (R language v4.2.2; R package 'car', v3.1-1; R foundation for statistical computing, Vienna, Austria). For the relative numbers of live-born and stillborn piglets, litter size as an additional co-variable was included. The pairwise comparison of the mean values between experimental piglet groups assigned due to breed × housing system × birth weight class was carried out using the Tukey post-hoc test. A chi-square test was carried out to test whether hypotrophic piglets die more often compared to heavier littermates. The effect of litter size on the number of piglets per birth weight class was tested using a linear model, as was the effect of inter-farrowing intervals on the number of stillborn piglets.

Differences in plasma parameter profiles between the birth weight classes were assessed using a permutation test (R package 'RVAideMemoire', v0.9-83-7). Moreover, metabolite data were interrelated by birth weight class using a Partial Least Squares Discriminant Analysis (R package 'mixOmics', v6.24) (Rohart et al., 2017). The variable selection and classification processes were considered two components. For the statistical evaluation of plasma metabolites, a rank-based inverse normal transformation was applied as raw data showed deviation from a normal distribution (R package 'RNOmni', v1.0.1.2). In a repeated measurements approach, the influence of breed, housing system, birth weight class, and time as fixed effects as well as the interactions of breed × housing system, breed × birth weight class, housing system × birth weight class, and breed × housing system × birth weight class were analysed (R package 'stats'). Additionally, each individual time point was evaluated via a linear model with breed, housing system, and birth weight class as fixed effects as well as the interactions of breed × housing system, breed × birth weight class, housing system × birth weight class, and breed × housing system × birth weight class (R package 'stats'). In order to evaluate potential temporal effects on the total plasma protein (0–6 h vs day 1) and plasma triglyceride levels (day 1 vs day 4 vs day 20), the linear model included the effect of sampling time point. The difference between age at sampling [min] and first colostrum intake [min], representing the individual duration for digestion, was considered as co-variable at the first time point. The pairwise comparison of the mean values between experimental groups was carried out using the Tukey posthoc test. The significance level was set at $P < 0.05$. All results are presented as mean ± SEM.

Results

Farrowing characteristics

In order to achieve the required number of piglets per experimental group, the number of litters varied due to the partly homogeneous birth weights and the need for a complete time series (Table 2). Notably, 3 of 12 sows in group GS (pen) were kept in the analyses of farrowing characteristics but none of their piglets were included in blood analyses due to incomplete time series. The breed-specific conditions regarding gestation length were mimicked with the applied *partus* induction protocol. All GL sows received both $PGF_{2\alpha}$ and carbetocin, but only 29.4% of GS sows received carbetocin at 24 h after $PGF_{2\alpha}$ administration, because farrowing had already started. Details on farrowing characteristics, litter size, litter weight and the numbers of live-born and stillborn piglets as well as mummies observed in the respective sow groups are shown in Table 2. Neither farrowing length (breed: $P = 0.131$; housing system: $P = 0.706$) nor individual farrowing intervals (breed: $P = 0.728$; housing system: $P = 0.767$) were different between GL and GS and between farrowing crates and pens. Litter size ($P = 0.018$) as well as the number of live-born piglets ($P = 0.013$) were higher in GL compared to GS, but the litter weight was influenced neither by the breed ($P = 0.128$) nor by the housing system ($P = 0.784$). The analyses revealed an effect of the housing system on stillborn piglets ($P = 0.025$) whereby the absolute number of stillbirth was higher in the farrowing pens than in the farrowing crates. As shown in Table 2, no other litter characteristics were affected by breed or housing system. There was no effect of the inter-farrowing intervals for the number of stillborn piglets ($P = 0.659$). The preweaning mortality was independent of breed ($P = 0.683$) and housing system ($P = 0.487$), but hypotrophic piglets died more often than there heavier littermates ($P = 0.047$).

Vitality score and rectal temperature

The vitality score of the 96 in-depth phenotyped piglets was affected by the housing system (farrowing crate: 7.2 ± 0.2; farrowing pen: 7.0 ± 0.2; $P = 0.033$), while the factor breed showed no effect (GL: 7.2 ± 0.2; GS: 7.2 ± 0.2; $P = 0.305$). At 0–6 h *postnatum*, the body temperature was dependent on the birth weight class (hypotrophic: 36.9 ± 0.2 °C, control littermates: 37.4 ± 0.1 °C;

Table 2
Farrowing parameters in German Landrace (GL) and German Saddleback (GS) sows kept in farrowing crates one day prior to the estimated parturition for a period of five days and farrowing pens. All farrowings were induced with $PGF_{2\alpha}$ (Prostaglandin $F_{2\alpha}$) at 115 (GL) or 112 (GS) days *postconceptionem* (dpc). Carbetocin was administered 24 h later to all GL sows and to 29.4% of the GS sows. Data are presented as mean ± SEM.

Item	GL		GS		SEM	*P*-value		
	Farrowing crate	Farrowing pen	Farrowing crate	Farrowing pen		B	H	B × H
No. of observed litters	5	5	5	12				
Farrowing length [min]	267.6	284.5	185.0	152.7	17.88	0.131	0.706	0.982
Inter-farrowing interval [min]	17.8	15.7	15.7	17.1	1.73	0.728	0.766	0.687
Litter size [n]	16.4	19.0	12.2	11.9	0.73	0.018	0.129	0.195
Live-born piglets [n]	16.0	15.8	11.2	10.3	0.72	0.013	0.911	0.750
Stillborn piglets [n]	0.4	3.2	1.0	1.7	0.38	0.176	0.025	0.176
Live-born piglets [%]	97.5	83.3	92.0	86.7	2.43	0.351	0.150	0.484
Stillborn piglets [%]	2.5	16.7	8.0	13.3	2.43	0.351	0.150	0.484
Mummies [n]	0.4	0.2	0.6	0.5	0.19	0.761	0.761	0.907
Litter weight [kg]	20.6	21.3	16.7	15.3	0.88	0.128	0.784	0.539
Hypotrophic piglets [n]	4.8	4.0	1.6	1.6	0.55	0.070	0.639	0.725
Eutrophic piglets [n]	7.2	5.8	4.0	3.8	0.57	0.083	0.436	0.264
Hypertrophic piglets [n]	4.2	6.6	5.6	4.8	0.64	0.526	0.281	0.949
Preweaning mortality [%]	14.6	22.0	14.6	18.3	2.10	0.683	0.487	0.386
Weaned piglets [n]	13.4	11.6	9.6	8.3	0.58	0.309	0.020	0.002

B = breed; H = housing system.

$P = 0.008$), whereas no effect of breed (GL: 37.3 ± 0.1 °C; GS: 37.2 ± 0.2 °C; $P = 0.127$) and housing system was observed (crate: 37.2 ± 0.2 °C; pen: 37.3 ± 0.1 °C; $P = 0.903$). On day 1, the rectal temperature was affected by breed (GL: 37.8 ± 0.1 °C; GS: 38.1 ± 0.1 °C; $P = 0.013$), while the applied housing system showed no difference (crate: 38.1 ± 0.1 °C; pen: 37.8 ± 0.1 °C; $P = 0.244$).

Evaluation of BW

The GS piglets showed a higher average birth weight ($P = 0.049$) than the GL piglets when considering all 329 live-born piglets (GS: 1.5 ± 0.03 kg; GL: 1.3 ± 0.03 kg). While the GL had 15.9 ± 0.95 live-born piglets, the GS had only 10.5 ± 0.62 live-born piglets ($P = 0.013$; Table 2). The number of hypotrophic and eutrophic piglets was depending on the number of total born piglets (hypotrophic: $P < 0.001$; eutrophic: $P = 0.002$), but the number of hypertrophic piglets was independent of the litter size ($P = 0.971$). When considering the 96 piglets selected by birth weight, the repeated measurement analysis revealed that the BW was affected by breed ($P = 0.026$), birth weight class ($P < 0.001$), and time ($P < 0.001$), and a tendency due to the housing system ($P = 0.056$) (Table 3). An interaction for the bodyweight was observed between the housing system × the birth weight class in the repeated measurement approach. When analysing the individual time points, no effect of the single factors breed or housing system on BW was found. Analyses of BW showed an interaction between breed × birth weight class on day 4 ($P = 0.024$) and between breed × housing system on day 20 ($P = 0.008$). Hypotrophic piglets had consistently lower BWs compared to the control littermates at all applied time points (Fig. 3), with a lowered BW by 34.2% on day 1 and by 18.8% less on the day *post*weaning.

Evaluation of plasma metabolites via partial least squares-discriminant analysis

According to the results of the partial least squares-discriminant analysis based on the plasma metabolites data (Fig. 4), hypotrophic piglets were partially discriminated from eutrophic piglets (adjusted $P = 0.026$; Fig. 4A), whereas the discrimination of hypotrophic vs hypertrophic littermates showed a trend (adjusted $P = 0.063$; Fig. 4B). Moreover, animals assigned to the eutrophic and hypertrophic birth weight classes had a similar metabolic profile (adjusted $P = 0.272$; Fig. 4C). From these, i.e., both eutrophic and hypertrophic piglets, the hypotrophic piglets were partially discriminated (adjusted $P = 0.025$; Fig. 4D). Therefore, the subsequent analysis focussed on the differences between piglets with a low birth weight (800–1 100 g) and their larger littermates with a birth weight of > 1 100 g, referred to as control littermates.

Comprehensive longitudinal evaluation of plasma metabolites

The repeated measurement analyses revealed effects on the plasma lactate level (Supplementary Table S4) due to breed and housing system as well as due to the three-way interaction between breed, housing system, and birth weight class. Both insulin and glucose levels were dependent on the birth weight class, whereas the latter were additionally influenced by the housing

Table 3
BW of neonates and suckling piglets at 0–6 h, day 1, day 4, day 20, and one–day *post*weaning. The data were collected from selected piglets (n = 96) assigned to two birth weight classes of German Landrace (GL) and German Saddleback (GS) breeds born either in farrowing crates or farrowing pens. Data are presented as mean ± SEM.

Parameter per time point	B		H		BWC		SEM	*P*-values for interactions of B × H
	GL	GS	Farrowing crate	Farrowing pen	800–1 100 g	>1 100 g		
BW								
0–6 h [kg]	1.36	1.40	1.36	1.40	1.04^{A}	1.54^{B}	0.032	0.958
Day 1 [kg]	1.36	1.46	1.39	1.43	1.05^{A}	1.59^{B}	0.035	0.767
Day 4 [kg]	1.88	2.01	1.93	1.96	1.51^{A}	2.15^{B}	0.047	0.242
Day 20 [kg]	6.08	6.08	6.01	6.14	5.12^{A}	6.49^{B}	0.136	0.024
*Post*weaning [kg]	7.78	8.19	7.77	8.22	6.87^{A}	8.50^{B}	0.185	0.186

B = breed; H = housing; BWC = birth weight class.
^{A,B}Different superscripts indicate statistical significance per individual time point within birth weight class ($P < 0.05$).

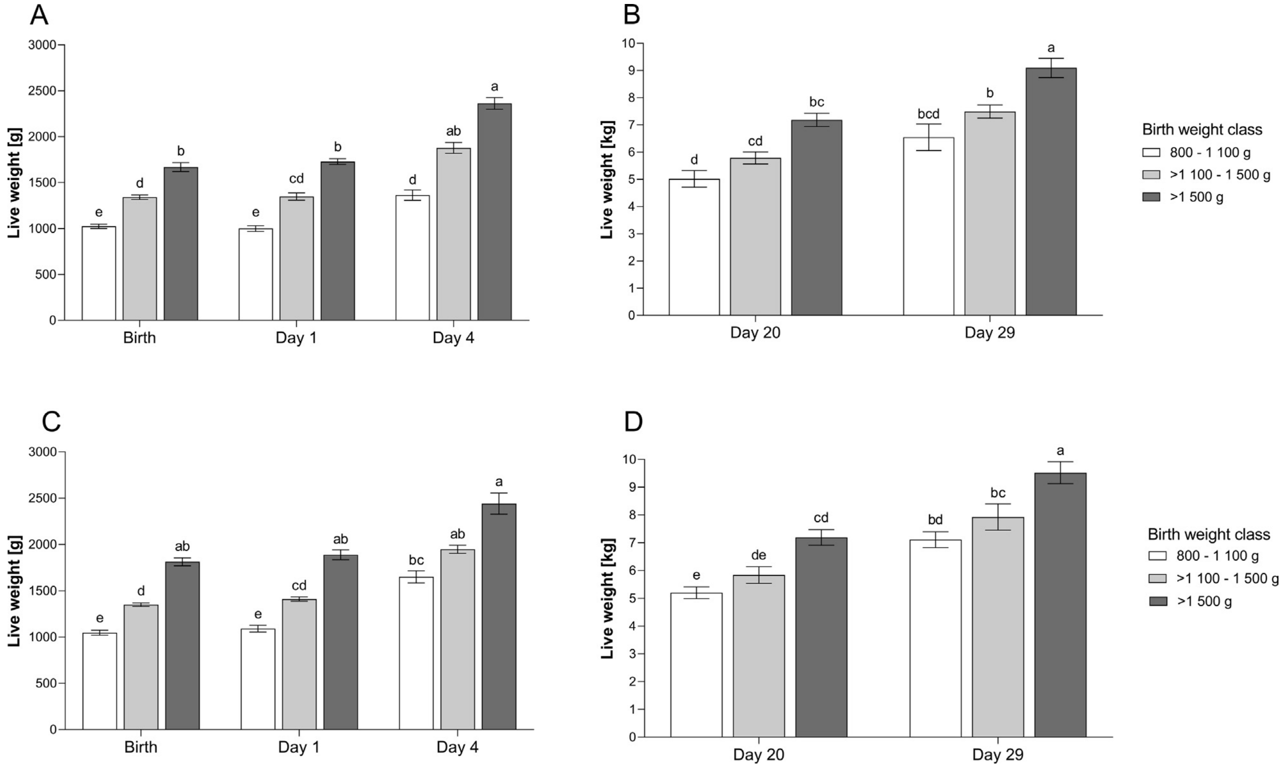

Fig. 3. BWs of German Landrace (A, B) and German Saddleback (C, D) piglets assigned to hypotrophic (800–1 100 g), eutrophic (1 100–1 500 g), and hypertrophic (> 1 500 g) piglets during the neonatal adaptation period (A, C) as well as at day 20 and one–day postweaning (B, D). Data are presented as mean ± SEM. ^{a,b,c,d,e} Different superscripts highlight significant differences ($P < 0.05$).

system. Moreover, a significant two-way interaction between the breed and housing system was observed for plasma glucose. The plasma inositol levels were dependent on the housing system, birth weight class, and time. For plasma fructose, which was quantified only within 0–6 h *postnatum* (undetectable at day 1 and day 4), the two-way interaction between breed and housing system was significant. The plasma non-esterified fatty acid concentrations showed significant effects due to the housing systems and time. Plasma triglycerides showed effects due to time. Both plasma total protein and albumin levels were dependent on breed and time. Plasma urea levels were affected by time and the two-way interaction between breed and birth weight class, whereas ammonia levels were dependent on breed. The plasma creatinine concentration was dependent on the housing system, birth weight class, time, and the two-way interaction between breed and housing system. For uric acid, the analyses showed significant effects of breed, birth weight class, and time. The plasma triiodothyronine concentration was independent of the experimental factors investigated. The haptoglobin levels revealed a significant two-way interaction between breed and housing system. The plasma cortisol levels were dependent on the housing system and time. The plasma levels for the electrolytes sodium and chloride were dependent on breed. Additionally, sodium levels were dependent on birth weight class and time, while for chloride, there was a significant two-way interaction between the housing system and birth weight class.

Plasma metabolites related to energy metabolism per time point

The plasma lactate levels (Table 4) were 25% lower in GS piglets compared to GL piglets at day 1 ($P = 0.025$) and 41% lower at day 4 ($P = 0.004$). Pen-born piglets had significantly lower plasma lactate levels at day 1 compared to piglets born to crated dams. There was a three-way interaction on plasma lactate concentrations between breed, housing system and birth weight class at day 4. Plasma lactate levels were independent from birth weight class. There was a significant two-way interaction on the plasma lactate concentration between the breed and housing system at day 4. Plasma insulin concentrations were higher in GS piglets compared to GL piglets on day 1 ($P = 0.024$) and day 4 ($P = 0.027$), but insulin levels were unaffected by the housing system and birth weight class. Plasma glucose levels were higher in GL piglets compared to GS piglets on day 4 ($P = 0.002$). The glucose levels in piglets born in the farrowing pens were reduced compared to piglets born to sows kept in crates on day 1 ($P = 0.018$) and day 4 ($P = 0.010$). The birth weight class showed an effect as plasma glucose levels were 21% lower on day 1 ($P = 0.031$) and 4% lower on day 4 ($P = 0.006$) in hypotrophic piglets compared to control littermates. For plasma inositol, which was only detectable at 0–6 h and day 1, piglets born in the pen showed lower levels compared to crate-born piglets with reductions of 14% at initial sampling *postnatum* ($P = 0.013$) and 7% at day 1 ($P = 0.014$). There were significant two-way interactions between breed and housing system on inositol levels 0–6 h *postnatum* and between housing system and birth weight class at day 1. Plasma inositol levels were independent of breed and birth weight class. Plasma non-esterified fatty acid levels were similar between breeds and housing systems, while hypotrophic piglets showed an increase of 42% compared to control piglets at day 4 ($P = 0.013$). Plasma triglycerides showed an increase ($P < 0.001$) from day 1 (55.2 ± 3.62 mg/dl) compared to day 4 (147.4 ± 6.42 mg/dl), followed by a decline ($P < 0.001$) until day 20 (61.0 ± 3.0 5). Hypotrophic piglets had 20% lower plasma triglyceride concentrations compared to control piglets at day 1 ($P = 0.038$). Plasma triglyceride levels were independent of breed and housing system. Compared to GL piglets, the GS piglets showed an increase of plasma total protein levels of 21% at day 4 ($P = 0.006$) and of 11%

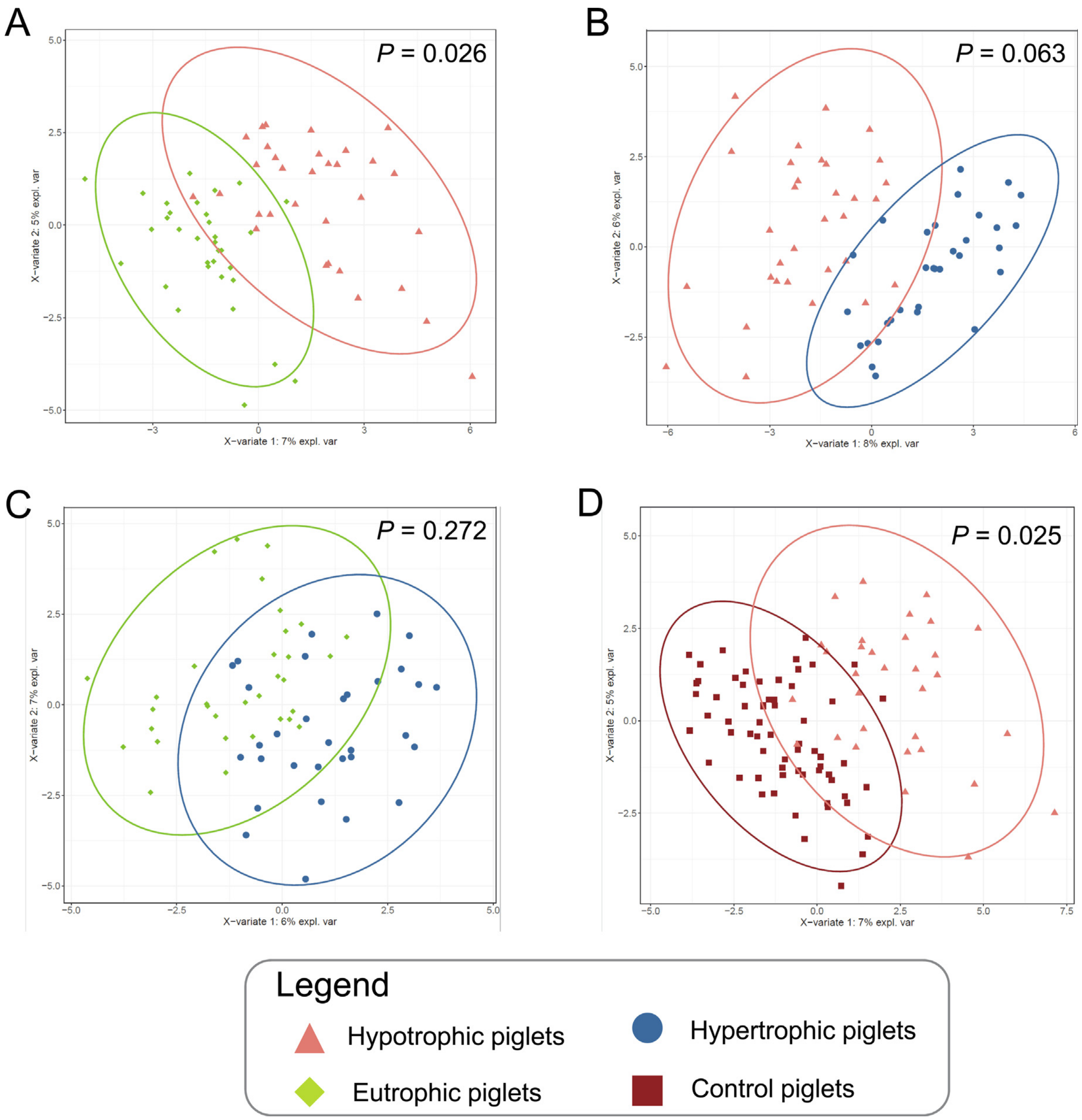

Fig. 4. Partial least squares-discriminant analysis according to birth weight classes using the available plasma metabolite data. The panel shows comparisons between (A) hypotrophic and eutrophic piglets, (B) hypotrophic and hypertrophic piglets, and (C), eutrophic and hypertrophic piglets. (D) The applied partial least squares-discriminant analysis further discriminated between hypotrophic piglets (800–1 100 g) and their eutrophic and hypertrophic littermates (> 1 100 g). Eutrophic and hypertrophic piglets were summarised as control littermates. The corresponding symbols represent individual animals and the circles indicate the 95% confidence interval for each group.

at day 20 (P = 0.001). There were two-way interactions between the housing system and birth weight class for the total protein at 0–6 h *postnatum* (P = 0.044) and between breed and birth weight class at day 1 (P = 0.017). Furthermore, two-way and three-way interactions between breed, housing system, and birth weight class appeared on day 20. Plasma total protein levels were increased by 93% (P < 0.001) between a few hours *postnatum* (2.7 ± 0.07 g/dl) and day 1 (5.2 ± 0.11 g/dl). No effect of the individual factors housing system and birth weight class was observed for plasma total protein levels. The plasma triiodothyronine levels remained unchanged due to breed, housing system, and birth weight class. Hypotrophic piglets had 50% (P = 0.025) higher plasma cortisol levels compared to control piglets on day 1. The difference remained until day 4, where the hypotrophic piglets showed 32% (P = 0.011) higher plasma cortisol levels. There was a two-way interaction effect between breed and birth weight class for the plasma cortisol at day 20 (P = 0.019). For plasma cortisol, there was no significant effect of the single factors breed and housing system observed.

Plasma metabolites related to tissue maturation per time point

Fructose and haptoglobin levels appeared to be unaffected by breed, housing system and birth weight class. However, numerically higher haptoglobin levels were measured at day 1 (42%) and day 4 (131%) in GS compared to GL piglets. The analyses revealed two-way and three-way interactions on haptoglobin at day 1 and day 20. This parameter increased during the neonatal adaptation period. Plasma albumin (Table 5) concentrations were 9% higher in piglets born in the pen compared to piglets born to crated sows a few hours *postnatum* (P = 0.036). Albumin levels appeared to be unaffected by breed and birth weight class. The

Table 4
Plasma metabolites covering the energy metabolism assessed during the suckling period (0–6 h, day 1, day 4, day 20), and one–day *post*weaning. The data were collected from selected piglets (n = 96) assigned to birth weight classes of German Landrace (GL) and German Saddleback (GS) breeds born either in farrowing crates or farrowing pens. Data are presented as mean ± SEM.

Parameter per time point	B		H		BWC		SEM	*P*-values for interactions of B × H
	GL	GS	Farrowing crate	Farrowing pen	800–1 100 g	>1 100 g		
Cortisol [ng/ml]								
0–6 h	91.4	104.9	97.5	99.0	114.2	90.9	5.98	0.222
Day 1	123.2	85.7	116.0	93.4	134.4§	90.0$^{\$}$	9.16	0.483
Day 4	71.3	39.6	70.5	39.7	65.6§	49.9$^{\$}$	4.39	0.628
Day 20	35.0	26.0	36.0	24.9	26.7	32.0	2.65	0.836
*Post*weaning	32.7	48.4	45.5	36.8	41.6	40.9	2.85	0.184
Glucose [mmol/l]								
0–6 h	5.9	6.7	6.6	6.0	5.2	6.8	0.24	0.402
Day 1	5.9	5.9	6.2^{A}	5.6^{B}	5.0§	6.3$^{\$}$	0.18	0.056
Day 4	7.0^{a}	6.6^{b}	6.9^{A}	6.7^{B}	6.6§	6.9$^{\$}$	0.15	0.053
Inositol [mmol/l]								
0–6 h	4.4	5.3	5.2^{A}	4.5^{B}	6.3	4.2	0.21	0.049
Day 1	3.0	2.8	3.0^{A}	2.8^{B}	3.5	2.6	0.12	0.169
Insulin [mU/l]								
0–6 h	31.1	33.4	28.9	36.1	19.8	36.8	3.30	0.748
Day 1	9.9^{a}	17.8^{b}	16.5	12.8	9.9	16.7	1.95	0.258
Day 4	11.2^{a}	11.3^{b}	10.7	11.8	13.8	10.1	0.93	0.018
Lactate [mmol/l]								
0–6 h	4.3	4.0	4.3	3.9	3.7	4.3	0.26	0.076
Day 1	5.6^{a}	4.2^{b}	5.4^{A}	4.4^{B}	5.1	4.8	0.19	0.965
Day 4	6.6^{a}	3.9^{b}	5.5	4.9	5.1	5.3	0.26	0.154
NEFA [µmol/l]								
0–6 h	107.6	128.5	121.7	114.6	91.5	130.9	7.61	0.757
Day 1	125.5	139.1	126.2	138.1	137.8	129.5	4–34	0.503
Day 4	223.1	183.7	193.3	213.5	254.4§	179.5$^{\$}$	8.97	0.135
Day 20	275.9	305.9	313.5	270.4	300.5	287.8	14.95	0.590
*Post*weaning	335.8	419.2	243.0	507.8	532.3	313.4	40.78	0.269
Total protein [g/dl]								
0–6 h	2.7	2.6	2.6	2.7	2.3	2.8	0.07	0.057
Day 1	4.7	5.8	5.3	5.1	5.1	5.3	0.11	0.066
Day 4	4.4^{a}	5.3^{b}	4.8	4.9	4.8	4.9	0.07	0.090
Day 20	4.5^{a}	4.9^{b}	4.8	4.7	4.8	4.7	0.08	0.032
Postweaning	4.5	4.8	4.7	4.6	4.7	4.7	0.06	0.331
Triglyceride [mg/dl]								
0–6 h	35.1	37.4	38.7	33.8	28.9	39.6	2.79	0.439
Day 1	51.3	59.2	56.2	54.3	47.3§	59.0$^{\$}$	3.63	0.887
Day 4	168.5	126.7	147.5	147.3	158.5	142.0	6.49	0.308
Day 20	63.3	58.8	62.7	59.3	66.0	58.8	3.14	0.685
*Post*weaning	39.2	44.0	38.3	44.9	50.2	38.1	2.93	0.207
Triiodothyronine [ng/ml]								
0–6 h	3.9	3.1	3.4	3.7	3.0	3.8	0.25	0.885
Day 4	6.1	3.9	4.9	5.0	4.7	5.1	0.30	0.703

Different superscripts indicate statistical significance per individual time point ($P < 0.05$) within breed (^{a,b}), within housing system (^{A,B}), and within birth weight class ($^{\S,\$}$).
B = breed; H = housing; BWC = birth weight class; NEFA = Non-esterified fatty acids.

GS piglets had higher plasma urea levels compared to GL piglets on day 20 (*P* = 0.020). Piglets born in the pen had higher plasma urea concentrations compared to piglets born to crated sows a few hours *postnatum* (*P* = 0.023). Plasma urea concentrations were 36% elevated in hypotrophic piglets compared with control piglets on day 4 (*P* = 0.002). There were significant two-way interactions between breed and birth weight class on day 4 and day 20. The plasma ammonia level was 24% lower in GS piglets compared to GL piglets on day 1. For plasma ammonia concentration, a significant three-way interaction between breed, housing system, and birth weight class was obtained one–day postweaning. For ammonia, no impact of the housing system and birth weight class was observed. Plasma creatinine levels were affected by the breed (0–6 h: *P* = 0.001; day 1: *P* = 0.025; *P* = 0.001) and housing system (0–6 h: *P* = 0.003; day 1: *P* < 0.001; day 4: *P* < 0.001) during the neonatal adaptation phase. The GS piglets had higher creatinine concentrations compared to GL piglets a few hours *postnatum* (*P* = 0.001) and lower levels at day 1 (*P* = 0.025) and day 4 (*P* = 0.001). Piglets born in the pen had higher plasma creatinine concentrations compared to piglets born to crated sows during the neonatal adaptation period (0–6 h: *P* = 0.003, day 1: *P* < 0.001; day 4: *P* < 0.001) and *post*weaning (*P* < 0.001). There was a significant two-way interaction between breed and housing system on plasma creatinine throughout the neonatal adaptation period. There was a significant three-way interaction between breed, housing system, and birth weight class one–day *post*weaning, but no significant effects were found due to birth weight class. Compared to the GL piglets, GS piglets had 25% and 33% higher

Table 5

Plasma metabolites covering the tissue maturity assessed during the suckling period (0–6 h, day 1, day 4, day 20), and one–day *post*weaning. The data were collected from selected piglets (n = 96) assigned to birth weight classes of German Landrace (GL) and German Saddleback (GS) breeds born either in farrowing crates or farrowing pens. Data are presented as mean ± SEM.

Parameter per time point	B		H		BWC		SEM	*P*-values for interactions of B × H
	GL	GS	Farrowing crate	Farrowing pen	800–1 100 g	>1 100 g		
Albumin [g/dl]								
0–6 h	1.1	1.2	1.1^{A}	1.2^{B}	1.0	1.2	0.04	0.320
Day 1	1.8	2.1	2.0	1.9	1.9	2.0	0.05	0.153
Day 4	2.2	2.5	2.3	2.4	2.3	2.4	0.05	0.160
Day 20	3.9	4.0	3.9	4.0	4.1	3.9	0.06	0.227
*Post*weaning	3.8	4.0	3.8	4.0	3.9	3.9	0.06	0.366
Ammonia [µg/dl]								
0–6 h	183.6	143.2	160.0	166.5	162.2	163.6	6.65	0.661
Day 1	168.3^{a}	128.6^{b}	153.3	143.8	150.0	147.7	5.19	0.667
Day 4	146.2	93.7	120.9	118.4	114.1	122.3	5.82	0.001
Day 20	125.5	115.0	122.2	117.9	116.1	121.8	6.73	0.814
*Post*weaning	85.8	84.1	79.5	90.0	83.6	85.4	3.67	0.823
Chloride [mmol/l]								
0–6 h	88.3	89.3	89.2	88.4	$88.3^{\S}$	$89.0^{\$}$	0.62	0.994
Day 1	89.5	91.2	90.9	89.7	91.7	89.8	0.68	0.601
Day 4	90.0	91.4	91.3^{A}	90.2^{B}	$90.2^{\S}$	$91.0^{\$}$	0.57	0.527
Day 20	87.7^{a}	94.9^{b}	92.1	90.8	92.5	91.0	0.85	0.837
*Post*weaning	92.7^{a}	97.9^{b}	95.8	95.1	$95.2^{\S}$	$95.6^{\$}$	0.92	0.446
Creatinine [mg/dl]								
0–6 h	1.63^{a}	1.87^{b}	1.70^{A}	1.80^{B}	1.75	1.74	0.062	0.010
Day 1	0.92^{a}	0.86^{b}	0.83^{A}	0.95^{B}	0.94	0.86	0.028	<0.001
Day 4	0.75^{a}	0.66^{b}	0.70^{A}	0.71^{B}	0.65	0.74	0.021	<0.001
Day 20	0.85	0.92	0.79	0.99	0.83	0.92	0.023	0.102
*Post*weaning	0.98	0.97	0.80^{A}	1.14^{B}	0.94	0.99	0.028	0.671
Fructose [mmol/l]								
0–6 h	2.0	2.2	2.1	2.1	2.2	2.1	0.07	0.171
Haptoglobin [µg/ml]								
0–6 h	51.7	52.7	46.7	57.7	33.0	61.3	5.25	0.832
Day 1	120.7	171.2	121.2	169.7	157.7	139.8	8.61	0.006
Day 4	159.8	369.7	293.4	238.8	400.2	200.8	48.18	0.192
Day 20	337.8	281.1	316.0	299.5	359.5	284.1	65.03	0.080
*Post*weaning	474.22	380.1	439.0	408.3	504.7	388.1	43.39	0.914
Sodium [mmol/l]								
0–6 h	126.4^{a}	123.8^{b}	124.4	125.7	$121.4^{\S}$	$126.6^{\$}$	0.59	0.364
Day 1	130.5^{a}	127.1^{b}	129.1^{A}	128.4^{B}	127.9	129.1	0.55	0.126
Day 4	129.9^{a}	125.5^{b}	127.7	127.5	125.7	128.5	0.52	0.809
Day 20	120.2	119.0	120.1	118.7	118.0	120.2	0.88	0.201
*Post*weaning	121.3	119.6	119.4	121.4	$118.2^{\S}$	$121.2^{\$}$	0.78	0.232
Urea [mg/dl]								
0–6 h	11.9	11.7	11.4^{A}	12.2^{B}	11.6	11.9	0.25	0.051
Day 1	19.5	20.1	19.6	20.0	20.3	19.6	0.57	0.830
Day 4	8.4	6.7	7.2	7.8	$9.1^{\S}$	$6.7^{\$}$	0.42	0.760
Day 20	5.9^{a}	6.3^{b}	6.4	5.8	5.6	6.3	0.26	0.107
*Post*weaning	5.8	6.1	5.6	6.3	6.4	5.8	0.26	0.832
Uric acid [mg/dl]								
0–6 h	0.4^{a}	0.5^{b}	0.5	0.4	0.5	0.4	0.01	0.003
Day 1	0.5	0.6	0.5	0.5	0.6	0.5	0.01	0.696
Day 4	0.6	0.6	0.6	0.5	$0.6^{\S}$	$0.5^{\$}$	0.01	0.432
Day 20	0.3^{a}	0.4^{b}	0.3	0.3	0.3	0.3	0.01	0.391
*Post*weaning	0.3	0.4	0.3	0.3	0.3	0.3	0.01	0.981

Different superscripts indicate statistical significance per individual time point ($P < 0.05$) within breed (^{a,b}), within housing system (^{A,B}), and within birth weight class ($^{\S,\$}$).
B = breed; H = housing; BWC = birth weight class.

plasma uric acid concentrations a few hours *postnatum* ($P = 0.006$) and at day 20 ($P = 0.007$), respectively. In hypotrophic piglets, plasma uric acid levels were increased by 20% compared to control piglets on day 4 ($P = 0.018$). There was a significant two-way interaction between the breed and housing system a few hours after birth. For plasma uric acid, there was no effect of the housing system. The plasma sodium levels of GS piglets were significantly lower compared to those of GL piglets during the neonatal adaptation period and ranged from 2% lower a few hours *postnatum* to 3% lower on day 4. Piglets born in the pen had lower plasma sodium levels compared to piglets born to a crated sow on day 1 ($P = 0.044$). Hypotrophic piglets had 4% ($P = 0.011$) lower plasma sodium levels compared to control piglets a few hours *postnatum* and 3% ($P = 0.007$) lower one day after weaning. There were two-way interactions between the housing system and birth weight class on day 1 and one–day *post*-weaning. The GS piglets had 8%

(*P* = 0.001) higher plasma chloride levels compared to GL piglets at day 20 and 6% (*P* = 0.027) higher levels one–day postweaning. The plasma chloride concentrations were lower in piglets born in the pen compared to those born to a crated sow at day 4 (*P* = 0.035). Hypotrophic piglets had lower plasma chloride levels compared to control piglets a few hours *postnatum* (*P* = 0.035), at day 4 (*P* = 0.013), and one–day *post*weaning (*P* = 0.039).

Discussion

Farrowing characteristics

Results refer to the dynamics of neonatal adaptation and vitality parameters of newborn piglets with divergent genetic background, and housing conditions at farrowing, and birth weight classes. The relative proportions of live-born piglets were not different between the breeds indicating unaffected piglet viability. In fact, the observed differences in absolute litter size between commercial and traditional dam lines were to be expected and are in line with previous results (König et al., 2021; Ponsuksili et al., 2024; Gladbach, 2022). The results show that the housing conditions did not influence the length of the expulsion phase and there was no effect of the inter-farrowing intervals on the number of stillborn piglets. Nevertheless, management could affect the number of stillbirths, as indicated by the significantly higher numbers of stillbirth retrieved from farrowing pens compared to farrowing crates in this study. A number of studies analysed stillbirth rates in different housing systems with inconsistent results (Glencorse et al., 2019; Goumon et al., 2022) due to differences in prolificacy and the provision of enrichment such as straw or pen size. The preweaning mortality corresponds to the literature data of 15–20% on average (Kielland et al., 2018; Nuntapaitoon et al., 2018) and thus appears to be similar for the modern and traditional breeds analysed and the farrowing crates and farrowing pens used.

Vitality score and rectal temperature

The vitality scores appeared to be similar between GL and GS piglets, but were lower due to pen housing compared to the crate housing system. This goes along with the higher number of stillborn piglets in the pen. The rectal temperature of hypotrophic piglets was lower compared to control piglets at 0–6 h *postnatum*. In fact, hypotrophic piglets cool down more quickly due to the less favourable body surface-to-volume ratio (Herpin et al., 2002) and consequently positive correlation between birth weight and rectal temperature was reported (Baxter et al., 2008). Therefore, the selected hypotrophic neonatal piglets in this study indeed represent a vulnerable subgroup. At 24 h of life, GS piglets had higher rectal temperatures than GL, indicating different development. An effect of breed on body temperature was already observed in commercial crossbreeds, where birth weight was assumed to be a relevant factor (Schild et al., 2020).

Development of BW and discrimination of hypotrophic piglets from eutrophic and hypertrophic piglets

Considering all live-born piglets (n = 329), the higher average birth weight of GS piglets and the tendency for a higher number of hypertrophic piglets in GS compared to GL might reflect less intrauterine crowding and suitable nutrient availability during foetal development in traditional breeds (Vázquez-Gómez et al., 2018). Indeed, average birth weight decreases with litter size (mean and SD total number born: 15.1 ± 3.5 piglets) (Vernunft et al., 2018) and became a problem in modern pig breeds during the last decades (Knap et al., 2023). In our study, the repeated measurement analysis including 96 selected piglets revealed a significant effect due to breed on BW development, which was found to be numerically higher for GS piglets at all selected time points. BW development appeared to be independent of the housing system used, suggesting that maternal environmental perceptions of available space and physical activity are not significant for nutrient allocation or colostrum production. Regarding the effects of birth weight, hypotrophic piglets consistently had lower BWs than control piglets at each selected time point until weaning, which is consistent with previous reports (Škorjanc et al., 2007; López-Vergé et al., 2018; Vodolazska et al., 2023). Blood parameter patterns of hypotrophic piglets could be separated from their heavier littermates via partial least squares-discriminant analysis analyses, with particular differences in plasma metabolites related to energy supply, organ maturation, and stress response. This allows to identify compensatory mechanisms for successful neonatal adaptation and catch-up growth.

Energy metabolism thorough neonatal adaptation

Energy is a fundamental requirement for biological processes in organisms and can be derived from endogenous reserves or exogenous sources through dietary intake. The current results show that hypotrophic piglets exhibit a fully developed thyroid hormone system which indicates a sufficiently developed orchestration of the energy metabolism (Ritacco et al., 1997; Morise et al., 2008). Newborn piglets mainly rely on limited glycogen reserves, which become depleted within approximately 10 h after birth, necessitating the restoration of glucose levels from lactate (Mota-Rojas et al., 2011). Although there might be a genetic contribution to muscle glycogen content in pigs (Liu et al., 2019), porcine neonates of breeds with pronounced differences in body composition such as Meishan and Large White exhibited similar glycogen levels (Le Dividich et al., 1991). An unaffected glycogen content might be assumed for GL and GS neonates, although glycogen contents have not been analysed in the present study. However, the GL piglets showed higher blood lactate levels compared to the GS piglets on day 1 and day 4, indicating an increased anaerobic metabolism in GL compared to GS neonates. In turn, the GS piglets might have received a higher lipid supply via the colostrum in order to maintain their energy stores. Differences in milk composition between GL and GS sows are conceivable, contributing to the observed variations in total protein content in the plasma of their respective piglets, as was described for Meishan and Yorkshire (Zou et al., 1992). The observed course of increased blood insulin levels also indicates an active regulation of lipid and carbohydrate metabolism in GS piglets, potentially aimed at replenishing glycogen stores. It is widely known that pigs of different breeds, especially those bred divergently for lean mass, exhibit differences in energy metabolism which also applies to their piglets (Nürnberg et al., 1997; Ponsuksili et al., 2024). Total protein levels were found to be higher in GS piglets on day 4 and day 20. Protein supplementation in suckling piglets was demonstrated to lead to higher total protein levels in plasma (Kósa et al., 2020).

The farrowing environment was also found to affect the carbohydrate metabolism of the piglets during the neonatal adaptation period. Although the parameters glucose, inositol, and lactate did not exhibit consistent changes over the time points evaluated, their levels were consistently lower in piglets born in farrowing pens compared to those in farrowing crates. Interpreting these observations is challenging, as the farrowing environment and the time elapsed between the last suckling and blood collection are often not comparable across studies (Nowland et al., 2019). However, a plausible explanation for the observed effects might be the increased freedom of movement afforded to sows in farrowing pens, which makes it more difficult for piglets to access the udder, requiring greater physical activity compared to their counterparts in farrowing crates. This increased locomotor activity could potentially contribute to alterations in carbohydrate metabolism and utilisation in neonatal piglets, although there were no differences in BWs between housing systems.

The birth weight class of newborn piglets exerts effects on blood glucose levels on day 1 and day 4, but not at initial sampling *postnatum*. Accordingly, previous studies had not found a significant correlation between umbilical cord blood glucose levels and birth weight (Quesnel et al., 2023). Due to their lower muscle mass, altered body composition, and variable rates of hepatic glycogen mobilisation (Vanden Hole et al., 2019), low birth weight piglets are more dependent on exogenous glucose sources and are more susceptible to dietary fluctuations in the first days of life compared to their counterparts with normal birth weights. This observation is further supported by similar blood lactate values across the birth weight classes per time point, which indicate high plasma lactate levels as a general characteristic of newborn piglets (Uddin et al., 2022). Other parameters related to carbohydrate metabolism, e.g. insulin or lactate, were not affected by birth weight class at the individual time points evaluated in the present study. In previous investigations (Morise et al., 2008; Quesnel et al., 2023), plasma insulin levels were also shown to be independent of birth weight. Inositol, an important component of cell membranes and receptors, is known to exhibit elevated values in cases of intrauterine growth restriction (IUGR) (Gao et al., 2022). However, in the present study, hypotrophic piglets had comparable inositol levels, but it has to be mentioned that piglets with a birth weight < 800 g were excluded from the study to minimise the influence of IUGR on the observed parameters. Total protein content in plasma serves as an indicator of colostrum intake in neonatal piglets (Devillers et al., 2011; Quesnel et al., 2012). In the present study, the observed levels of total protein in the plasma of hypotrophic piglets suggest that these animals had sufficient colostrum intake during the early postnatal period.

Cortisol may be transferred from the sow to the piglets (Grün et al., 2013; Morgan et al., 2021), but the short-term housing of the sows in the two different farrowing environments had no effect on the stress response measurable at the piglet level. Physiological functions of cortisol comprise immunomodulation (Li et al., 2019), and stimulation of the lung function (Czock et al., 2005) essential for neonatal adaptation (Diehl et al., 2022). In this context, the observed higher cortisol release in hypotrophic piglets can be seen as a compensatory mechanism. Moreover, the catabolic effect of cortisol via mobilisation of body reserves via increased gluconeogenesis, lipolysis and protein turnover contributes to meeting the required energy metabolites of hypotrophic piglets during neonatal adaptation. Since the observed hypotrophic neonates are susceptible to the development of a hypoglycaemia-hypothermia complex, an increased release of cortisol indicates an efficient counter-control.

The high energy requirements and low endogenous reserves in hypotrophic piglets lead to elevated non-esterified fatty acid concentrations on day 4, as observed in the present study and reported previously (Stange et al., 2020). This phenomenon is likely attributable to the mobilisation of lipid reserves, although limited, to meet the increased energy demands of these piglets during the early postnatal period. Even though the hypotrophic piglets in our study show specific metabolic adaptation processes, the data indicate a sufficiently developed energy metabolism to survive. Interestingly, lipids might accumulate during the neonatal adaptation period, as the digestive kinetics increase more rapidly than the metabolic capacity (Odle, 1997).

Proxies for tissue maturation of liver and kidney

The analysed proxies for assessing tissue maturation in neonates revealed reduced ammonia and creatinine levels in the plasma of GS compared to GL piglets during the neonatal adaptation period. Despite a shorter gestation length in GS compared to GL, this might be attributed to an increased hepatic detoxification of ammonia and an improved renal clearance of creatinine in GS piglets, as suggested previously in determining kidney maturity (Bauer et al., 2000). The metabolite results depend in part on the timing of the sucking event, which was not controlled in the experimental design prior to the initial blood sampling at 0.5–6 h. However, this bias is present in all 12 experimental groups and the measurements should therefore be regarded as informative. Plasma sodium showed a consistent breed difference, with the GS piglets having lower values and thus exhibiting physiological values of around 125 mmol/l early *postnatum*. Breed-specific differences in litter size could obviously contribute to differences in the hydration status of newborn piglets and consequently influence their blood sodium concentration in the early postnatal period (Devillers et al., 2007; Quesnel et al., 2012).

Haptoglobin levels in the blood reflect the balance between haemolysis and erythrocyte production, but can fluctuate depending on hepatic synthesis function, acute phase responses, genetic factors, and age (Alayash, 2018). Directly *postnatal*, haptoglobin is absorbed via the colostrum, thereby the neonate receiving stimulation for the hepatic synthesis (Hiss-Pesch et al., 2011). In the current study, the increase in haptoglobin levels during neonatal adaptation was consistent with results obtained for the first week of life in piglets (Martin et al., 2005), although the reported time-dependent increase in blood haptoglobin was more prominent.

Housing conditions showed elevated plasma creatinine levels in piglets born in farrowing pens compared to piglets born in farrowing crates throughout the neonatal adaptation period. This could reflect a higher level of physical activity or higher total muscle mass (James et al., 2002). Other markers of tissue maturation such as plasma albumin, sodium, chloride, and urea showed no systematic change. Elevated plasma urea and albumin levels immediately after birth could be related to the utilisation of proteins for energy production (Dazuk et al., 2019). Overall, the housing system did not indicate a major impact on organ maturity.

Newborn piglets possess low endogenous fat reserves and are heavily reliant on the intestinal absorption of triglycerides from colostrum and milk (Zhao et al., 2021). Therefore, it is conceivable that the plasma triglyceride profile of hypotrophic piglets may reflect the maturity of cells and organs, particularly their ability to metabolise ingested lipids. Additionally, the effects of teat competition among littermates could play a role, as hypotrophic piglets generally suckle on teats with lower colostrum quality and additionally ingest usually smaller amounts of colostrum compared to their heavier littermates (Milligan et al., 2002; Oliviero, 2023).

Fructose levels are used as an indicator of maturity in neonatal piglets, with higher levels observed in immature neonates compared to mature piglets (Gondret et al., 2018; Diehl et al., 2022; Quesnel et al., 2023). Thus, the hypotrophic piglets in this study appeared to be sufficiently developed, as evidenced by their fructose levels. In the hypotrophic piglets, plasma urea and uric acid levels were both elevated compared to the control piglets at day 4. The time-dependent pattern shows a decrease in the values along the suckling period, which might reflect differences in metabolic status or tissue maturation. Higher urea levels in hypotrophic piglets are thought to be caused by reduced protein synthesis, which was associated with lower muscle growth in suckling piglets (Getty et al., 2015). As the kidneys are not yet fully developed at birth (Bostedt and Walser, 2008), uric acid appears to accumulate in hypotrophic piglets during the neonatal adaptation phase, although compensation was achieved during further development. In summary, hypotrophic piglets appear to have a slight delay in organ maturation.

Conclusion

Our results provide new insights into piglet vitality and the dynamics of plasma metabolite concentrations during the suckling period in relation to different genetic background, housing conditions at farrowing, and birth weights following artificial birth induction. Both GL and GS breeds subjected to divergent housing systems exhibited breed-specific metabolite profiles to maintain neonatal adaptation. The GS piglets appeared to exhibit a higher level of tissue maturity than GL piglets, suggesting that the time of birth induction in GS at gestation day 112 is corresponding to the physiological time of birth in this breed. The farrowing environment revealed an impact on plasma glucose, inositol and lactate in neonatal piglets, potentially due to higher physical activity to access the udder in farrowing pens. The hypotrophic piglets remained small during the suckling phase and were characterised by the co-occurrence of low blood glucose levels as well as reduced body temperature, i.e., a hypoglycaemia-hypothermia complex. This can have significant implications for neonatal health and development but might be mitigated by an increased release of cortisol. Additionally, lipid metabolism appears to develop more slowly in hypotrophic piglets.

Supplementary material

Supplementary Material for this article (https://doi.org/10.1016/j.animal.2025.101460) can be found at the foot of the online page, in the Appendix section.

Ethics approval

The trial was carried out in accordance with the German Animal Welfare Act, approved by the Animal Welfare Committee of the Research Institute for Farm Animal Biology (FBN), Dummerstorf. The study was approved by the Ethics Committee of the federal state of Mecklenburg-Western Pomerania, Germany (LALLF M-V/TSD/7221.3-1-030/21).

Data and model availability statement

None of the data were deposited in an official repository. The data that support the study findings are available from the authors upon request.

Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work the author(s) did not use any AI and AI-assisted technologies.

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Declaration of interest

None.

Acknowledgements

The authors would like to express special thanks to Angela Garve, Gina Fiedler, Leon Borowski, Tina Illner, Magdalena Rudkowska, and Sonja Uplegger for their excellent technical help. The authors appreciate the work performed by Benjamin Diehl, Adewunmi O. Omotoso, and Maruf Hasan and the staff of the Experimental Pig Facility at FBN.

Financial support statement

The project was supported by the non-profit Tönnies Forschung gGmbh.

References

Alayash, A.I., 2018. Oxidative pathways in the sickle cell and beyond. Blood Cells, Molecules, and Diseases 70, 78–86.
Baude, B.-M., Krugmann, K., Diers, S., Tholen, E., Krieter, J., 2022. Short-term fixation of sows in farrowing pens using different opening procedures. Livestock Science 264, 105051.
Bauer, R., Walter, B., Zwiener, U., 2000. Comparison between inulin clearance and endogenous creatinine clearance in newborn normal weight and growth restricted newborn piglets. Experimental and Toxicologic Pathology 52, 367–372.
Baxter, E., Jarvis, S., D'eath, R., Ross, D., Robson, S., Farish, M., Nevison, I., Lawrence, A., Edwards, S., 2008. Investigating the behavioural and physiological indicators of neonatal survival in pigs. Theriogenology 69, 773–783.
Blim, S.M., 2020. Über das Geburtsgeschehen bei Schweinen einer hochproliferativen Linie unter verschiedenen Haltungsbedingungen: Quantifizierung der partusrelevanten Belastung anhand klinischer, stoffwechselbezogener und ethologischer Parameter. PhD thesis, Justus Liebig University Giessen, Giessen, Germany.
Bostedt, H., Walser, K., 2008. Neugeborenen-und Säuglingskunde der Tiere. Special study edition of the. Enke Verlag, Stuttgart, Germany.
Czock, D., Keller, F., Rasche, F.M., Häussler, U., 2005. Pharmacokinetics and pharmacodynamics of systemically administered glucocorticoids. Clinical Pharmacokinetics 44, 61–98.
Dazuk, V., Rocha Gebert, R., dos Reis, J.H., Baldissera, M.D., Paiano, D., da Silva, A.S., 2019. Glucose and urea levels in suckling piglets. Comparative Clinical Pathology 28, 567–569.
Devillers, N., Farmer, C., Le Dividich, J., Prunier, A., 2007. Variability of colostrum yield and colostrum intake in pigs. Animal 1, 1033–1041.
Devillers, N., Le Dividich, J., Prunier, A., 2011. Influence of colostrum intake on piglet survival and immunity. Animal 5, 1605–1612.
Diehl, B., Oster, M., Vernunft, A., Wimmers, K., Bostedt, H., 2022. Intrinsic challenges of neonatal adaptation in swine. Archives Animal Breeding 65, 427–438.
Gao, H., Chen, X., Zhao, J., Xue, Z., Zhang, L., Zhao, F., Wang, B., Wang, L., 2022. Integrative analysis of liver metabolomics and transcriptomics reveals oxidative stress in piglets with intrauterine growth restriction. Biology 11, 1430.
Getty, C., Almeida, F., Baratta, A., Dilger, R., 2015. Plasma metabolomics indicates metabolic perturbations in low birth weight piglets supplemented with arginine. Journal of Animal Science 93, 5754–5763.
Gladbach, C., 2022. Untersuchungen über den Einfluss der Gen-Umwelt-Interaktion auf klinische, endokrinologische und metabolische Parameter im Verlauf der Geburt bei einer Schweinerobustrasse (Angler Sattelschwein) und einer

modernen reproduktiv leistungsstarken Schweinerasse (Deutsche Landrasse). PhD thesis, Justus Liebig University Giessen, Giessen, Germany.

Glencorse, D., Plush, K., Hazel, S., D'Souza, D., Hebart, M., 2019. Impact of non-confinement accommodation on farrowing performance: a systematic review and meta-analysis of farrowing crates versus pens. Animals 9, 957.

Gondret, F., Guével, B., Pere, M.-C., Quesnel, H., Billon, Y., Com, E., Canario, L., Louveau, I., Liaubet, L., 2018. Proteomic analysis of adipose tissue during the last weeks of gestation in pure and crossbred Large White or Meishan fetuses gestated by sows of either breed. Journal of Animal Science and Biotechnology 9, 1–16.

Goumon, S., Illmann, G., Moustsen, V.A., Baxter, E.M., Edwards, S.A., 2022. Review of temporary crating of farrowing and lactating sows. Frontiers in Veterinary Science 9, 811810.

Grün, V., Schmucker, S., Schalk, C., Flauger, B., Weiler, U., Stefanski, V., 2013. Influence of different housing systems on distribution, function and mitogen-response of leukocytes in pregnant sows. Animals 3, 1123–1141.

Herpin, P., Damon, M., Le Dividich, J., 2002. Development of thermoregulation and neonatal survival in pigs. Livestock Production Science 78, 25–45.

Hiss-Pesch, S., Daniel, F., Dunkelberg-Denk, S., Mielenz, M., Sauerwein, H., 2011. Transfer of maternal haptoglobin to suckling piglets. Veterinary Immunology and Immunopathology 144, 104–110.

Höbel, C., 2019. Untersuchungen zum Verhalten von Sauen und Ferkeln sowie zu den Produktionsdaten in verschiedenen Abferkelsystemen. PhD thesis, Ludwig-Maximilians-Universität München, Munich, Germany.

James, B., Goodband, R., Unruh, J., Tokach, M., Nelssen, J., Dritz, S., 2002. A review of creatine supplementation and its potential to improve pork quality. Journal of Applied Animal Research 21, 1–16.

Kammersgaard, T.S., Pedersen, L.J., Jørgensen, E., 2011. Hypothermia in neonatal piglets: interactions and causes of individual differences. Journal of Animal Science 89, 2073–2085.

Kielland, C., Wisløff, H., Valheim, M., Fauske, A., Reksen, O., Framstad, T., 2018. Preweaning mortality in piglets in loose-housed herds: etiology and prevalence. Animal 12, 1950–1957.

Kilbride, A.L., Mendl, M., Statham, P., Held, S., Harris, M., Cooper, S., Green, L.E., 2012. A cohort study of preweaning piglet mortality and farrowing accommodation on 112 commercial pig farms in England. Preventive Veterinary Medicine 104, 281–291.

Knap, P.W., Knol, E.F., Sørensen, A.C., Huisman, A.E., Van Der Spek, D., Zak, L.J., Granados Chapatte, A., Lewis, C.R., 2023. Genetic and phenotypic time trends of litter size, piglet mortality, and birth weight in pigs. Frontiers in Animal Science 4, 1218175.

König, N.L., Wähner, M., Seeger, J., Sigmarsson, H.L., Kauffold, J., 2021. An investigation into uterine capacity based on litter and placental characteristics in two sow lines with different prolificacy (Danish Landrace x Danish Yorkshire versus German Saddleback). Reproduction in Domestic Animals 56, 34–45.

Kósa, B., Bárdová, K., Lešková, L., Reichel, P., Novotný, J., Link, R., Húska, M., Kyzeková, P., Csörgö, A., 2020. The effect of a feed additive supplemented with porcine plasma protein on growth performance and selected biochemical indices of nursing piglets. Acta Veterinaria Brno 88, 393–399.

Langendijk, P., Plush, K., 2019. Parturition and its relationship with stillbirths and asphyxiated piglets. Animals 9, 885.

Le Dividich, J., Mormède, P., Catheline, M., Caritez, J., 1991. Body composition and cold resistance of the neonatal pig from European (Large White) and Chinese (Meishan) breeds. Neonatology 59, 268–277.

Le Dividich, J., Rooke, J., Herpin, P., 2005. Nutritional and immunological importance of colostrum for the new-born pig. The Journal of Agricultural Science 143, 469–485.

Lee, G., Haley, C., 1995. Comparative farrowing to weaning performance in Meishan and Large White pigs and their crosses. Animal Science 60, 269–280.

Li, Z., Kanitz, E., Tuchscherer, M., Tuchscherer, A., Metges, C.C., Trakooljul, N., Wimmers, K., Murani, E., 2019. Kinetics of physiological and behavioural responses in endotoxemic pigs with or without dexamethasone treatment. International Journal of Molecular Sciences 20, 1393.

Liu, X., Zhou, L., Xie, X., Wu, Z., Xiong, X., Zhang, Z., Yang, J., Xiao, S., Zhou, M., Ma, J., Huang, L., 2019. Muscle glycogen level and occurrence of acid meat in commercial hybrid pigs are regulated by two low-frequency causal variants with large effects and multiple common variants with small effects. Genetics Selection Evolution 51, 1–16.

López-Vergé, S., Gasa, J., Farré, M., Coma, J., Bonet, J., Solà-Oriol, D., 2018. Potential risk factors related to pig body weight variability from birth to slaughter in commercial conditions. Translational Animal Science 2, 383–395.

Marchant, J., Rudd, A., Mendl, M.T., Broom, D.M., Meredith, M., Corning, S., Simmins, P., 2000. Timing and causes of piglet mortality in alternative and conventional farrowing systems. Veterinary Record 147, 209–214.

Martin, M., Tesouro, M., González-Ramón, N., Piñeiro, A., Lampreave, F., 2005. Major plasma proteins in pig serum during postnatal development. Reproduction, Fertility and Development 17, 439–445.

Metges, C.C., Görs, S., Lang, I.S., Hammon, H.M., Brüssow, K.-P., Weitzel, J.M., Nürnberg, G., Rehfeldt, C., Otten, W., 2014. Low and high dietary protein: carbohydrate ratios during pregnancy affect materno-fetal glucose metabolism in pigs. The Journal of Nutrition 144, 155–163.

Milligan, B.N., Dewey, C.E., de Grau, A.F., 2002. Neonatal-piglet weight variation and its relation to pre-weaning mortality and weight gain on commercial farms. Preventive Veterinary Medicine 56, 119–127.

Morgan, L., Meyer, J., Novak, S., Younis, A., Ahmad, W., Raz, T., 2021. Shortening sow restraint period during lactation improves production and decreases hair cortisol concentrations in sows and their piglets. Animal 15, 100082.

Morise, A., Louveau, I., Le Huërou-Luron, I., 2008. Growth and development of adipose tissue and gut and related endocrine status during early growth in the pig: impact of low birth weight. Animal 2, 73–83.

Mota-Rojas, D., Orozco-Gregorio, H., Villanueva-Garcia, D., Bonilla-Jaime, H., Suarez-Bonilla, X., Hernandez-Gonzalez, R., Roldan-Santiago, P., Trujillo-Ortega, M., 2011. Foetal and neonatal energy metabolism in pigs and humans: a review. Veterinarni Medicina 56, 215–225.

Nicolaisen, T., Lühken, E., Volkmann, N., Rohn, K., Kemper, N., Fels, M., 2019. The effect of sows' and piglets' behaviour on piglet crushing patterns in two different farrowing pen systems. Animals 9, 538.

Noblet, J., Etienne, M., Blanchard, A., Fillaut, M., Meziere, N., Vachot, C., Dubois, S., 1987. Body composition, metabolic rate and utilization of milk nutrients in suckling piglets. Reproduction Nutrition Développement 27, 829–839.

Nowland, T.L., van Wettere, W.H.E.J., Plush, K.J., 2019. Allowing sows to farrow unconfined has positive implications for sow and piglet welfare. Applied Animal Behaviour Science 221, 104872.

Nuntapaitoon, M., Muns, R., Tummaruk, P., 2018. Newborn traits associated with pre-weaning growth and survival in piglets. Asian-Australasian Journal of Animal Sciences 31, 237.

Nürnberg, K., Kuhn, G., Ender, K., Nürnberg, G., Hartung, M., 1997. Characteristics of carcass composition, fat metabolism and meat quality of genetically different pigs. Lipid/fett 99, 443–446.

Odle, J., 1997. New insights into the utilization of medium-chain triglycerides by the neonate: observations from a piglet model. The Journal of Nutrition 127, 1061–1067.

Oliviero, C., 2023. Offspring of hyper prolific sows: Immunity, birthweight, and heterogeneous litters. Molecular Reproduction and Development 90, 580–584.

Panzardi, A., Bernardi, M., Mellagi, A., Bierhals, T., Bortolozzo, F., Wentz, I., 2013. Newborn piglet traits associated with survival and growth performance until weaning. Preventive Veterinary Medicine 110, 206–213.

Pedersen, L., Berg, P., Jørgensen, G., Andersen, I., 2011. Neonatal piglet traits of importance for survival in crates and indoor pens. Journal of Animal Science 89, 1207–1218.

Ponsuksili, S., Siengdee, P., Li, S., Kriangwanich, W., Oster, M., Reyer, H., Wimmers, K., 2024. Effect of metabolically divergent pig breeds and tissues on mesenchymal stem cell expression patterns during adipogenesis. BMC Genomics 25, 407.

Quesnel, H., Brossard, L., Valancogne, A., Quiniou, N., 2008. Influence of some sow characteristics on within-litter variation of piglet birth weight. Animal 2, 1842–1849.

Quesnel, H., Farmer, C., Devillers, N., 2012. Colostrum intake: Influence on piglet performance and factors of variation. Livestock Science 146, 105–114.

Quesnel, H., Resmond, R., Merlot, E., Père, M.-C., Gondret, F., Louveau, I., 2023. Physiological traits of newborn piglets associated with colostrum intake, neonatal survival and preweaning growth. Animal 17, 100843.

Ritacco, G., Radecki, S., Schoknecht, P., 1997. Compensatory growth in runt pigs is not mediated by insulin-like growth factor I. Journal of Animal Science 75, 1237–1243.

Rohart, F., Gautier, B., Singh, A., Lê Cao, K.-A., 2017. mixOmics: An R package for 'omics feature selection and multiple data integration. PLOS Computational Biology 13 (11), e1005752.

Schild, S.-L.-A., Foldager, L., Rangstrup-Christensen, L., Pedersen, L.J., 2020. Characteristics of piglets born by two highly prolific sow hybrids. Frontiers in Veterinary Science 7, 355.

Schodl, K., Revermann, R., Winckler, C., Fuerst-Waltl, B., Leeb, C., Willam, A., Knapp, P., Pfeiffer, C., 2019. Assessment of piglet vitality by farmers-validation of a scoring scheme and estimation of associated genetic parameters. Animals 9, 317.

Škorjanc, D., Brus, M., Čandek Potokar, M., 2007. Effect of birth weight and sex on pre-weaning growth rate of piglets. Archives Animal Breeding 50, 476–486.

Stange, K., Miersch, C., Sponder, G., Röntgen, M., 2020. Low birth weight influences the postnatal abundance and characteristics of satellite cell subpopulations in pigs. Scientific Reports 10, 6149.

Theil, P., Cordero, G., Henckel, P., Puggaard, L., Oksbjerg, N., Sørensen, M., 2011. Effects of gestation and transition diets, piglet birth weight, and fasting time on depletion of glycogen pools in liver and 3 muscles of newborn piglets. Journal of Animal Science 89, 1805–1816.

Tuchscherer, M., Puppe, B., Tuchscherer, A., Tiemann, U., 2000. Early identification of neonates at risk: traits of newborn piglets with respect to survival. Theriogenology 54, 371–388.

Tucker, B.S., Petrovski, K.R., Kirkwood, R.N., 2022. Neonatal piglet temperature changes: effect of intraperitoneal warm saline injection. Animals 12, 1312.

Uddin, M.K., Hasan, S., Peltoniemi, O., Oliviero, C., 2022. The effect of piglet vitality, birth order, and blood lactate on the piglet growth performances and preweaning survival. Porcine Health Management 8, 52.

Vanden Hole, C., Ayuso, M., Aerts, P., Prims, S., Van Cruchten, S., Van Ginneken, C., 2019. Glucose and glycogen levels in piglets that differ in birth weight and vitality. Heliyon 5, e02510.

Vázquez-Gómez, M., García-Contreras, C., Torres-Rovira, L., Astiz, S., Óvilo, C., González-Bulnes, A., Isabel, B., 2018. Maternal undernutrition and offspring sex determine birth-weight, postnatal development and meat characteristics in traditional swine breeds. Journal of Animal Science and Biotechnology 9, 1–15.

Vernunft, A., Maass, M., Brüssow, K.-P., 2018. Placental characteristics of german landrace sows and their relationships to different fertility parameters. Czech Journal of Animal Science 63, 339–346.

Vodolazska, D., Feyera, T., Lauridsen, C., 2023. The impact of birth weight, birth order, birth asphyxia, and colostrum intake per se on growth and immunity of the suckling piglets. Scientific Reports 13, 8057.

Zaleski, H., Hacker, R., 1993. Comparison of viability scoring and blood gas analysis as measures of piglet viability. Canadian Journal of Animal Science 73, 649–653.

Zhao, J., Tao, C., Chen, C., Wang, Y., Liu, T., 2021. Formation of thermogenic adipocytes: What we have learned from pigs. Fundamental Research 1, 495–502.

Zou, S., McLaren, D., Hurley, W., 1992. Pig colostrum and milk composition: comparisons between Chinese Meishan and US breeds. Livestock Production Science 30, 115–127.