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Influence of genotype-environment interaction on stress parameters during spontaneous farrowing in modern and traditional pig breeds housed in crates and pens

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ABSTRACT

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The transition from farrowing crates to farrowing pens aims to improve animal welfare by enabling the expression of maternal behavioural profiles. This study examines the spontaneous farrowing process in both farrowing crates and pens for modern German Landrace (GL) and traditional German Saddleback (GS) pigs — two breeds with different breeding histories and adaptations to housing systems. The goal is to investigate whether, and how, both breeds benefit equally from farrowing pens. From the birth of the first piglet until 1 h after the last delivery (*intrapartum*; \dot{p}), half-hourly blood samples were collected from catheterized sows in addition to blood samples retrieved from *antepartum* (ap) and *postpartum* (pp) periods. After spontaneous, noninduced farrowing, the traditional GS breed exhibited a significantly shorter gestation length, smaller litter weight, and a lower incidence of labour dystocia compared to modern GL sows. Breed effects were observed for profiles of heart rate (ap: GL > GS), cortisol (ap: GL < GS; ap: GL < GS), adrenaline (ap: GL < GS), non-esterified fatty acids (ap: GL < GS; ap: GL < GS), glucose (ap: GL > GS), and ap-hydroxybutyrate (ap: GL < GS) at distinct *peripartum* periods. Effects due to housing appeared for heart rate (ap: crate > pen) as well as respiratory rate (crate < pen) and adrenaline (crate > pen) at distinct time points. Taken together, breed-specific endocrine control and energy-related metabolic properties might suggest a need for tailored housing conditions during parturition for modern and traditional sows.

1. Introduction

The husbandry system of breeding pigs during gestation, farrowing, and lactation constitutes a particular challenge in order to reconcile the demands of society and breeders for pricing, animal welfare, economic value, and work safety. For decades, sows were kept in crates during farrowing and lactation, which might offer piglets some protection against crushing [1], but are also associated with restrictions in behavioural needs [2–4]. In fact, several European countries such as Sweden, Finland, Norway, and Switzerland have already banned the housing of sows in farrowing crates during late gestation and lactation. In other countries, such as Germany, legislators have only recently

mandated improvements for animal welfare [5].

As in all other mammals, the farrowing process in pigs proceeds in distinct phases termed stage 1 (antepartum period; last hours to days before labour; includes endocrine changes, nesting behaviour, and colostrum production preceding birth of the first piglet), stage 2 (intrapartum period; typically 2–12 h; includes onset of labour and expulsion of fetuses), and stage 3 (expulsion of placentas which may commence in stage II). The postpartum period begins after parturition and includes initial recovery for 12–24 h, while uterine involution lasts 2–4 weeks. Farrowing is initiated or maintained by several important endocrine and metabolic processes and requires the interplay of progesterone, estrogen, 13,14-dihydro 15-keto-prostaglandin $F_{2\alpha}$ metabolite (PGFM),

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oxytocin, cortisol, and catecholamines. Some well-known endocrine control dynamics of the farrowing process include an increase in estradiol and a decrease in progesterone levels [6]. The latter initiates the end of gestation as progesterone promotes immobilization of the myometrium by extracellular binding of calcium [7]. The altered ratio between progesterone and estradiol stimulates the release of PGFM from the endometrium [8], which increases considerably at the onset of farrowing [9]. These endocrine key players are precisely coordinated which is evidenced by the fact that PGFM induces an increase in oxytocin receptors in the uterus at the onset of partus, thereby achieving a direct as well as indirect effect on myometrial contraction [10]. The increase of foetal corticosteroids might contribute to this cascade of events, although its relevance in the pig has been questioned [11-13]. The physiological changes in the farrowing dam are further demonstrated by clinical parameters, as body temperature in particular rises antepartum indicating increased heat production [6,14]. The heart rate and respiratory rate also increase antepartum and remain elevated until the end of parturition [15-17]. Consequently, temperature preferences differ throughout gestation, i.e., late-gestation sows prefer lower temperatures compared to mid-gestation or non-pregnant sows [18].

The farrowing process can be delayed or even disrupted by exogenous or endogenous factors which may include housing conditions [19, 20], age of an individual, i.e., parity number [21], and genetics [22]. Different environments revealed effects on the endocrine status of sows in gestation, birth and lactation, but the results were not always consistent. Basal levels of catecholamines [23] were found to be breed-specific, with Large White pigs showing lower adrenaline and noradrenaline concentrations compared to Piétrain and Meishan breeds. Moreover, differences in basal cortisol levels in pigs have been attributed to a causal genetic variant [24].

In recent decades, litter size has increased significantly in modern pig breeds and highly productive sow lines have been established [17]. However, while productivity appears to be based in part on uterine capacity [25,26], the ability to complete a spontaneous parturition without intervention or complications has not been a selection criterion although the metabolic demands for maternal performance have increased due to the elevated number of piglets with potential implication on animal welfare as discussed for decades [27-31]. In fact, management practices such as standard partus induction by hormone administration and frequent use of contraction-enhancing measures have been rarely questioned [32]. There is a concern whether the use of exogenous hormonal birth-controlling measures has resulted in abnormalities in the farrowing process itself. It is expected that such adaptation to anthropogenic interventions has not occurred in traditional, non-commercial or traditional breeds such as Saddleback pigs not subjected to intensive selection in recent decades. Saddleback pigs are considered robust, undemanding animals and particularly suitable for extensive free-range or organic farming [33]. Moreover, saddleback pigs showed higher backfat thickness, higher body fat and lower lean meat compared to Landrace pigs [34].

We hypothesized, that genetics and housing conditions impact on the farrowing process of sows. The aim of the study was to investigate the spontaneous farrowing process of a modern dam line (German Landrace) and a traditional breed (German Saddleback), i.e. breeds representing different body compositions, in farrowing crates and pens. Analyses on genotype-environment interaction comprised clinical, metabolic, and endocrine parameters throughout the *antepartum*, *intrapartum*, and *postpartum* periods. Preliminary results have been previously reported in abstract form [35].

2. Material and methods

2.1. Animals and study design

The study comprised repeated blood samples to investigate endocrine stress parameters and metabolites throughout farrowing of sows of

the modern German Landrace (GL; n = 25 farrowings) and the traditional German Saddleback (GS; n = 17 farrowings) kept in crates or pens in a 2 × 2 factorial arrangement as previously described by Gladbach [36]. The farrowings were replicated over time in 16 batches, each with 1-4 healthy sows which were in their first, second or third parity (Supplemental Table S1 and Supplemental Table S2). Detailed information referring to the number of sows used per experimental batch, i. e., numbers referring to sows per breed, parity, and housing environment is displayed in Supplemental Table S2. The individual farrowings represent the experimental unit (n = 42). To exclude any potential confounding of parity and housing conditions, a subgroup of 15 sows (GL: n = 9; GS: n = 6) was subjected to both housing conditions as a cross-over design (Supplemental Table S1). Accordingly, the 15 sows mentioned were examined twice, namely in the first and second parity. A total of n = 4 GL sows and n = 4 GS sows were kept in pens for the first parturition and housed in crates during the second parturition (vice versa: n = 5 GL sows; n = 2 GS sows). Additional sows in their first, second, and third parity (GL: n = 7; GS: n = 5) were randomly assigned to the housing system. All sows were subjected to spontaneous, non-initiated onset of parturition.

After confirmation of pregnancy on day 28 of gestation, sows were group-housed until day 105 of gestation. Sows were moved into single farrowing units (5.8 m²). On day 110 of gestation, units were either left unchanged as farrowing pens (5.8 m²; GL: n=11; GS: n=8) or restricted following conventional standards as farrowing crate (1.2 m²; GL: n=14; GS: n=9). Both housing conditions were situated in the same room, equipped with semi-slatted floors and nest-building material in the form of canvas bags.

From day 105 of gestation, sows received 3.2 kg/day of a commercial gestation feed with 12.2 MJ ME/kg (Supplemental Table S3). From day 109 of gestation, sows were fed 3.2 kg/day of a commercial lactation feed containing 13.2 MJ ME/kg (Supplemental Table S3). Feed quantity was reduced to 2.5 kg/day per individual sow on day 113 of gestation, and further to 2 kg/day per individual sow on day 112 of gestation. Feed was offered in two daily meals at 0700 h and 1400 h. Feed quantity was gradually increased after farrowing starting from 1 kg/day. Feed intake was recorded on a daily basis. Water was supplied *ad libitum*. The ambient temperature in the farrowing units ranged between 18 and 25 $^{\circ}$ C.

2.2. Catheterization, pain medication, and infection metaphylaxis

In order to obtain frequent blood samples, a central venous catheter was implanted into the jugular vein via the ear vein of the sows (V. auricularis lateralis) on the 112th day of gestation using the method described by Blim et al. [31]. All animals were lightly sedated for the procedure (Azaperon, Stresnil®, Elanco Tiergesundheit AG, Germany, 0.5-1 ml per 20 kg BW). In some animals, short anesthesia (ketamine hydrochloride; Ursotamin®, Serumwerk Bernburg AG, Germany, 0.2 ml/kg BW) was additionally necessary. For implantation of the catheter, the ear was cleaned and disinfected and the ear veins were blocked. The catheter (Cavafix® Certo®; B. Braun; Melsungen, Germany; 14 G $1.1 \times$ 1.7 mm; 45 cm or 30 cm long) was then implemented via the ear vein into the jugular vein. The catheter was fixed at the puncture site by individual stiches and a self-adhesive plaster. In nine cases (only GS sows), the insertion of the catheter via ear vein was not possible. Due to anatomical variations in the course of the ear veins, it was not possible to advance the catheter beyond the envelope at the base of the ear into the central veins. In these cases, direct catheterization of the jugular vein was used as described by Brüssow et al. [37] and Niiyama et al. [38]. For this purpose, the animals were given a dose of anaesthetic (azaperone, Stresnil®, 0.5-1 ml per 20 kg BW and ketamine hydrochloride; Ursotamin®, 0.2 ml/kg BW) and turned onto their backs. After cleaning and disinfection of the right side of the neck, the jugular vein was exposed after cutting the skin and blunt pre-preparation. A silicone catheter was implanted directly into the vein and fixed by several individual staples.

The end of the catheter was guided subcutaneously to the dorsal side using a metal probe to position the end of the catheter dorsal to the scapula for blood sampling. The surgical wound was closed by muscle, subcutaneous and skin sutures, and the catheter end was fixed in a small bag on the sow's shoulder for protection. All catheterised animals received pain prophylaxis (Meloxicam, Melovem®, Boehringer Ingelheim Vetmedica GmbH, Germany, 2 ml/100 kg BW) after implantation and antibiotic care (Sulfadimidine sodium + Trimethoprim, Trimethosel®, Selectavet Dr. Otto Fischer GmbH, Germany, 1 ml/10–15 kg BW) for several days. Catheter care was performed twice per day by flushing with 5–10 ml of a 0.9 % heparin sodium chloride solution (0.1 ml heparin sodium (25,000 IU/5 ml), Rotexmedica GmbH Arzneimittelwerk Trittau, Germany dissolved in 1000 ml sodium chloride solution, B. Braun, Melsungen, Germany).

2.3. Blood sampling

Blood samples were derived from 20 GL to 17 GS farrowings (Fig. 1; Supplemental Table S1 and Supplemental Table S2). Sampling included stage I, which covers cervical dilation (antepartum; ap), stage II which represents the onset of labour until the placentas are delivered (intrapartum; ip), and early lactation (postpartum; pp). Within 10 min of the birth of the first piglet, investigators were present to continuously collect blood samples and monitor sows and neonates. Blood samples were collected in half-hourly intervals throughout the intrapartum period, beginning at onset of parturition (marked as expulsion of the first piglet) until 1 h after birth of the last piglet. The intrapartum period differs in duration from one individual to another and depends, e.g., on the litter size. The end of parturition was defined by the number and weight of placentas (>1000 g). Blood samples obtained before (gestational days 112, day 114, and day 116, if applicable) and after farrowing (lactation days 1, 2, and 3) were collected between 1000 h-1100 h. Blood samples from day 112 of gestation were taken via jugular puncture prior to surgery. At each sampling time point, the first 3 mL of fluid was discarded to remove the heparinized saline which ensured patency between sample collections. Blood collection of approximately 20 ml each was performed in both EDTA and serum tubes (Sarstedt, Nümbrecht, Germany). EDTA tubes were placed on ice. A few drops of EDTA-full blood were used for glucose analyses. Serum tubes were stored at room temperature (30 min) to ensure complete coagulation. Serum and plasma samples were prepared by centrifugation at 3500×g for 10 min at 4 °C and stored at -80 °C.

2.4. Farrowing process and clinical parameters

The birth interval was recorded. Prolonged farrowing, i.e., labour dystocia, was defined as a birth interval between single piglets

exceeding 60 min which resulted in respective obstetric interventions, i. e., manual vaginal exploration with compliance to obstetric hygiene rules. A farrowing process can therefore include one or multiple dystocia events. The number of sows having labour dystocia was determined for each experimental group. Numbers of total born piglets, live born piglets, and stillborn piglets were recorded. The individual birth weights of delivered piglets were recorded. Veterinary examination was performed at half-hour intervals prior to the scheduled blood samplings. Records included the measurement of heart rate by cardiac auscultation with a stethoscope counting the carotid artery pulse over 30 s [1/min], rectal temperature with a thermometer [°C], and respiratory rate by counting complete breath cycles for 60 s [1/min]. The overall duration of farrowing [min] and birth intervals between piglets [min] were monitored.

2.5. Analyses of metabolites and stress hormones in blood

Blood glucose was measured via a commercially available blood glucose meter with test strips (VetMate, Berger Med GmbH, Gießen, Germany). Concentrations of serum non-esterified fatty acids (NEFA) and β -hydroxybutyrate (BHB) were determined via commercial assays using an enzymatic analyser (ABX Pentra 400, HORIBA Medical, Montpellier, France). Serum levels of cortisol were determined in duplicate using commercially available ELISA according to the manufacturer's protocols (DRG, Marburg, Germany). Both adrenaline and noradrenaline were analysed in plasma via HPLC (Shimadzu, Kyoto, Japan) as previously described by Otten et al. [39]. Quantification of adrenaline and noradrenaline were performed via single-point calibration curves using dihydroxybenzylamine as internal standard (Recipe, Munich, Germany). The limit of detection (LOD) is 4 pg/ml for adrenaline and 2 pg/ml for noradrenaline.

2.6. Statistical analysis of data

Data on farrowing characteristics were analysed including breed, housing condition, breed \times housing interaction, and parity as fixed effects (R language v4.2.2; R package stats; R package car, v3.1-1; R Foundation for Statistical Computing, Vienna, Austria). A chi-squared test was carried out to analyse the prevalence of dystocia.

According to the onset of parturition, sampling time points from the *ante partum* period were expressed as negative values. Sampling time points collected during the ante partum period were expressed according to the onset of parturition: 3 days, -2 days, and -1 days prior parturition. Due to the large individual differences in the length of the parturition process, the data were analysed up to 240 min after the birth of the first piglet. For the time points after 240 min, the number of sows decreased significantly due to termination of parturition, hence these data were not analysed.

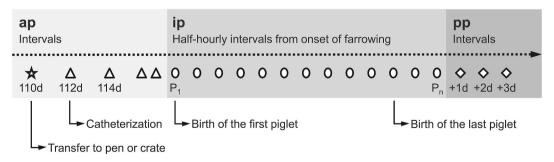


Fig. 1. Experimental design. Sows of German Landrace (GL) and German Saddleback (GS) breeds were subjected to farrowing crates or farrowing pens at day 110 of gestation as indicated by the star. Catheterization was conducted at day 112 of gestation. Triangles, circles and diamonds represent time points for blood sampling and clinical examination. The frequency of blood sampling before farrowing depended on the duration of gestation (day 112, day 114, day 116, if applicable). The ante partum time points were assigned retrospectively in a daily manner according to the individual onset of parturition (–3 days, –2 days, and –1 days prior parturition). The expulsion of the first piglet was defined as the starting point of the *intrapartum* period. Subsequently, the sampling and clinical examination scheme followed half-hourly intervals until 1 h after birth of the last piglet. Additional blood samples were collected at daily intervals during the lactation period. Ap – *antepartum*; pp – *postpartum*.

For statistical analysis of hormone and metabolite data, residuals have been calculated using the breed, the housing condition, the breed \times housing interaction, and the parity as fixed effects. As residuals showed deviation from normal distribution, data was transformed via the rank-based inverse normal transformation as presented in Supplemental Fig. 1 (R package RNOmni, v1.0.1.2).

The data of clinical, endocrine and metabolic parameters were analysed as repeated measurements (correlation structure: compound symmetry) for each of the three farrowing periods ap (-3 to -1 days prior onset of parturition), ip (onset of parturition until 1h after birth of the last piglet), and pp (+1 to +3 days after parturition). Analyses included the breed, the housing condition, the breed \times housing interaction, and the parity as fixed effects using R language (package stats). Moreover, data was analysed for each time point as a single trait taking into account the breed, the housing condition, the breed \times housing interaction, and the parity as fixed effects using a linear model (R package stats).

Effects of the anaesthetic protocol in combination with the catheterization methods on serum cortisol, plasma adrenaline and noradrenaline was evaluated using the housing condition, the parity, and the catheterization method as fixed effects (R package stats). Differences were considered significant at $P \leq 0.05$. All results were presented as mean \pm SEM.

3. Results

3.1. Farrowing characteristics

In total, the farrowing of 23 primiparae (farrowing crates: n=13; farrowing pens: n=10) and 19 pluriparae (farrowing crates: n=10; farrowing pens: n=9) were sampled. The average gestation number of all studied sows was 1.50 ± 0.09 (mean \pm SEM). For the pluriparae, the parity number was 2.0 for GL and 2.3 for GS sows on average. The gestation period of GL sows was approximately 1.2 days longer compared to GS sows (Table 1). Since no artificial birth induction was applied, these data represent the biological conditions. The GL sows showed a higher litter weight compared to GS (P=0.025). The percentage of live born piglets was not significantly different between breeds and was 96.5% for GL and 97.9% for GS (excluding mummified piglets; P=0.152). In GL sows, farrowing was associated more often (11/25) with dystocia (P=0.027) than in GS sows (2/17).

The total farrowing length was numerically 94 min longer in GL sows compared to GS (P = 0.111). Housing conditions showed no impact on total farrowing length (P = 0.825). For the birth interval, neither breed (P = 0.509) nor housing conditions (P = 0.550) or their interaction (P = 0.573) showed effects. Farrowing took place regardless of the time of

day for all sow groups.

3.2. Clinical parameters

The *P*-values of the evaluation of the clinical data on body temperature (n = 565), respiratory rate (n = 537), and heart rate (n = 556) per farrowing period are shown in Table 2 and Fig. 2. For body temperature,

Table 2

Statistical evaluation (*P*-values) of clinical parameters, concentrations of plasma hormones, and metabolites at distinct farrowing periods. Data were retrieved from German Landrace (GL) and German Saddleback (GS) pigs kept in farrowing crates and farrowing pens throughout the entire *peripartum* period. The results include stage I, i.e., cervical dilatation (*antepartum*; ap), and stage II, i.e., the onset of parturition until delivery of the placenta (*intrapartum*; ip), as well as early lactation (*postpartum*; pp). Significant effects are highlighted in bold.

Item	Breed	Housing	$Breed \times Housing \\$		
ap period					
Body temperature	0.527	0.335	0.592		
Respiratory rate	0.216	0.869	0.727		
Heart rate	0.619	0.015	0.014		
Blood concentrations					
Cortisol	0.026	0.380	0.404		
Adrenaline	0.029	0.334	0.966		
Noradrenaline	0.701	0.180	0.577		
Glucose	0.047	0.728	0.119		
NEFA	0.007	0.856	0.343		
BHB	0.019	0.376	0.258		
ip period					
Body temperature	0.756	0.693	0.755		
Respiratory rate	0.367	0.436	0.476		
Heart rate	0.014	0.456	0.733		
Blood concentrations					
Cortisol	< 0.001	0.240	0.011		
Adrenaline	0.178	0.638	0.803		
Noradrenaline	0.048	0.796	0.816		
Glucose	0.618	0.756	0.251		
NEFA	0.008	0.590	0.263		
ВНВ	0.224	0.412	0.293		
pp period					
Body temperature	0.270	0.410	0.207		
Respiratory rate	0.799	0.856	0.656		
Heart rate	0.076	0.148	0.167		
Blood concentrations					
Cortisol	0.849	0.724	0.775		
Adrenaline	0.118	0.643	0.749		
Noradrenaline	0.656	0.381	0.811		
Glucose	0.456	0.923	0.497		
NEFA	0.324	0.339	0.051		
BHB	0.642	0.768	0.889		

Abbreviations: NEFA – non-esterified fatty acids; BHB – $\beta\text{-hydroxybutyrate.}$

Table 1
Body weight, feed intake and farrowing characteristics in German Landrace (GL) and German Saddleback (GS) pigs kept in farrowing crates and farrowing pens throughout the entire *peripartum* period. Data are presented as mean.

Item	GL in crate	GL in pen	GS in crate	GS in pen	SEM	P-value Breed	P-value Housing	P-value Breed x Housing
N	14	11	9	8				
Body weight of sows at farrowing, kg	233.2	224.9	219.2	235.6	4.99	0.678	0.446	0.318
Feed intake antepartuma, kg	6.1	5.8	5.1	8.1	0.34	0.023	0.007	0.017
Feed intake postpartum ^b , kg	5.9	6.6	2.9	2.9	0.37	< 0.001	0.964	0.584
Gestation length, d	115.8	115.9	115.0	114.3	0.22	0.013	0.270	0.348
Total farrowing length, min	262.4	272.1	166.3	179.5	19.38	0.111	0.825	0.952
Birth interval, min	18.0	19.2	18.7	14.5	1.98	0.509	0.550	0.573
Litter weight, kg	19.3	19.1	17.1	14.3	0.75	0.025	0.182	0.385
Birth weight, kg	1.29	1.45	1.37	1.38	0.05	0.646	0.732	0.409
Total born piglets, N	15.2	13.8	11.4	11.4	0.58	0.102	0.959	0.552
Live born piglets, N	14.7	13.2	10.9	11.4	0.55	0.184	0.764	0.328
Stillborn piglets, N	0.5	0.6	0.6	0.0	0.15	0.160	0.240	0.246
Stillborn piglets, %	2.7	4.3	4.3	0.0	1.00	0.152	0.179	0.147
Labour dystocia, N	6	5	1	1	_	0.027	0.938	0.176

^a Summarized for ap days -3, -2, -1.

^b Summarized for pp days +3, +2, +1.

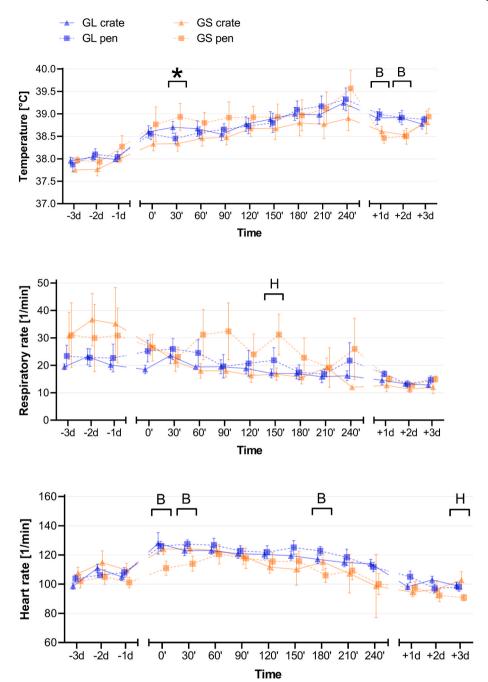


Fig. 2. Representation of the clinical parameters body temperature, respiratory rate, and heart rate in German Landrace (GL) and German Saddleback (GS) pigs kept in farrowing crates or farrowing pens throughout the entire *peripartum* period. Data are presented as mean \pm SEM and cover the time series for GL sows (blue) and GS sows (orange) kept in farrowing crates (triangles; solid line) or farrowing pens (squares; dashed line). The time points -3d until -1d represent the *antepartum* period, time points 0 min until 240 min represent the *intrapartum* period, and the time points +1d until +3d represent the *postpartum* peSignificant difference due to breed at single time pointriod. * Significant difference due to breed × housing interaction at single time point (P < 0.05); B Significant difference due to breed at single time point (P < 0.05). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

the analyses via repeated measurements revealed no differences due to breed, housing, and their interaction. For the evaluation per time point, a significant interaction of breed and housing was found at 30 min of parturition. Additionally, analysis revealed a significantly higher body temperature at +1 d and +2 d *postpartum* in GL sows compared to GS sows.

The respiratory rate was unaffected by breed, housing, and their interaction following the repeated measurement analyses throughout

the three *peripartum* periods. For individual time points, there was a significant impact of the housing conditions at 150 min of parturition, when the respiratory rate of sows in pens was higher than that of sows in crates.

Heart rate analysis revealed significant effects for the interaction of breed and housing conditions in the ap period. Moreover, heart rate appeared to be significantly affected by breed in the ip period, with higher levels in GL sows compared to GS sows. For the evaluation per

time point, this significance was shown with higher levels in GL than in GS at start of parturition (0 min), as well as 30 min and 180 min of parturition. Moreover, a higher heart rate was shown in sows kept in crates compared to sows kept in pens at day 3 of lactation.

3.3. Stress hormones

One GS sow had exceptionally high serum cortisol levels (up to 700 ng/ml) and was excluded from analysis. Results of the blood levels of the

stress hormones cortisol (n = 415), adrenaline (n = 430) and noradrenaline (n = 430) throughout the distinct *peripartum* periods are shown in Table 2 and Fig. 3. The cortisol values retrieved from the ip period showed a significant interaction of breed and housing condition via repeated measurements. Moreover, the evaluation for effects due to breed revealed significantly higher serum cortisol levels for GS sows compared to GL sows at ap and ip periods. In the statistical analysis at specific time-points, cortisol levels were significantly higher for GS sows compared to GL sows at -1 d ap, at expulsion of the first piglet (0 min) as

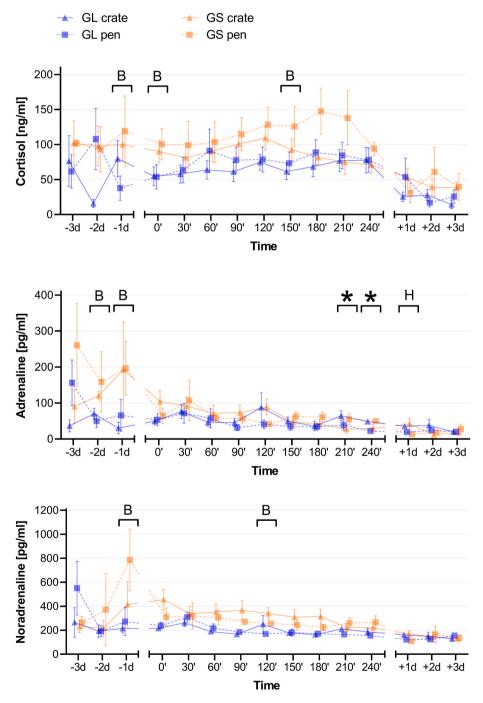


Fig. 3. Representation of serum cortisol as well as plasma adrenaline and noradrenaline levels in German Landrace (GL) and German Saddleback (GS) pigs kept in farrowing crates and farrowing pens throughout the entire *peripartum* period. Data are presented as mean \pm SEM and cover the time series for GL sows (blue) and GS sows (orange) kept in farrowing crates (triangles; solid line) or farrowing pens (squares; dashed line). The time points -3d until -1d represent the *antepartum* period, time points 0 min until 240 min represent the *intrapartum* period, and the time points +1d until +3d represent the *postpartum* period. * Significant difference due to breed × housing interaction at single time point (P < 0.05); B Significant difference due to housing at single time point (P < 0.05). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

well as at 150 min of parturition.

For plasma adrenaline, GS animals had significantly higher concentrations than GL animals in the ap period as shown by the repeated measurement analyses. For time point-specific evaluation, the interaction of breed and housing condition showed a significant effect at 210 min and 240 min of parturition. Moreover, GS sows showed significantly higher values for plasma adrenaline levels at $-2~\mathrm{d}~ap$ and at $-1~\mathrm{d}~ap$ compared to GL sows. Sows kept in the farrowing crate revealed significantly higher values for plasma adrenaline at $+1~\mathrm{d}~pp$ compared to sows kept in farrowing pens.

The noradrenaline profiles were affected by breed in the ip period with significantly higher levels in GS sows compared to GL sows. Regarding the statistical evaluation at specific time-points, the plasma noradrenaline levels were significantly higher for GS sows compared to GL sows at -1 d ap, at expulsion as well as at 120 min of parturition. Housing conditions showed no significant effects at respective time points.

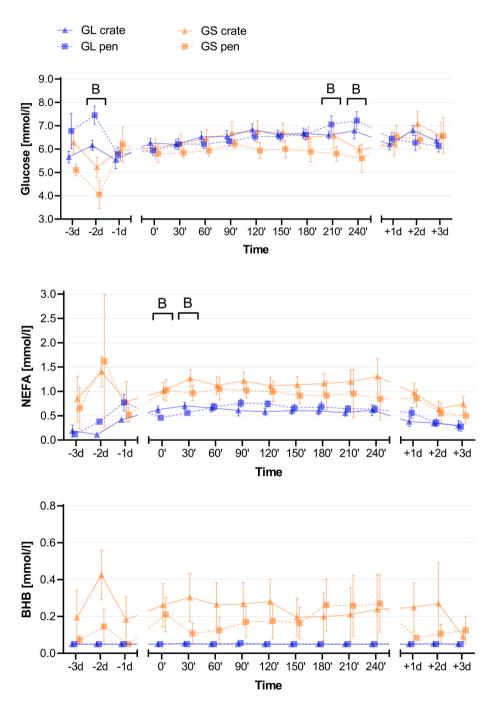


Fig. 4. Representation of blood glucose and serum NEFA, and BHB levels in German Landrace (GL) and German Saddleback (GS) pigs kept in farrowing crates and farrowing pens throughout the entire *peripartum* period. Data are presented as mean \pm SEM and cover the time series for GL sows (blue) and GS sows (orange) kept in farrowing crates (triangles; solid line) or farrowing pens (squares; dashed line). The time points -3d until -1d represent the *antepartum* period, time points 0 min until 240 min represent the *intrapartum* period, and the time points +1d until +3d represent the *postpartum* period. * Significant difference due to breed \times housing interaction at single time point (P < 0.05); B Significant difference due to breed at single time point (P < 0.05); H Significant difference due to housing at single time point (P < 0.05). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

3.4. Metabolites

The results of the statistical analysis of blood glucose (n = 438), serum NEFA (n = 433), and serum BHB (n = 352) per farrowing period is shown in Table 2 and Fig. 4. The blood glucose levels were significantly different between GL and GS in the ap period as shown by results obtained from the repeated measurement analyses. Results showed no impact of the housing condition at the distinct farrowing periods. For the evaluation per time point, analysis revealed significantly higher blood glucose levels at -2 d ap as well as at 210 min and at 240 min of parturition in GL sows compared to GS sows. Housing conditions showed no significant effects on glucose levels at respective time points.

The profile of NEFA levels was significantly affected by breed with higher levels in GS sows compared to GL sows at *ap* and *ip* periods. For time point-specific evaluation, serum NEFA levels were significantly elevated in GS sows compared to GL sows at onset of parturition (0 min) and at 30 min of parturition.

For serum BHB, most values for GL individuals were below the dynamic range of the applied quantification method of 0.10 mmol/l. Overall, the monitoring of serum BHB levels revealed no symptoms of ketosis. The statistical evaluation revealed a breed effect with higher levels in GS compared to GL within the *ap* period. No effect of housing condition on serum BHB levels was observed.

3.5. Impact of the anaesthetic regimen on stress-associated parameters

No significant effect of the anaesthetic protocol in combination with the applied catheterization method on serum cortisol (P=0.665), plasma adrenaline (P=0.476), or plasma noradrenaline (P=0.091) concentrations was detected.

4. Discussion

Effects of crate and pen housing systems applied to modern and traditional pig breeds was evaluated throughout farrowing on clinical parameters, endocrine physiology and blood metabolites.

The GL sows had a gestation period that was 1.2 days longer compared to the GS sows [36]. The impact of maternal genotype on gestation length has been demonstrated in several studies. Breed-specific gestation lengths with deviations of a few days are known for the various pig breeds, with the majority of sows farrowing in the range of 114–117 days [40–42]. Large field studies have analysed data from commercial pig farms and found that a shorter gestation length is associated with a larger litter size [41,43,44], which might be in contradiction to the results of this study. However, breed-effects involved in the regulation of gestation length must be taken into account, as shown in other polytocous species such as dogs [45]. In fact, the gestation length appears to ultimately affect farrowing process and neonatal outcome [40,46].

The study showed that the housing system had no effect on both farrowing length and occurrence of dystocia in both genotypes. This is in line with previous reports that found no effect on farrowing length due to varying housing systems [47]. However, other studies suggested a shorter total farrowing length of sows kept in crates compared to pens [48] or that loose-housed sows had a shorter farrowing length compared to crated sows [49]. Sows of the traditional GS groups exhibited a significantly reduced labour dystocia compared to modern GL sows. Although there were clear differences in NEFA and BHB levels between genotypes, the relevant mechanisms have not yet been identified. Overall, the current study shows that the farrowing is characterized by transient breed-specific differences in endocrine status and blood metabolites related to the stress response of modern and traditional pig breeds.

Azaperone and ketamine used for sedation and short-term anesthesia have been investigated for their effects on plasma concentrations of hormones and metabolites including cortisol, which was elevated until 180 min after injection [50]. Consistent with the experimental design of this study, the results showed that the anesthesia regimen had no specific effects on stress-associated parameters in the *peripartum* period. Moreover, farrowing took place regardless of the time of day for all sow groups. Hence, the comprehensive blood sampling in the *ip* period represent conditions largely unaffected by circadian rhythms.

The overall profile of cortisol, which is increasingly released by the adrenal cortex during stress and hypoglycemia, was significantly influenced by breed. The cortisol concentrations of the GS sows were ap and ip at a higher level than those of the GL. The impact of genetics on plasma cortisol concentration is known from the literature [23,24]. The higher cortisol profiles in the ante- and intrapartum period in GS animals compared to GL animals could be due to the different body fat percentage or fat distribution pattern and might not necessarily reflect a stress situation [23,51]. In fact, the GS animals had a significantly increased proportion of adipose tissue amounting to 40.9 % compared to 28.2 % in the GL animals [34]. In addition, intramuscular fat was reported to be 2.9 % in GS animals and 1.3 % in GL animals [34]. In humans, long-term cortisol levels are elevated in obese individuals, which may be due to the higher density of glucocorticoid receptors in visceral adipose tissue [52]. Studies of genetics on cortisol concentrations at farrowing showed a tendency for an earlier antepartum rise of cortisol in Meishan compared to Large White [22]. Cortisol is involved in modulating the sow's energy requirements and the maturation of the fetal organs as well as in triggering parturition [53]. The antepartum increase in fetal and maternal cortisol in many species is part of the significant endocrine reorganization that initiates farrowing and is considered a biological stress. If this effect of cortisol is taken into account, the significantly higher cortisol concentrations in traditional GS animals could be related to the shorter gestation length as well as to the lower dystocia rate in this breed. This would imply that the cortisol concentrations in GL animals may not be sufficient to effectively induce parturition and allow labor to proceed without protractions, especially considering the longer farrowing length which require constant flow of energy stores. This scenario might be supported by the results of Lehn [3], in which animals of the db. Viktoria line exhibiting a dystocia rate of 50-60 % showed a cortisol level similar to that of GL animals. However, cortisol also inhibits prostaglandin synthesis and the importance of cortisol in the mechanism of inducing labor in pigs has been debated [11,12]. The catabolic effect of cortisol on protein turnover contributes to meeting the required energy needs of the sow during parturition, whereas excessive cortisol production can be attributed to overstraining of the maternal organism [54]. An effect of housing conditions on the peripartum cortisol level in parturient animals cannot be deduced at any time. This is consistent with the findings of Lehn [3], Oliviero et al. [20], and Jarvis et al. [55]. In contrast, pregnant sows that were housed antepartum in a farrowing crate showed higher cortisol levels than sows that were kept in the farrowing pen [56,57].

The catecholamines adrenaline and noradrenaline are key factors in the fight-or-flight response and trigger functional adaptations in the organism in response to psychological and physical stressors. In the present study, the sows of the GS breed showed higher adrenaline and noradrenaline concentrations in stages I and II of farrowing under natural, spontaneous farrowing conditions than sows of the GL breed. The impact of genetics on basal levels of catecholamines has already been shown in commercial breeds, with Large White pigs having the lowest concentrations of both adrenaline and noradrenaline compared to Meishan pigs [23]. A positive correlation was found between body fat percentage and basal catecholamine concentration [23]. The higher body fat percentage of GS compared to GL animals supports this assumption [34]. The study by Rosochacki et al. [58] on the stress response in two different pig breeds also indicates a significant breed difference in the cortisol, adrenaline and noradrenaline responsiveness. This should therefore be reflected in the management and handling guidelines of the respective pig breeds, as it is conceivable that the increased psychological stress level in the GS sows is expressed in

restlessness and consequently in an increased activity level. The fact that the measurements of the heart rates do not show any abnormalities suggests that overstress is not responsible for the higher adrenaline and noradrenaline values in GS animals. In contrast, the GL sows exhibited numerically higher heart rates at ip period compared to sows of the GS breed. The comparison of housing conditions showed no significant differences for catecholamines in the ante- and intrapartum period. An effect of housing conditions as well as breed × housing interaction has been found only for the adrenaline profiles at the transition to the early postpartum period. Therefore, the observed catecholamine levels might indicate that the sows coped well with farrowing pens. However, both husbandry systems could equally be regarded as prolonged or chronic stressors. For the assessment of individual housing systems with regard to the welfare of pregnant sows and their piglets, the genetic requirements of the pig breeds should therefore be taken into account to a greater extent than in the past [59].

The farrowing process of sows require a complex physiological response to meet energy needs of labour. The glucose profiles were subject to differences between breeds in the ap period and the late stage of the *ip* period. Due to the farrowing process and the related physical activity, both cortisol and adrenaline are likely to be involved in the mobilization of glucose from hepatic stores. A previous study showed that plasma cortisol was significantly negatively correlated with hepatic D-glucose and lactate [60]. In this study, glucose levels remained within physiological ranges (GL: 5.43-5.92 mmol/l; GS: 5.25-5.84 mmol/l) which matches previous reports for the ip period in sows [13,61]. In this study, both NEFA and BHB concentrations were dependent on breed and remained at breed-specific levels. The ap and ip periods were characterized by significantly higher NEFA concentrations in GS animals compared to GL sows. Similarly, BHB concentrations were significantly higher in GS than in GL over the study period. Serum NEFA serve as an indicator for lipid mobilization in a catabolic state and are metabolized to ketone bodies, which provide a rapidly available energy source for the body. At the end of gestation, the metabolic rate increases with adipose and muscle tissue as the most important source of energy. The observed increase in NEFA is therefore an indication of a catabolic state in the two pig breeds investigated in this study. Other studies in sows also showed increasing NEFA concentrations antepartum [61,62]. In contrast to the results of Le Cozler et al. [13], the NEFA concentrations within the expulsion phase were subject to only minor variation. Consistently, the NEFA concentration have been reported to decrease in the postpartum period [13,61,63]. The significantly higher NEFA and BHB concentrations in GS sows could be explained by their higher proportion of adipose tissue and thus their ability to cover their energy requirements to a greater extent by lipolysis than GL sows. We observed that the GS sows showed pronounced reductions in feed intake during the ap and pp periods compared to the GL sows, which certainly contributed to the metabolite pattern described above. The mobilization of body reserves via increased lipolysis could be facilitated by the increased cortisol level in GS. However, the individual insulin sensitivity should be monitored in this context [62]. The observed ketone body level was at a rather low level in the two breeds. Excessive formation of ketone bodies can result in ketoacidosis, however, this postpartum pathological condition appears not as relevant in pigs as it is a known phenomenon for cattle [63]. Overall, the monitoring of serum BHB levels suggests no ketosis in agreement with no excess energy depot mobilization. In the current study, housing conditions had no influence on the blood metabolites of glucose, NEFA, and BHB. Previous studies showed a trend for higher NEFA concentrations in early lactation in sows kept in free farrowing environments than those kept in crates [64]. The combination of a reduced energy intake towards the end of gestation and the energetically highly demanding birth process almost inevitably leads to a temporary energy imbalance, which in turn causes the release of NEFA as an available source of energy. Clearly, both over- and undernutrition as well as the body condition are factors influencing reproductive health and perinatal outcomes [65,66].

5. Conclusions

The study showed breed-specific characteristics regarding the gestational length, with a longer gestation length in the breed with the larger litter size. Throughout the farrowing process, endocrine stress physiology at farrowing, i.e. plasma levels of cortisol, adrenaline and noradrenaline, which reflect the perception of exogenous and endogenous stressors, indicate that the genetic requirements of pig breeds should be given greater consideration to maintain genetic diversity within and among pig breeds. Temporary significant interactions between breed \times housing condition on heart rate, body temperature, serum cortisol, and plasma adrenaline levels support concepts for tailored management conditions at parturition for modern and traditional breeds. Data form the basis for genotype-environment interaction analysis and help to reconcile husbandry and management measures in terms of birth physiology, animal welfare and economic aspects.

CRediT authorship contribution statement

M. Oster: Writing - review & editing, Writing - original draft, Visualization, Validation, Supervision, Software, Project administration, Investigation, Formal analysis, Data curation. C.A. Gladbach: Writing – review & editing, Writing - original draft, Visualization, Validation, Software, Investigation, Formal analysis, Data curation. A. Vernunft: Writing - review & editing, Visualization, Validation, Supervision, Investigation, Formal analysis, Data curation. H. Reyer: Writing - review & editing, Visualization, Validation, Supervision, Software, Project administration, Investigation, Formal analysis, Data curation. W. Otten: Writing - review & editing, Resources, Investigation, Formal analysis, Data curation. C.C. Metges: Writing - review & editing, Resources, Investigation, Data curation. E. Muráni: Writing - review & editing, Resources, Investigation. S. Ponsuksili: Writing - review & editing, Investigation. K. Frölich: Writing - review & editing, Investigation, Funding acquisition, Conceptualization. K. Wimmers: Writing - review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. H. Bostedt: Writing - review & editing, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

Ethics approval

The trial on female reproductive pigs was carried out in accordance with the ARRIVE guidelines, the EU Directive 2010/63, and the German Animal Welfare Act, approved by the Animal Welfare Committee of the FBN and licensed by the Ethics Committee of the federal state of Mecklenburg-Western Pomerania, Germany (LALLF 7221.3–1.1-026/18).

Availability of data and materials

The dataset analysed during the current study is available from the corresponding author on reasonable request.

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

The authors did not use any artificial intelligence assisted technologies in the writing process.

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Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: K. Wimmers reports financial support was provided by Hessian Ministry for the Environment, Climate Protection, Consumer Protection and Agriculture, Germany. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Abbreviations

GL German Landrace GS German Saddleback

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.theriogenology.2025.117394.

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