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Piglets' behaviour and performance in relation to sow characteristics

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ABSTRACT

The importance of maternal care in commercial pig production is largely ignored. The sow has little possibility to interact with her piglets, and piglets are often subjected to early weaning or artificial rearing. This study aimed to investigate aspects of physiological and behavioural maternal provisioning that contribute to offspring outcomes. We hypothesised that better maternal care and nutritional provisioning would relate positively to piglet immunity, growth and behaviour. Nineteen sows and their litters were studied in free-farrowing pens. Oxytocin and tumour necrosis factor- α in colostrum/milk and salivary cortisol were sampled from sows throughout lactation. Sows were assessed for dominance rank, response to handling, maternal defensiveness, suckling initiation and termination, posture and sow-piglet contact. Piglets were weighed, measured for body mass index (BMI) and sampled for blood (Immunoglobulin G; at birth). After weaning, they experienced a human approach test (HAT) and novel object test. Correlations were explored between individual sow characteristics, individual piglet outcomes, and between sow characteristics and piglet outcomes averaged by litter. Significant correlations between sow and piglet factors were analysed at the litter level in mixed models with piglet outcomes as response variables and sow characteristics as predictor variables, while accounting for sow parity, litter size and batch. Litters grew faster when their sow had lower cortisol values ($P = 0.03$), while sows with lower cortisol levels had more successful suckling bouts and engaged in greater amounts of sow-piglet contact. Litters had a lower BMI at weaning when the sow had a higher milk fat percentage at d3. Litters of the most dominant sows took longer to approach the human in the HAT, while litters of sows with higher cortisol at d0 took longer to approach the novel object when assessed on correlations ($r = 0.82$, $P < 0.001$) but not when the model accounted for parity and litter size ($P = 0.35$). Only some of the measured nutritive and non-nutritive sow factors influenced litter performance and behaviour, with parity and litter size also playing a role. Given the continued increase in litter size, but also the interest in loose-housed lactation pens for sows, further research on sows' maternal investment and how it can be optimised is warranted.

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Implications

In commercial farm environments, the possibility for contact between the dam and her offspring is typically limited or fully absent. This assumes a limited role of the mother, or a largely nutritional role only. This study looked at the role of the sow in offspring development. The results show that sows vary widely in their maternal provisioning but that this, only to a limited extent, translates into piglet performance. Sows with low cortisol concentrations showed a better nursing capacity, therefore reducing sow stress is recommended.

Introduction

Many studies have proven the importance of maternal contact for offspring's health, physical, and behavioural development (e.g., Nowak et al., 2000; Beery and Francis, 2011), and its beneficial effects for stress coping abilities (Francis et al., 1999). That young mammals need their mothers seems like an obvious notion, but within the livestock industry, it is challenged by numerous husbandry practices including abrupt and early weaning, artificial rearing, and cross-fostering (e.g., Newberry and Swanson, 2008). Maternal investment, i.e. provisioning and care, varies amongst mammalian livestock species, but nearly all intensive farms separate the mother from their young much earlier than in a natural situation (Newberry and Swanson, 2008). While motherless reared

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farm animals are provided with the required nutrition, they may develop abnormal behaviour and suffer from impaired health (e.g., Rzezniczek et al., 2015; Schmitt et al. 2019; Newberry and Swanson, 2008).

In commercial pig production, sow-piglet interactions are compromised due to the conventional use of farrowing crates, which restrict the sow's movements and her ability to make contact with her piglets, such as snout contact (e.g., Jensen and Stangel, 1992; Rosvold et al. 2019). In some cases, piglets are artificially reared following removal from the mother as early as a few days old. Artificial, i.e., motherless, rearing of piglets impairs piglet welfare through an increase in abnormal behaviour (Rzezniczek et al., 2015) and reduced growth performance and emotional state (Schmitt et al., 2019). The housing and management of lactating commercial sows therefore largely ignores the potential role of the mother beyond the provision of nutrition.

Studies on maternal care often focus on the impact of its variation (reviewed by Beery and Francis, 2011). In sows, the focus has been on variations in maternal behaviour that cause piglet mortality, such as savaging and accidental piglet crushing by the sow (reviewed by Edwards and Baxter, 2015). How maternal behaviour can benefit piglets has, however, received comparatively little attention, in part because porcine maternal care is more rudimentary compared to the relationship observed in other livestock (Nowak et al., 2000). Good maternal behaviour of sows is characterised by more passive care involving lateral lying with the udder exposed (Nowak et al., 2000). Active behaviours (e.g., nest-building) are more apparent prepartum and have been shown to influence maternal behaviour and physiology and thus affect offspring. For example, engaging in satisfying nest-building activity results in calmer sows during farrowing, reduces the farrowing length and increases colostrum quality (reviewed in Yun and Valros, 2015), and thus can be considered part of the maternal investment (Ocepek and Andersen, 2017; Rosvold et al. 2019). 'Calmness' is a term used to describe a sow's activity and reactivity, particularly around farrowing and during early lactation in particular (Jarvis et al., 1999; Špinka et al., 2000).

The knowledge gap on how variation in maternal behaviour can affect piglet development needs to be addressed in order to assess the consequences of management practices. Previously, we looked at the nutritional and biochemical aspects of maternal provisioning (Hall et al., 2021). The aim of the current study was to investigate the influence of sow maternal behaviour and physiology on piglet immunity, growth and behaviour. We hypothesised that better maternal care (including a greater amount of sow-piglet non-nutritive contact), and more optimal nutritional provisioning (such as higher milk fat), would relate positively to piglet outcomes.

Material and methods

The research was conducted at the research pig unit of Scotland's Rural College (SRUC), Midlothian, Scotland. Twenty Landrace × Large White sows (Pig Improvement Company, Kingston, Oxfordshire, United Kingdom) (average parity 4.05 ± 1.43 (SD), range 2–6), pregnant from American Hampshire boars, were randomly selected from the research herd. Sows farrowed over two batches of ten sows each.

Sows were housed in the "PigSAFE" system (Baxter et al., 2015, Supplementary Fig. S1 in Supplementary File 1), a high-welfare zero-confinement farrowing pen, measuring 2.2 m × 3.6 m (7.9 m²), including a 0.5 m wide feeding stall and a covered piglet nest area of 0.75 m². Pens had solid concrete flooring throughout apart from in the slatted dunging area (2.2 m × 1.2 m). For nesting, the sow received 2 kg of long-stemmed straw, which was replenished daily until day seven postpartum, then reduced to 1 kg of

straw daily until weaning. Sows were fed twice a day and initially received a 3 kg/d lactation diet (17% CP, 13.75 MJ DE.kg⁻¹) which was increased by 0.5–1 kg daily up to a maximum of 12 kg/d until weaning. Farrowing room temperature was maintained at 20 °C for the first week after farrowing and then reduced to 16 °C for the remainder of lactation. The piglet nest (creep) was bedded with a thin layer of sawdust and underfloor heating of 30 °C which was reduced gradually after two weeks to 25 °C.

One sow had to be removed from the study due to overly maternally defensive behaviours limiting data collection. All piglets received an intramuscular iron injection (Gleptosil®, Alstoe Animal Health) on day three post farrowing. No further piglet handling was conducted (no castration of male piglets and no tail docking or tooth resection). In batch 1, some cross-fostering of the largest piglets (if possible in sibling pairs) was required to maximise piglet survival. Cross-fostering was conducted only after 12 h post farrowing. Data for fostered piglets were recorded against the foster sow. Piglets received a creep feed (Elite starter feed, Primary Diets) from two weeks of age which was replenished daily until the end of the trial. All animals had ad libitum access to water via nipple drinkers. Piglet mortality was recorded, and the cause of death was identified by visual examination by highly experienced technical staff, following Table 1. At weaning, at approximately 26 days postpartum, sows were removed from the farrowing pens and piglets were ear tagged and vaccinated (Ingelvac CircoFLEX®, Boehringer Ingelheim Vetmedica, Inc.). After weaning, piglets were kept in their litter groups in the farrowing pen for a further seven days until the end of the trial.

Sow data collection

Approximately five days before their expected due date, before being moved into farrowing accommodation, sows were weighed (kg), condition scored (on a scale from 0: thin to 5: obese) and had their backfat thickness measured (mm). Backfat was measured using a Piglog 105 backfat scanner (Frontmatec®, Skive, Denmark). The scanner probe is positioned at the P2 site on the sow, approximately 6.5 cm from the midline of the back.

Food competition test

A food competition test was conducted three weeks prior to entry into the farrowing accommodation, which enabled accounting for the potential effects of sow dominance rank on offspring outcomes (e.g., Kranendonk et al., 2007). Sows were housed across four stable groups with a maximum of six sows per pen. Sows were fed their standard ration at 7 am. No earlier than 10 am, a trained staff member entered the pen, cleaned the pen floor from excreta, and then presented the group with a maximum 4.5 kg of feed (0.5 kg per sow), evenly spread in a line on the pen floor. The per-

Table 1
Descriptions of causes of piglets' death.

Cause of death	Definition
Stillborn	Fully formed piglet with periople still present on hooves, often found in placental fluids
Crushed	Piglet found squashed or bruised in appearance or with broken limbs
Starvation	Piglet very thin, dehydrated skin with pin bones and individual ribs visible, vertebrae prominent
Other	Scour, blind anus, splayed legs, deformations, disease and any unidentified causes. Often euthanised.

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son left the pen immediately and sows were observed live for 10 minutes for attacks received (defeats) as per Ison et al. (2010). Dominance ranks (1–6) were assigned by ordering pigs by [number of defeats/number of group mates interacted with]. This results in 1 = highest ranking (fewest defeats) and 6 = lowest ranking (most defeats), with a maximum of four sows per rank.

Response to handling

Sows were moved to their farrowing accommodation, approximately five days before their due date, by two trained members of staff equipped with pig handling boards. The ease with which the sows moved into their farrowing accommodation was scored by one member of staff for all sows on the study and encompassed the movement process. Scores were (1) walks or runs to farrowing accommodation voluntarily; (2) walks easily and only hesitates to show interest; (3) hesitates but recommences movement without human contact; (4) stops, but shows no physical resistance to movement on human contact; and (5) stops, offers physical resistance to movement on human contact. Sows were assessed for lameness (yes/no) during this test, and all were scored as not lame.

Maternal defensiveness

On six days (days 1, 3, 5, 10, 14 and 21 postpartum), when piglets were being handled and removed from the pen for sampling, the sow's response to removal of her piglets was scored as a measure of maternal defensiveness. First, sows were shut in their feeding stalls when consuming their feed. Immediately after, piglets were gathered and the sow's response to temporary piglet removal was scored as (1) calm, does not react; (2) alert, looks up frequently but consumes feed; (3) restless, moving and vocalising but consumes feed; and (4) reactive, moving and vocalising strongly, acts aggressively, does not consume all feed. For the full ethogram, see [Supplementary Table S1](#). The six scores were averaged across the observations to obtain a single (continuous) variable.

Nursing behaviour

Video recordings were made for 24 h on days (d) 3, 6 and 22 postpartum. Closed-circuit television (CCTV) cameras (LL20, infra-red cameras, RF concepts, Ireland) connected to the GeoVision Digital Surveillance (computer) System and software (ezCCTV Ltd, Herts, UK) were mounted above each pen to record the sow and her piglets. Three trained observers watched videos balanced across sow parity and batch. They had, between them, experience with observing pig behaviour for over 20 years and were trained and instructed by the same researcher. Several videos were observed by all observers to ensure milk ejection by the sow was being correctly recognised. The following four behaviours were recorded:

- (i) Successful suckling bouts (frequency): the number of successful and unsuccessful suckling bouts was recorded for 24 h each recording day. A successful suckling bout was one where milk ejection (let-down) could be seen. Signs of milk ejection included a change in piglet behaviour from massaging of teats and non-nutritive suckling to a focused rapid suckling motion with the mouth (Špinková and Illmann, 2015).
- (ii) Suckling bouts initiated and terminated by the sow (percentage): from 0700 to 1600 h, it was noted whether the sow initiated the suckling bout and whether she terminated it (two binary scores per suckling bout), based on Špinková and Illmann (2015). Initiation by the sow was scored when she

assumed a lateral lying position, exposing her udder and starting to rhythmically grunt. Termination by the sow was scored when she changed posture whilst the piglets were still engaged in teat massage, thereby denying them further access to the teats. If it was not clear who had initiated or terminated, then 'both' was recorded to maintain the accurate number of suckling bouts. The percentage of suckling bouts initiated and terminated across the three observation days was calculated to obtain a single (continuous) variable for initiation and a variable for termination.

- (iii) Lying laterally (percentage): sow posture was recorded as lying lateral (as indication of nursing facilitation), lying ventral, kneeling, sitting, or standing at 10 min before, during and at 10 min after the suckling bout, resulting in three observations per suckling bout. The percentage of lying lateral was calculated across all observations to obtain a single (continuous) variable of lateral lying.
- (iv) Sow-piglet contact (percentage): the number of piglets present at the sow's udder was counted at 10 and 5 min prior to, during, and at 5 and 10 min post milk let-down, resulting in five observations in the 20 minutes around each suckling bout. The percentage of piglets within the litter that was present at the udder was averaged per time point (time points: -10, -5, 0, 5, 10), and averaged across all observations to obtain a single percentage of contact behaviour.

Sow saliva samples

Sows were saliva sampled 15 min pre- (basal) and post removal of their piglets for piglet data collection on d0, 3, 5, 10, 14, and 21 postpartum. Sows were offered and readily accepted (without training) two large cotton buds at a time (Millpledge Veterinary, Clarbrough, Nottinghamshire, UK) on which to chew for approximately 30 seconds or until saturated with saliva. The cotton buds were placed into Salivette tubes (SARSTEDT AG & Co., Nümbrecht, Germany), which were promptly sealed and centrifuged for 5 min at 1 400g (centrifuge set at 5 °C). The supernatant was stored at -20 °C. Sows' salivary cortisol (ng/ml) was measured using an ELISA (ALPCO #11-CORHU-E01-SLV). Samples were read at 450 nm using a spectrophotometer with Thermo SkanIt software (Multiskan, Thermo Scientific, USA). All assays included positive quality controls (QCs) and assays were only accepted if R2 was above 0.98, curve fit percentage recovery was within the 70–130% range and intra-plate and inter-plate CV% had a threshold for acceptance of below 20%. Individual sample results were only accepted if they had a CV% of <20%. For the analysis, only the basal value was used. The pre- (basal) and post sample did not significantly differ (Hall et al., 2021) and while the pre sample was standardised across sows, the duration between pre and post varied between sows due to different durations of piglet removal (as a consequence of litter size). Full details are provided in Hall et al. (2021).

Sow colostrum and milk samples

Sows in the trial had a natural milk production (i.e., no use of synthetic oxytocin to enable milk sampling), with natural variation between sows. Colostrum and milk were obtained when the piglets returned to the sow after piglet data collection (on d0, 3, 5, 10, 14, 21 postpartum). As a natural response, most sows allowed the piglets to suckle quickly after reunion. A trained experimenter (always the same person) quietly entered the pen after the sow started her nursing grunt. Then, without disrupting the suckling bout, colostrum/milk was collected in rimmed plastic beakers (50 ml ThermoFisher Scientific) from as many teats as possible at the moment of milk ejection (for a video of the milk sampling technique, see [Supplementary File 2](#)). Ejection lasts ca. 20 s and is

characterised by cascading of milk from the anterior to posterior teat pairs and the piglets showing a focussed rapid suckling motion with clear signs of milk consumption (Algers and Uvnäs-Moberg, 2007; Špinka and Illmann, 2015). The experimenter briefly removed piglets when collecting samples but did not displace piglets considered to be vulnerable (e.g., low BW) or piglets that had been blood sampled. Samples were pipetted into smaller 2.0 ml Eppendorf tubes and stored at -70°C . Colostrum and milk were analysed for fat, protein, immunoglobulin G (IgG), oxytocin, and tumour necrosis factor- α (TNF- α) as described in detail in Hall et al. (2021), see [Supplementary Material S1](#). Analysis of the pattern of milk and saliva biomarkers across the lactation phase indicated that d0 and d3 were significantly different from the other days, whereas d5–21 of lactation remained stable (Hall et al., 2021). Therefore, values for d0, d3 and d5–21 were assessed separately.

Piglet data collection

From the 19 sows, 271 piglets were born (48% females, 52% males), (246 born alive, 20 stillborn, 5 mummified). The average litter size at weaning was 11.3 ± 1.69 piglets (range 9–14). After birth (d0), data were collected between 12–24 h postpartum from the exact farrowing time (batch 1: average 14 h; batch 2: 13 h). For data collection, piglets were, by litter, removed from the sow and relocated into a heated area. At birth and weaning, piglets were weighed, chest circumference (cm) was measured, and the crown-rump length was measured (from the tail base to the top of the crown, in between the ears) to calculate body mass index ($\text{BMI} = \text{birth weight (kg)} / \text{crown-rump length (m)}^2$). Piglets were given a number on their back with a marker pen for individual recognition throughout the study. Pigs were also weighed on d3, 5, 10, 14, 21, 35 and 100.

Piglet behaviour

On d35 (7 days post weaning but within the farrowing pens), piglets underwent, within their litter groups, the human approach test (HAT) and novel object test (NOT). Both tests were conducted on the same day, randomised for litter order but with the HAT conducted first, followed by the NOT with a break in between of at least one hour. For the HAT, an unfamiliar staff member wearing a red non-farm overall entered the home pen and walked calmly to the end of the pen, and stood there still for five minutes (for illustration, see [Supplementary Fig. S2](#)). From video footage, the latency for piglets to enter a 50 cm semi-circle radius around the person and to contact the person was recorded. Scan samples were taken every minute to note which piglets were in contact or in the 50 cm vicinity of the person. The NOT was carried out in the same way as the HAT, but instead of a person, an unfamiliar blue water drinker was suspended 25 cm above the ground on the back wall of the pen (for illustration, see [Supplementary Fig. S2](#)) and scan samples were taken every minute to note which piglets were in contact or in the 50 cm vicinity of the object.

Piglet physiology

Piglets were blood sampled to determine IgG concentration at d0. Two male and two female piglets per litter of low and heavy birth weight (selected as being two SDs below or above the average birth weight of the litter) were sampled ($n = 76$) from the ear vein following the procedure of Ison et al. (2017) which involved a minimally invasive pin-prick of the most prominent ear vein, with the blood sample being collected in capillary tubes and stored at -70°C for later analysis (full details in [Supplementary Material S1](#)).

Samples were thawed on ice, centrifuged at 13 000 rpm for 3 min and diluted 1:100 in assay diluent (supplied with kit). Blood

IgG was measured using Pig IgG ELISA (Cusabio cat #CSB-E06804p) following the manufacturer's instructions. IgG was measured at 450 nm in a spectrophotometer (Multiskan, Thermo Scientific, USA) using Thermo SkanIt software. The quality control (QC) was 73% and 116.57% for batches 1 and 2, respectively. Intra-plate coefficient of variation (CV%) was $<16\%$ for batch 1 and $<3\%$ for batch 2, and the inter-plate CV% was $<10\%$ for both batches.

Data analysis

Data were analysed using SAS version 9.4 (SAS Institute Inc., Cary, NC, USA). Data were analysed with sow/litter as the experimental unit, except for analyses solely on piglet data.

Descriptive statistics of all variables were obtained, and the distributions of the data were assessed. Pearson correlations were conducted between potentially biologically meaningful relationships within sow variables, within piglet variables, and between sow and piglet variables. Only correlations of continuous variables with at least six samples were run and were reported in the text if they had a P -value of <0.05 and r of >0.50 (moderate correlation or higher).

To assess the differences between observation days for suckling bout initiation and termination (both binary), these two variables were analysed in a general linear mixed model (GLIMMIX procedure) with a binary distribution and logit link. The predictor variable was observation day while litter was specified as subject in the random statement to account for repeated observations per litter.

Piglet blood IgG at d0 post farrowing was analysed in a linear mixed model (MIXED Procedure) with piglet IgG as response variable and piglet sex (M/F), birth weight nested within the number of live-born piglets in the litter (as these variables are negatively correlated: $r = -0.76$; $P < 0.001$) and sow parity as predictor variables, with litter (sow) as the random variable.

The latencies in the HAT and NOT were analysed as response variables in a mixed model with piglet as the experimental unit. The latencies for the HAT were log-transformed to gain a normal distribution of the model residuals, while NOT latencies did not require transformation. The predictor variables were the sow/litter (to assess variation between litters), sex and BW at 35d of age. Batch was included as the random effect.

Due to the large number of sow outcomes, only correlations between the sow and piglet variables that had a P -value of <0.05 and r of >0.30 were entered into mixed models to assess the association between the sow and her litter. The response variables were averaged by litter: litter average daily gain (ADG from birth to weaning), average litter BMI at weaning, the average latency of the litter to approach in the HAT and NOT, and litter average for piglet blood IgG concentration. The predictor variables were the continuous sow variables that showed a significant correlation with the response variable, the categorical sow characteristics (condition score, dominance rank, response to handling), parity (category) and litter size (covariate), with batch as the random variable. Models were stepwise reduced based on achieving the lowest Akaike information criterion (AIC) and Bayesian information criterion (BIC) values. The models were assessed for the assumptions of homogeneity of variance and normal distribution of the residuals.

Results

Sow behaviour

Sows' average (means \pm SD) pre farrowing BW, condition score and backfat thickness were 275 ± 43 kg, 2.8 ± 0.96 and

18.9 ± 4.42 mm, respectively. Average number of live-born piglets was 13.6 ± 3.19 (range 5–18). On average, 1.2 piglets were stillborn and 0.3 were born mummified. Pre weaning live-born mortality (12.5%) included crushing by the sow (n = 7), savaging by the sow (n = 2), low viability (n = 11), starvation (n = 10), and other causes such as bloat or deformity (n = 4). Due to the low numbers, and equal spread of the causes between sows, mortality was not analysed further.

Sows' response to handling showed little variation; 12/19 sows scored 1 (calm), 5/19 scored 2 or 2.5 and the remaining two sows scored 3 and 3.5. Sows varied in their maternal defensiveness, with one sow having all six observations a maximum score of 5 and five sows having all observations the lowest score of 1. Their response was consistent over time, with strong and significant correlations between the six observations (r 0.75–0.98), except for the score at d0 (average r = 0.67). The average of the six scores (Table 2) therefore gives a good reflection of their maternal response. The correlations showed that maternal defensiveness was more profound in heavier (r 0.57, P = 0.01) and older (i.e., higher parity) sows (r 0.60, P = 0.001), but was unrelated to reproductive parameters. A stronger maternal defensiveness (average of six scores) was related to higher milk fat (Fig. 1.).

Nursing behaviour

A total of 1 610 suckling bouts were recorded across d3, 6 and 22 postpartum (average per day: 24, 28, 25 bouts, respectively; Table 2). The results from the binary model showed that sows initiated nursing more often on d3 (50.4% of suckling bouts) as compared to d6 (17.1%) and d22 (18.8%) (F_{2,54} = 3.30; P = 0.04). Individual sows varied in their nursing frequency with some sows nursing more than twice as much as others (Table 2). Sows who initiated a larger percentage of the bouts had on average a shorter amount of sow-piglet contact (r -0.86, P < 0.001). The suckling bout was 21.7% of the time terminated by the sow (17.3% it was unclear who terminated). There was no effect of day on who terminated the bouts (P = 0.40).

The number of successful suckling bouts (Table 2) was positively correlated with the amount of time the sow spent in a lateral posture (r 0.59, P = 0.007) and was negatively correlated with the percentage of suckling bouts terminated (r -0.69, P = 0.001), i.e., sows who terminated more suckling bouts had fewer successful suckling bouts. Most notably, correlational analysis showed that sows with more successful suckling bouts had lower saliva cortisol levels (Fig. 1).

Table 2
Sow behavioural variables (for n = 19 sows) in means with SD, minimum and maximum.

Measure	Mean	SD	Min	Max
Maternal defensiveness (average)	2.0	1.26	1.0	5.0
Suckling bouts (freq/d)	25.7	5.1	15	36
Sow nursing initiation (% of obs.)	17.6	14.5	0	42
Sow nursing termination (% of obs.)	21.7	24.9	0	69
Lying lateral (% of obs.)	77.6	7.3	65	91
Sow-piglet contact (% of obs.)	49.2	10.3	36	68

Abbreviations: freq: frequency; obs.: observations.

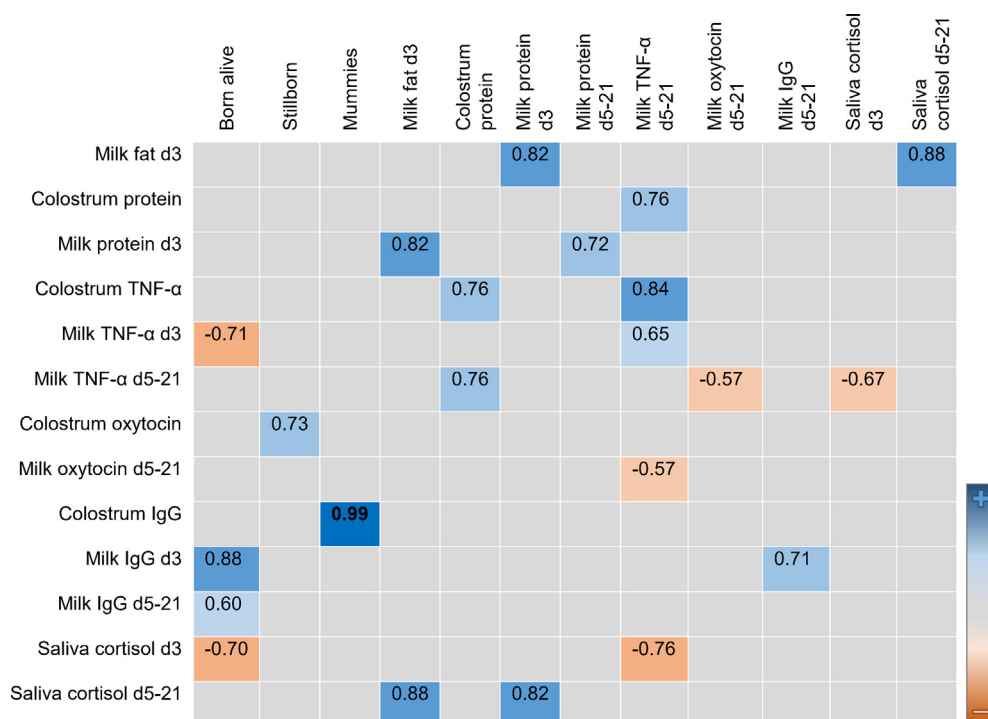


Fig. 1. Correlation coefficients between sow behaviour and physiology parameters. Only correlations with a P-value <0.05 are shown. Abbreviations: TNF-α: tumour necrosis factor-α; IgG: immunoglobulin G.

The majority of sows were lying laterally 10 min before nursing (at least 75% of the sows), during nursing (100% were lying laterally), and at 10 min post nursing (at least 70% of the sows). The percentage of time lying laterally (Table 2) positively correlated to the number of successful suckling bouts ($r = 0.59, P = 0.007$). Piglets were nearly all present at the udder during nursing ($94 \pm 11\%$), but fewer piglets were present in the specific moments of 10 and 5 min prior (both $22 \pm 32\%$) and at 5 and 10 min after the suckling bout ($56 \pm 36\%$ and $38 \pm 33\%$, respectively).

The percentage of sow-piglet contact (Table 2) positively correlated to the number of successful suckling bouts ($r = 0.56, P = 0.01$) and related to fewer nursing initiations ($r = -0.86, P = 0.01$) and terminations ($r = -0.78, P < 0.001$) by the sow. A greater amount of sow-piglet contact was related to higher milk TNF- α values (Fig. 1).

Sow colostrum/milk quality, physiology and reproductive performance

The analytes for colostrum at d0, and milk at d3 and d5–21 (described in Table 3) correlated across some or all of the sampling points for milk protein, milk IgG and TNF- α (Fig. 2). Most notable were that higher biomarker levels of inflammation (TNF- α) and stress (cortisol) on d3 were correlated with fewer live-born piglets. Additionally, IgG was strongly correlated to the number of mummified foetuses. Sow BW, backfat thickness and litter size did not correlate with any of the colostrum/milk or saliva parameters.

Piglet growth, behaviour and physiology

Piglets showed a good growth performance from birth to weaning and strong behavioural variation during the HAT and NOT (de-

scriptive statistics provided in Table 4). The mixed model on piglet blood IgG showed that the IgG concentration was strongly related to birth weight when the number of live-born piglets in the litter was taken into account ($F_{11,41} = 3.58; P = 0.001$), with piglets with a heavier birth weight showing a higher IgG (Fig. 3). Sex of the piglet did not influence blood IgG concentration ($F_{1,41} = 0.18; P = 0.68$).

Piglets' behaviour in the HAT showed a significant positive but negligibly low correlation with the behaviour in the NOT ($r = 0.23; P < 0.001$). In the mixed models, the response in the HAT strongly differed between litters ($F_{18,194} = 8.09; P < 0.001$), as was the case in the NOT ($F_{18,194} = 5.85; P < 0.001$). Heavier pigs had a shorter time to approach the human ($b = -0.12 \pm 0.049$ s/kg; $F_{1,193} = 5.64; P = 0.02$), but not to approach the object ($P = 0.45$). For both tests, the response was not influenced by the sex of the piglet ($P > 0.10$).

Relationship between sow factors and litter outcomes

From the eight behavioural characteristics of the sow, including maternal defensiveness, sow-piglet contact time and lying laterally, none of them were a significant predictor for any of the measured piglet outcomes (averaged by litter). From the twenty measures on sow physiology (fat, protein, IgG, cortisol, oxytocin and TNF- α across three phases of lactation), only the sow's milk fat at d3 and saliva cortisol concentration at d5–21 significantly influenced the litter outcomes, while the effect of parity and litter size overshadowed some of the sow characteristics (described below in detail).

The average ADG of the litter across lactation was negatively related to the sow's average saliva cortisol level from d5–21 of lactation, with a lower ADG when sows had higher salivary cortisol

Table 3
Means with SD and sample size (in brackets) of sow milk (colostrum for d0) and sow saliva analytes.

Analytes	d0	d3	d5–21
Milk fat (%)	13.6 ± 4.87 (9)	19.4 ± 7.15 (9)	10.9 ± 2.65 (15)
Milk protein (mg/ml)	90.5 ± 37.95 (9)	66.5 ± 29.88 (8)	44.3 ± 15.90 (15)
Milk TNF- α (pg/ml)	409 ± 492.3 (8)	162 ± 120.9 (10)	342 ± 383.9 (15)
Milk oxytocin (pg/ml)	48.3 ± 25.34 (11)	42.1 ± 19.26 (11)	36.8 ± 12.01 (18)
Milk IgG (mg/ml)	278.0 ± 32.74 (9)	87.63 ± 54.92 (9)	4.47 ± 3.85 (13)
Saliva cortisol (ng/ml)	25.3 ± 16.29 (9)	48.3 ± 35.28 (9)	23.9 ± 17.01 (14)

Abbreviations: TNF- α : tumour necrosis factor- α ; IgG: immunoglobulin G.

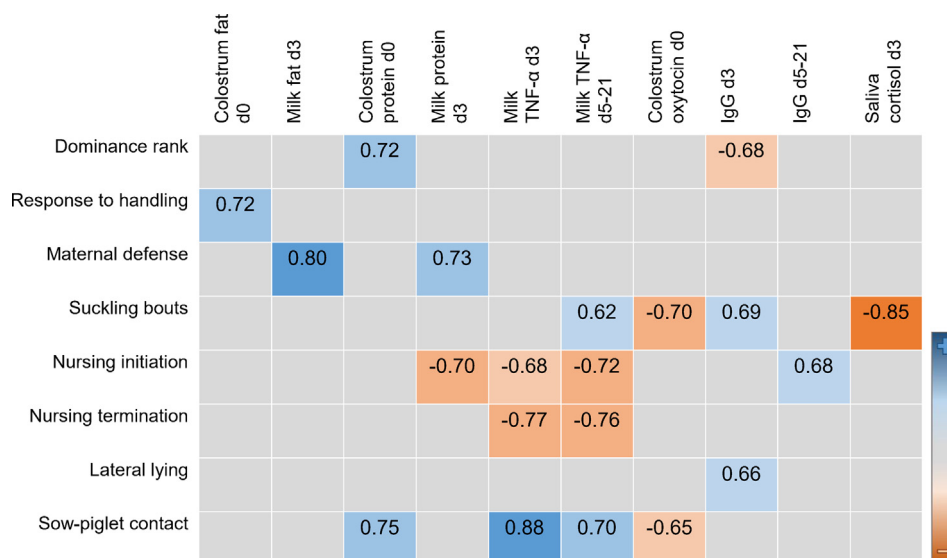


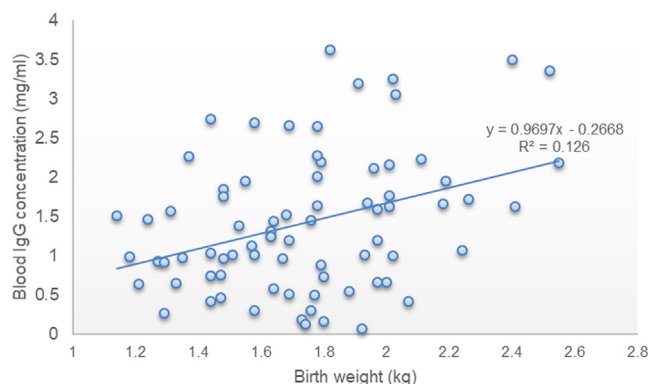
Fig. 2. Pearson correlations between analytes from sow colostrum (d0), milk and saliva and sow reproductive traits. Only correlations with a P-value <0.05 are shown. Abbreviations: TNF- α : tumour necrosis factor- α ; IgG: immunoglobulin G.

Table 4

Piglet performance, blood IgG and behavioural response, given in chronological order with sample size (n), mean, SD, minimum and maximum.

Measure	n	Mean	SD	min	max
Birth weight (kg)	274	1.62	0.42	0.56	2.81
Circumference d0 (cm)	274	26.0	2.84	13.7	32.5
BMI d0	274	21.8	3.12	13.5	48.8
Blood IgG d0 (mg/ml)	76	1.42	0.876	0.07	3.62
Weaning weight (kg)	214	8.75	1.58	4.70	12.57
Circumference weaning (cm)	214	46.0	3.04	37.0	54.0
BMI weaning	214	31.0	2.48	24.2	37.7
ADG (kg/d) d0-weaning	214	0.26	0.053	0.13	0.39
HAT latency (s)	214	47.2	73.4	1	300
NOT latency (s)	214	116.7	114.0	1	300
Weight d100 (kg)	151	58.9	7.6	31.0	75.0

Abbreviations: IgG: immunoglobulin G; BMI: Body Mass Index; ADG: Average Daily Gain; HAT: Human Approach Test; NOT: Novel Object Test.

**Fig. 3.** The relationship between piglet birth weight (kg) and piglet blood IgG (immunoglobulin G) concentration (mg/ml) on the day of birth (n = 76).

(mixed model, $b = -0.001 \pm 0.0004$ (g/d)/(ng/ml); $F_{1,7} = 7.48$; $P = 0.03$; Fig. 4a). The average litter ADG was lower when the sow had a larger litter ($b = -0.007 \pm 0.003$ (g/d)/piglet; $F_{1,7} = 5.72$; $P = 0.048$). A lower average BMI of the litter at weaning was related to a higher fat percentage in the sow's milk at d3 ($b = -0.15 \pm 0.03$ (g/d)%; $F_{1,4} = 30.47$; $P = 0.005$; Fig. 4b). The average litter IgG at d0 correlated with sow milk IgG at d3 ($r = -0.71$, $P = 0.03$; Fig. 4c), but this relationship was not significant once parity and litter size were considered in the mixed model ($F_{1,4} = 2.28$; $P = 0.21$). The average latency of the litter in the NOT showed a positive correlation with sow saliva cortisol taken at d0 ($r = 0.82$, $P < 0.001$; Fig. 4d) but this did not show a significant relationship ($P = 0.35$) once litter size and parity were taken into account, due to a statistical tendency for an interaction between saliva cortisol and parity ($F_{3,3} = 7.47$; $P = 0.07$). The average HAT latency did not significantly relate to the sow's dominance rank from the feed competition test (categorical variable) ($F_{4,8} = 1.99$; $P = 0.19$) but showed a linear decline with significant post-hoc differences (Fig. 4e). Sow parity did not influence litter ADG, BMI at weaning, IgG at d0 or HAT. Litter size tended to influence BMI ($P = 0.09$) and did not significantly influence litter IgG or HAT and NOT latency.

Discussion

The current study aimed to understand more about the physiological and behavioural aspects of maternal provisioning and how it relates to piglet development, including post weaning responses to challenges. The data showed substantial variation in maternal behaviour and physiology. However, only a few of the measured sow characteristics were predictive of the outcomes of her litter.

Sow nursing behaviour and maternal defensiveness

Sows who initiated the suckling bout had less sow-piglet contact, which may be because the sow calls the piglets to suckle (e.g., Algers, 1993), whereas when the piglets initiate a suckling bout, they are already present at the udder engaging in udder massage to encourage milk let-down. In other species (particularly studied in rodents; Beery and Francis, 2011), direct (non-nutritive) maternal care has been related to a higher rate of tactile (somatosensory) stimulation which includes brooding/huddling over, licking/grooming and side-by-side contact (Gromov, 2014). As pigs do not engage or engage much less in the former behaviours (Nowak et al., 2000; Ocepek and Andersen, 2017), contact with the udder is where maternal care might be more direct and quantifiable. Besides nutrition, contact with the udder provides thermal comfort, which is particularly important in the first few hours of life when piglets are very sensitive to cold stress (Edwards and Baxter, 2015). Other authors have suggested prolonged non-nutritive contact around nursing is an important component of the 'calmness' dimension of maternal behaviour, along with low frequencies of posture changes and carefulness when changing posture (Špinková et al., 2000). We found the majority of sows in our study allowed sustained piglet contact pre- and post-suckling. More successful suckling bouts were related to fewer terminations (and concomitantly fewer initiations) and a greater amount of sow-piglet contact. Additionally, sows with lower salivary cortisol levels had more often successful suckling bouts, which supports observations that calmer sows show better maternal behaviours (e.g., Jarvis et al., 1999; Ocepek and Andersen 2017).

Maternal defensiveness was highly consistent across lactation, except at 12 h postpartum, which might be due to the residual effects of the farrowing process, such as fatigue and/or pain impacting their behavioural reactivity (Martínez-Burnes et al., 2021). Heavier and older sows (the two being naturally related) were more defensive of their piglets. This is in contrast to Held et al. (2006) who found that maternal defensiveness declined with parity. Maternal defensiveness, like several other characteristics, showed a great variability and as the sample size was modest, repetition on a larger sample of sows is worthwhile.

Sow physiology

Colostrum showed a superior quality compared to milk, especially regarding protein, TNF- α and IgG (see also Hall et al., 2021). Sows with higher milk TNF- α , a biomarker of inflammation (Clark, 2007), and sows with higher salivary cortisol, a biomarker of stress (Martínez-Miró et al. 2016), recorded on d3 were those with fewer piglets born alive. Similarly, Hemsworth et al. (1999) found a correlation between fearfulness (towards stockpeople) in

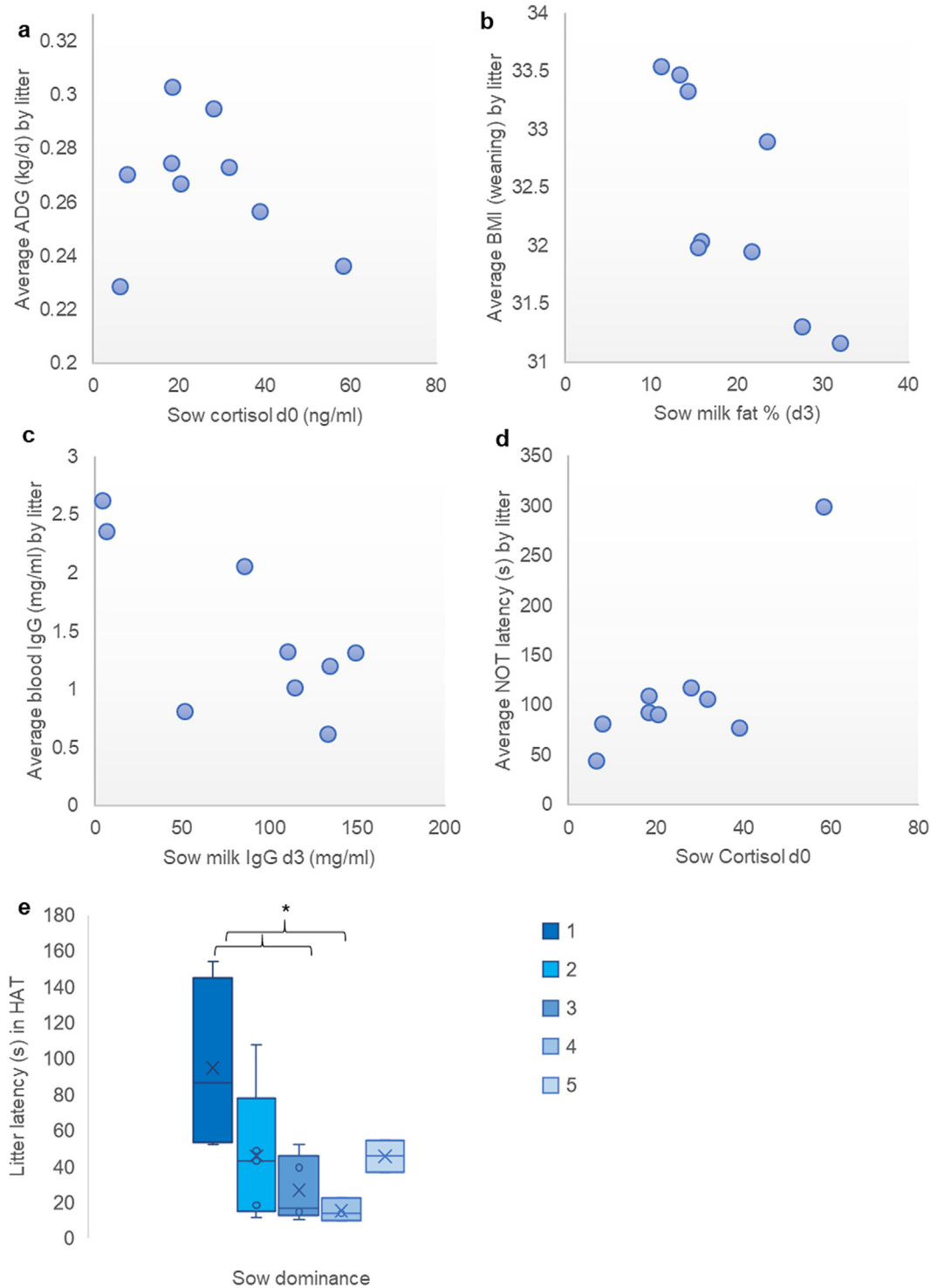


Fig. 4. Associations between sow and piglet variables for (a) sow salivary cortisol and average litter Average Daily Gain (ADG); (b) sow milk fat percentage on day 3 of lactation and average litter Body Mass Index (BMI) at weaning; (c) sow milk IgG (immunoglobulin G) on d3 and average litter blood IgG concentration at birth; (d) sow salivary cortisol and average litter latency in the Novel Object Test (NOT); and (e) the dominance rank of the sow from the feed competition test (1: highest rank (dominant) to 5: lowest rank (subordinate)) and average litter latency in the Human Approach Test (HAT). In the posthoc analysis, litters from the most dominant sow had a longer latency than sows from dominance ranks 3 and 4 ($P < 0.05$).

lactating sows and number of stillbirths. Whilst we did not specifically measure fearfulness in sows, the current results contribute to the body of literature linking stress with negative impacts on sow productivity (Hemsworth and Coleman, 2011).

Contrary to expectation, sows with higher colostrum oxytocin had fewer suckling bouts and less contact with their piglets. Potentially,

the greater oxytocin release may have antistress effects (Uvnäs-Moberg, 1997) and provide a qualitatively better (undisturbed) suckling bout, which therefore results in fewer bouts. Higher colostrum oxytocin on d0 was also related to more stillborn piglets. Whilst the evidence that synthetic oxytocin (and other uterotics) increases the risk of stillbirths (reviewed by Muro

et al., 2021), our study measured naturally occurring milk oxytocin and this was an unexpected result given that peripheral oxytocin levels are important for the onset and progress of parturition (Algers and Uvnäs-Moberg, 2007) which in turn impacts stillbirth rate.

Colostrum IgG was almost fully correlated ($r = 0.99$) with the number of mummies. However, there was only one sow with mummies (2 mummies) and a colostrum IgG measurement on d0 (93.6 mg/ml), and her IgG was more than seven times higher than others (on average 12.2 mg/ml). Papatsiros et al. (2022) had found a similar relationship when sampling 287 sows and hypothesised that the presence of mummies may trigger an increased immune activation in the sow.

Piglet behaviour and performance

Heavier piglets at birth had higher IgG blood levels on d0 (measured on an individual level), which likely reflects a superior intake of colostrum by larger piglets as found in other studies (e.g., Declerck et al., 2017). A weak correlation ($r = 0.23$) was found between the HAT and NOT latency times with the tests conducted on the same day, suggesting they reflect different traits. The response in the HAT and NOT was influenced by litter effects, and heavier piglets approached the human sooner. Several other studies found similar links between personality and BW (e.g., Scheffler et al., 2014), but a review of personality studies in pigs shows that the relationship with BW or growth is mostly inconclusive (O'Malley et al., 2019).

Relationships between sow factors and piglet outcomes

Sows with lower salivary cortisol had piglets with higher ADG, emphasising the importance of a calm sow (Ocepek and Andersen, 2017). Low saliva cortisol on d0 also correlated with a less fearful response of the litter in the NOT; however, this was not statistically significant when accounting for parity. Sows with a higher fat percentage in milk at d3 of lactation had piglets with lower BMI at weaning. This is contrary to expectations and seems driven by a single litter with low BMI values. At d3 of lactation, the colostrum changes into milk, which can result in different milk fat and protein levels that may be unrelated to the days later in lactation (Hall et al., 2021). The offspring of the most dominant sows were slower in the HAT responses, which is contrary to the findings of Kranendonk et al. (2007) who had a substantially larger sample of 62 high-ranking and 104 low-ranking sows. Similarly, we found no significant relationship between piglet blood IgG and sow colostrum IgG, while Devillers et al. (2011) did find a relationship between sow and piglet IgG when sampling 40 litters. Within our relatively low sample size, few sows with extreme but true values steered the direction of some relationships and therefore our results should be interpreted with caution.

Conclusions

Reduced maternal contact and motherless/artificial rearing are becoming more commonplace in commercial pig production, in part to manage supernumerary piglets as a result of selection pressure for large litter size. While in this study the relationship between sow maternal characteristics related relatively little to piglet outcomes, the results do show a role of the sow beyond the provision of milk, especially regarding non-nutritive sow-piglet contact contributing to suckling success. The results on cortisol levels point towards the importance of calm sows for better piglet performance. Given the growing interest in free-farrowing pens and temporary crating, the role of the sow and her maternal

ability, particularly her calmness, is of increased importance. We therefore encourage further research into sow's maternal ability, and to consider this as an essential aspect in the transition away from farrowing crates.

Supplementary material

Supplementary material to this article can be found online at <https://doi.org/10.1016/j.animal.2022.100699>.

Ethics approval

The experiment was reviewed and approved by SRUC's Animal Welfare Ethical Review Board (ED AE 23-2016), Edinburgh, UK, and conducted under Home Office Licence authority (PPL 60-4330).

Data and model availability statement

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

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Declaration of interest

None.

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