PITUITARY–ADRENAL ACTIVATION IN PRE-PARTURIENT PIGS (*SUS SCROFA*) IS ASSOCIATED WITH BEHAVIOURAL RESTRICTION DUE TO LACK OF SPACE RATHER THAN NESTING SUBSTRATE

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Previous research has shown that pre-parturient primiparous pigs (gilts) housed in behaviourally restrictive farrowing crates without straw redirect their nest-building behaviour to non-manipulable substrates such as the bars of the crate. These gilts also show elevated plasma adrenocorticotropic hormone (ACTH) and cortisol levels, particularly around the peak of nest-building activity, when compared to gilts in larger pens that have been provided with a manipulable substrate (straw). It remains unclear whether these behavioural and physiological responses to crating result from the lack of a suitable nesting substrate or from the restricted space. This study investigated the effects of space (crate [C] versus pen [P]) and straw (straw [S] versus no straw [NS]) using a 2 × 2 factorial design. Thirty-four gilts were implanted with an indwelling jugular catheter at around 12 days before parturition. They were moved to one of the four environments five days before parturition, and blood sampling and recording of behaviour were carried out during the pre-parturient period. Penned gilts (P), irrespective of straw availability, spent more time standing and walking and performed more total substrate-directed behaviour than crated (C) gilts. When straw was not available to penned gilts, a large proportion of their substrate-directed behaviour was redirected to the floor. Space also had an effect on ACTH and cortisol levels across the entire pre-parturient phase, with C gilts having higher levels than P gilts irrespective of straw availability, but particularly so at the peak of nest-building activity. There was no effect of straw on ACTH or cortisol levels. Overall, it appears that increased space, perhaps through allowing locomotion, increases substrate-directed behaviour of pre-parturient gilts. When space is available but straw is absent, pre-parturient gilts redirect their nest-building behaviour to the floor. The ability to express substrate-directed behaviour as a result of increased space is reflected in lower levels of indicators of physiological stress.

Keywords: *ACTH, animal welfare, cortisol, farrowing, gilt, nest-building, pig*

Introduction

Pre-parturient pigs, when given the opportunity, construct a nest into which they will give birth (Jensen *et al* 1987; Jensen 1989; Stolba & Wood-Gush 1989; Jensen *et al* 1993). This complex nest-building behaviour occurs during the 24 h before parturition, once the sow has

isolated herself from the herd. The sow selects a suitable nesting site and proceeds to dig a hollow into which she places grass and branches to construct her nest (Jensen *et al* 1987; Jensen 1989; Stolba & Wood-Gush 1989; Jensen *et al* 1993). The first part of nesting, characterised by much behaviour being directed towards the ground, has been suggested to be under internal control (Jensen 1993). The second phase, when the sow collects materials to complete the nest, is thought to be more strongly influenced by external stimuli such as availability of different types of substrates (Jensen 1993).

Nesting behaviour occurs spontaneously in naïve primiparous pre-parturient pigs (gilts). Previous research, using operant conditioning to measure motivation, showed that operant responding for access to a manipulable substrate (straw) increases as parturition approaches, suggesting that the pre-parturient pig has an increasing motivation for appropriate nest-building substrates (Arey 1992). There are many physiological changes occurring in the pre-parturient pig and the trigger for the onset of nesting behaviour is still unclear. Castren *et al* (1993) found some evidence that nesting coincided with a rise in prolactin; however, findings by Lawrence *et al* (1994) failed to support this. More recent work with pseudopregnant gilts has shown that administration of exogenous prostaglandin F2α (PGF2α) results in the performance of what appears to be nest-building behaviour (Boulton *et al* 1997; Burne *et al* 2000).

There has been much research investigating the effects of various types of housing on the behaviour and physiology of farrowing sows. The two main factors studied in relation to farrowing accommodation have been space and substrate availability. The general finding is that greater space allowance increases activity (Hansen & Curtis 1981; Cronin *et al* 1994; Jarvis *et al* 1997; Hartsock & Barczewski 1997; Cronin *et al* 1998) and the amount of nest-building behaviour that is performed by pre-parturient pigs (Cronin *et al* 1994; Hartsock & Barczewski 1997). Indeed, if sows are given a choice of farrowing crate widths, they will choose the widest, particularly if there is sufficient room to turn around (Phillips *et al* 1992). Similarly, if sows are given space they perform large amounts of locomotion during the pre-parturient phase (Haskell & Hutson 1994). In addition, if pre-parturient sows are housed in pairs they will use the space in such a way as to distance themselves from their penmate (Arey *et al* 1992).

Studies into the use of manipulable substrates have revealed an increase in nesting behaviours when substrates such as straw (Cronin & van Amerongen 1991; Thodberg *et al* 1999) and sawdust (Cronin *et al* 1993) are available during the pre-parturient phase. Similarly, in pseudopregnant gilts in which nesting behaviour is induced by exogenous PGF2α, more rooting and pawing behaviour is performed if straw is present (Burne *et al* 2000). Substrates can also alter the timing of nesting, with increased availability of straw increasing the length of the nesting period (Thodberg *et al* 1999) and availability of branches resulting in an earlier termination of nesting, perhaps because of feedback resulting from a more complete nest (Damm *et al* 2000). When manipulable substrates are absent, sows continue to express behaviour that has the characteristics of nest-building but which is now redirected towards less appropriate substrates for nest-building, such as solid floors and bars of the crate (Widowski & Curtis 1990; Lawrence *et al* 1994; Jarvis *et al* 1997).

Overall, despite domestication, pre-parturient pigs attempt to perform nest-building behaviour by making use of available space and substrates. Space restriction and absence of substrates, perhaps through interference with nest-building behaviour, can result in increased activation of the hypothalamic–pituitary–adrenal (HPA) axis. Results from our own experiments provide evidence that pre-parturient gilts housed in crates without straw, while

expressing redirected nest-building behaviour, had significantly higher plasma ACTH (Jarvis *et al* 1997) and cortisol (Jarvis *et al* 1997; Lawrence *et al* 1994) concentrations than gilts housed in larger pens with straw. However, from this experiment we could not conclude whether the elevation in physiological stress in the crated gilts was a result of space restriction or lack of straw.

The aim of this study was to investigate the effects of space and straw availability on the performance of nest-building behaviour of pre-parturient gilts. In addition, we examined whether any differences in expression of this highly motivated behaviour, resulting from differences in space and substrate availability, were reflected in circulatory levels of indicators of physiological stress.

Methods

Animals

This study was carried out under a UK Home Office project licence and personal licences in accordance with the Animals (Scientific Procedures) Act 1986. The experimental protocol was also reviewed and approved by the Animal Experiments Committee of the Scottish Agricultural College.

Thirty-four Large White × Landrace primiparous females (gilts; Cotswold Pig Development Co, Lincoln, UK) were used in this study. Groups of gilts were purchased at approximately six months of age, and each group was housed in a straw-bedded pen (2.6 × 4.1 m) which was cleaned as required with straw bedding being provided twice per week. They were fed 2.5 kg day^{-1} of a diet containing 13 MJ digestible energy (DE) per kilogram in one meal at 0800h. After a period of four weeks, a boar was introduced to the pen daily and the gilts were served on two consecutive days. The expected parturition day (EPD) was calculated as 114 days after the first service date. Once pregnancy was confirmed at around 32 days after service, the gilts were moved as a group to a strawed yard (9.6 × 6.0 m) where they were floor-fed 2.5 kg day^{-1} of the same commercial diet at 0800h. Similarly, the pens were cleaned and straw bedding provided twice per week.

Catheterisation

All gilts were weighed, and then a jugular catheter (Silastic, Osteotec Ltd, Christchurch, Dorset, UK) with internal diameter 1.47 mm and external diameter 1.93 mm was implanted under general anaesthesia around 13 days before the EPD (12.9 ± 0.2 days [SEM]). For full details of the procedure, see Lawrence *et al* 1992. The catheter was protected with an adhesive neck bandage, and a connecting tap at the back of the neck was used for the removal of blood. The catheters were flushed daily with saline and primed with heparinised saline (150 IU ml^{-1}) until sampling began four days before the EPD. After the operation, the gilts were housed individually in straw-bedded pens (2.0 × 2.0 m). The same commercial feed was offered in two meals at 0800h and 1600h (2.5 kg day^{-1}).

Experimental treatments

Five days before the EPD, the 34 gilts were moved at 1000h to one of two types of housing differing in space restriction: a conventional farrowing crate (Treatment C [n = 17]) measuring 2.25 × 0.45 m (l × w), or a pen (Treatment P [n = 17]) measuring 2.5 × 3.0 m (l × w). Within each of these environments, half of the gilts were provided with long straw at an approximate depth of 4 cm (Treatment S) and for the other half no straw was available (Treatment NS). This 2 × 2 factorial design therefore resulted in the following treatments: crate with no straw (CNS, n = 8); crate with straw (CS, n = 9); pen with no straw (PNS,

n = 9); and pen with straw (PS, n = 8). The crate had a solid floor with a slatted dunging area at the back, and the pen had a solid floor that was sloped to allow drainage. Both environments were cleaned daily between 0800h and 0900h, with fresh straw being given to pigs on the CS and PS treatments. The temperature of the housing was controlled (mean minimum temperature [°C] ± SEM = 15.04 ± 0.17; mean maximum temperature [°C] ± SEM = 21.14 ± 0.11), but both environments had a creep (heated area) for piglets outside the specified dimensions. The lights were on between 0800h and 1600h with dim lighting being used to allow observation during the night. The gilts were offered 3 kg day^{-1} of a food that provided 13.75 MJ DE kg^{-1} and contained 18% protein in two meals at 0800h and 1600h. After parturition the food level was gradually increased to appetite.

Behavioural observations

The behaviour of the gilts was recorded from their entry into the farrowing accommodation until the birth of the first piglet (BFP) using 24 h time-lapse video recording (Panasonic AG-6124). The 'Observer' system (Noldus *et al* 2000) was used to record behaviour continuously during the 24 h prior to the BFP. Posture and substrate-directed behaviours were recorded simultaneously using the ethogram shown in Table 1.

Table 1   The ethogram.

Posture	Description of posture	
Ventral lying	Lying on the floor on belly	
Lateral lying	Lying on the floor on side	
Standing	Standing on four legs	
Sitting	Sitting on the floor with front two feet on the floor	
Kneeling	Front legs knelt down while still standing on hind legs	
Walking	Moving about in the pen or stepping back and forth in the crate	
Behaviour	**Description**	**Substrates**
Nosing	Touching substrate with nose	Straw, bars, trough, drinker, floor
Pawing	Scratching movements with front legs	Straw, bars, trough, drinker, floor
Rooting	Digging/lifting movements with snout	Straw, bars, trough, drinker, floor
Biting	Gilt has object in her mouth/chewing	Straw, bars, trough, drinker, floor
Carrying	Picking up straw in mouth and carrying it	Straw

Blood sampling

Blood sampling began four days before EPD (day –4) and continued until the BFP. Samples were collected twice a day (1000h, 1400h) on day –4 and day –3 before EPD, and then every 4 h until the onset of nest-building. Samples were collected directly from the tap at the neck until the onset of nest-building behaviour (approximately 16 h before BFP), at which point a silastic catheter extension tube was fitted. The catheter extension minimised the disturbance to the gilts by allowing samples to be taken from outside the crate or pen. Samples were taken every 30 min during the nest-building phase until approximately 2 h before the BFP, when the sampling frequency was increased to every 10 min until the BFP. Saline was used to replace the volume of blood taken and the catheter and extension primed with heparinised saline (75 IU ml^{-1}). Heparinised monovette tubes (Sarstedt, Leicester, UK) were used to collect blood samples. The samples were spun at 3000 rpm at 4°C for 20 min. Aliquots of plasma were pipetted and stored at –20°C for later assay. Three days after parturition, the jugular catheter was removed and the gilts were returned to the commercial farm stock.

Hormonal analysis

Blood samples from different groups and treatments were balanced across assay runs. Plasma used for all assays had been thawed once only.

Cortisol

Cortisol was extracted using diethyl ether from 100 μl of plasma and concentrations were measured by radioimmunoassay of the extracted steroid (Duncan *et al* 1990). The intra- and inter-assay coefficients of variation were 8.9% and 15.6%, respectively, and the minimum detectable level of the assay was $0.156 \, \text{ng ml}^{-1}$. Single samples were extracted and then assayed in duplicate.

ACTH

Concentrations of ACTH were measured using 100 μl aliquots of plasma in duplicate. An immunoradiometric assay kit (Euro Path Ltd, Bude, Cornwall, UK) was used. Second antibody method was used, the samples spun and the pellet counted using a multigamma counter (Brooks 1992). The minimum detectable level of the assay was $5.0 \, \text{ng l}^{-1}$ and the intra- and inter-assay coefficients of variations were 13.3% and 12.3%, respectively.

Statistical analysis

Gilt information

Gilt weight and gestation length were compared across the four treatments using a one-way analysis of variance (Minitab, release 7.2).

Behavioural observations

The total number of posture changes, as well as the percentage of time spent in each of the postures and carrying out various aspects of substrate-directed behaviour, were calculated for each of four periods: Period 1, 24–16 h before BFP; Period 2, 15.5–8 h before BFP; Period 3, 7.5–4 h before BFP; Period 4, 3.5–0 h before BFP. All behaviours directed towards particular substrates were added together. Data were checked for normality and, if necessary, were log transformed. A repeated measures analysis of variance (Genstat, version 5) was used to analyse the data across all periods (investigating effects of period, space, straw and interactions between space and straw).

Hormonal data

The cortisol and ACTH results for each time-sample during the 24 h pre-parturition were divided into the same four periods as described for the behavioural observations. Baseline blood samples were taken at 1000h on day –4 and day –3, and the mean of these values was subtracted from all subsequent blood-sample results to account for individual differences in ACTH and cortisol. A repeated measures analysis of variance was used to analyse the data across all periods (investigating effects of period, space, straw and interactions). Least significant difference (LSD) tests were used to investigate space × period and straw × period interactions.

Results

Gilt information

The weight of the gilts did not differ between the four treatments (mean weight [kg] ± SEM for CNS = 191.4 ± 5.1; for CS = 181.0 ± 5.2; for PNS = 190.9 ± 3.8; for PS = 190.81 ± 4.82; $F_{3,30} = 1.17$, $P = 0.338$). Similarly, the length of gestation was not affected by space or straw

availability (mean gestation length [days] ± SEM for CNS = 113.9 ± 0.3; for CS = 114.7 ± 0.5; for PNS = 114.4 ± 0.5; for PS = 114.0 ± 0.46; $F_{3,30} = 0.66$, $P = 0.581$).

Behavioural observations
Posture
The general pattern was for gilts in all treatments to increase activity from Period 1 to Period 3, before their activity declined in Period 4 as the BFP approached (Figure 1). Overall, therefore, the percentage of time spent standing (including walking) (Figure 1c, Period: $F_{3,90} = 28.3$, $P < 0.001$) and walking (Figure 1d, Period: $F_{3,90} = 26.7$, $P < 0.001$) increased during Periods 1–3, before decreasing during Period 4. Overall, gilts expressed similar patterns for ventral lying (Figure 1b, Period: $F_{3,90} = 4.91$, $P < 0.01$), sitting (Figure 1e, Period: $F_{3,90} = 10.78$, $P < 0.001$) and posture changes (Figure 1f, Period: $F_{3,90} = 38.96$, $P < 0.001$). In a converse pattern, the time spent in lateral lying (an indication of reduced activity) fell during Periods 1–3, before increasing in Period 4 as the gilts quietened before the BFP (Figure 1a, Period: $F_{3,90} = 31.57$, $P < 0.001$).

Within this general pattern there were important differences between gilts experiencing variation in space availability. In general, penned gilts expressed greater levels of behavioural activity than crated gilts, spending longer standing (including walking) (Figure 1c, Space: $F_{1,30} = 13.56$, $P < 0.001$), and walking (Figure 1d, Space: $F_{1,30} = 58.82$, $P < 0.001$). Similarly, penned gilts spent longer lying ventrally (Figure 1b, Space: $F_{1,30} = 14.81$, $P < 0.001$) and made more posture changes (Figure 1f, Space: $F_{1,30} = 9.50$, $P < 0.01$) than crated gilts. Conversely, crated gilts showed higher levels of lateral lying (Figure 1a, Space: $F_{1,30} = 9.30$, $P < 0.01$) and sitting (Figure 1e, Space: $F_{1,30} = 26.9$, $P < 0.001$) than penned gilts. None of these postural variables were affected by provision of straw.

Substrate-directed behaviour
The percentage of time spent carrying out behaviour directed to substrates followed a similar pattern to active postures in that there was an increase in total substrate-directed behaviour during Periods 1–3 and then a decrease as the gilts quietened down prior to BFP (Figure 2a, Period: $F_{3,90} = 43.0$, $P < 0.001$). Although this temporal pattern was similar in both crated and penned gilts, the penned gilts carried out more total substrate-directed behaviour overall (Figure 2a, Space: $F_{1,30} = 16.12$, $P < 0.001$). The total substrate-directed behaviour carried out by the gilts was not affected by the presence of straw.

Of the two treatments that had straw available to them, the penned gilts used the straw significantly more than the crated gilts (Figure 2b, Space: $F_{1,15} = 13.55$, $P < 0.01$). Gilts that did not have straw present used non-straw substrates (floor, bars, trough and drinker) more than those with straw (Figure 2c, Straw: $F_{1,30} = 132.7$, $P < 0.001$). However when we looked at floor-directed behaviour only across all four treatments, it was apparent that the penned gilts (Figure 2d, Space: $F_{1,30} = 50.57$, $P < 0.001$) and gilts without straw (Figure 2d, Straw: $F_{1,30} = 321.8$, $P < 0.001$) spent longer performing floor-directed behaviour. Indeed, an interaction between space and straw was found, with the PNS gilts using the floor significantly more than gilts in the other three treatments (Figure 2d, Space × straw: $F_{1,30} = 4.92$, $P < 0.05$).
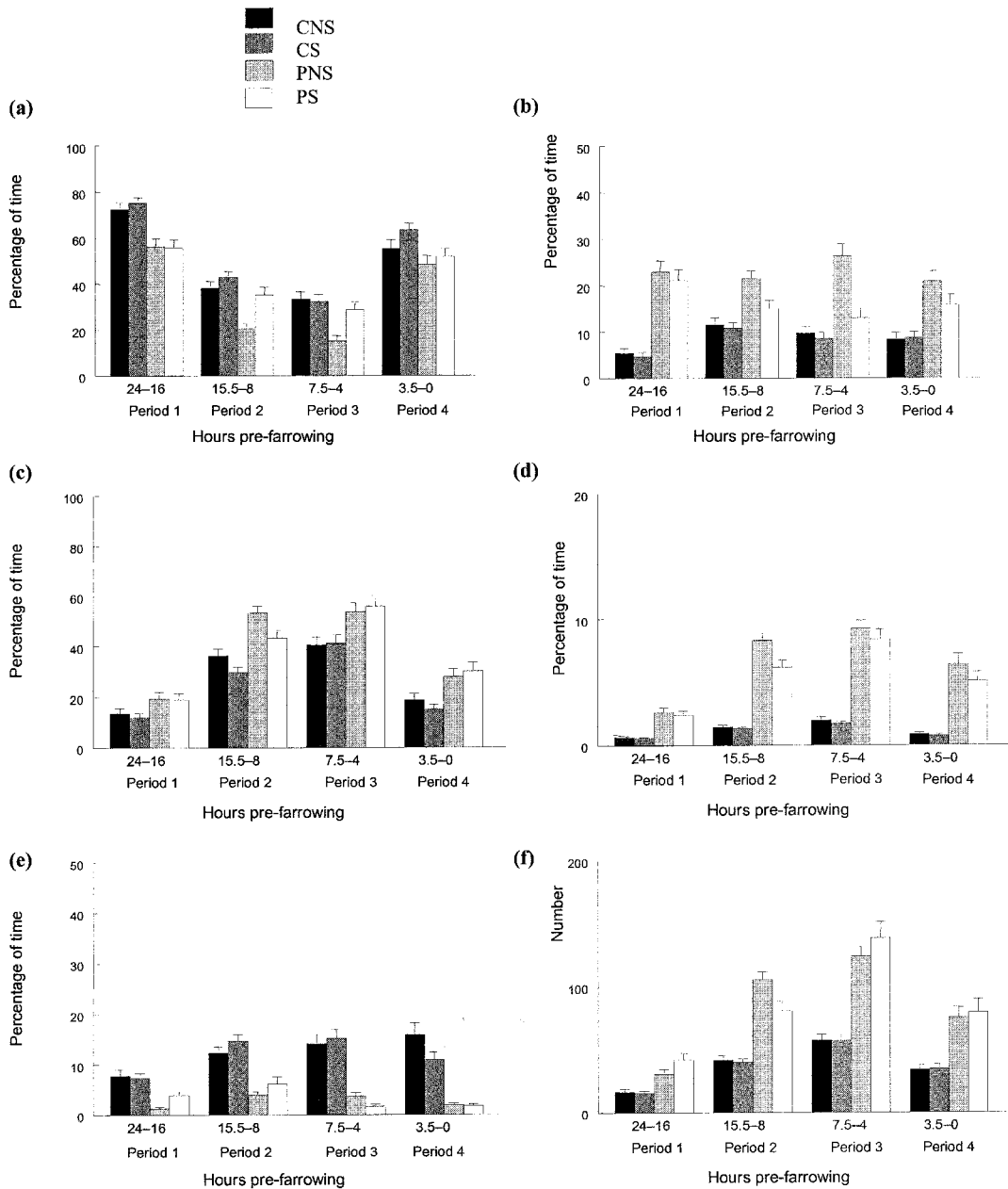
Figure 1   Percentage of total time spent (a) lying laterally, (b) lying ventrally, (c) standing (including walking), (d) walking, and (e) sitting. (f) The frequency of posture changes during the 24 h pre-parturition period in gilts housed in crates, no straw (CNS, n = 8); crates with straw (CS, n = 9), pens, no straw (PNS, n = 9) and pens with straw (PS, n = 8). Note different maxima on y-axes.
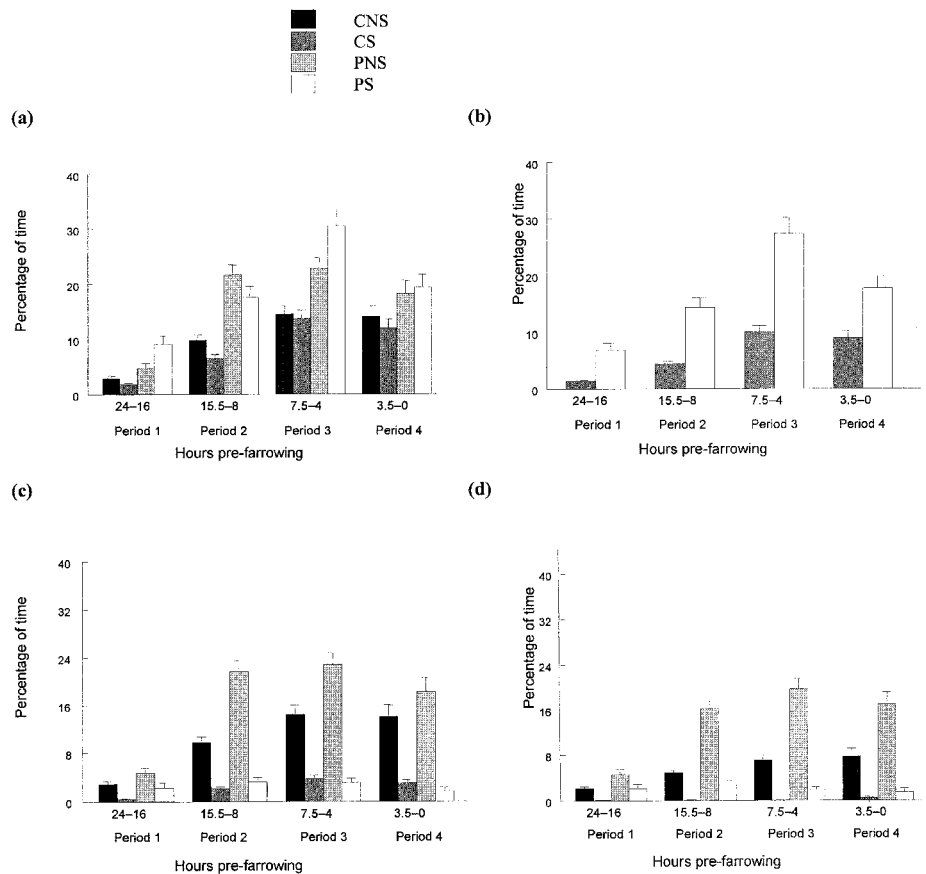
Figure 2   Percentage of total time spent (a) performing all substrate-directed behaviour, (b) using straw, (c) using non-straw substrates, and (d) using the floor during the 24 h pre-parturition period in gilts housed in crates, no straw (CNS, n = 8), crates with straw (CS, n = 9), pens, no straw (PNS, n = 9) and pens with straw (PS, n = 8).

Hormonal data
ACTH
Generally, plasma ACTH increased over time and reached a peak during Period 2 with a drop occurring in the last hours before the BFP (Figure 3a, Period: $F_{3,85} = 2.51$, $P = 0.064$). Across all periods there was a tendency for gilts in crates to have higher levels of ACTH than penned gilts (Space: $F_{1,29} = 4.13$, $P = 0.051$), but there was no effect of straw availability.

When we looked at space and straw effects within periods (Figure 3a) it was found that ACTH was higher in crated gilts during Period 2 (LSD: $P < 0.01$) and Period 3 (LSD: $P < 0.05$). There were no effects of straw availability on ACTH within any of the periods.

Cortisol
Cortisol followed a similar pattern to ACTH across the 24 h pre-farrowing, with a rise in cortisol occurring over Periods 1–3, followed by a decrease just prior to the BFP (Figure 3b, Period: $F_{3,85} = 3.85$, $P < 0.05$). Similarly, there was no effect of straw availability on plasma

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cortisol concentrations during the nesting period; however, there was a significant effect of space, with crated gilts having elevated levels of cortisol compared to penned gilts (Figure 3b, Space: $F_{1,30} = 6.41, P < 0.05$).

When we looked within periods we found that space affected plasma cortisol during Period 2 (LSD: $P < 0.05$) and Period 3 (LSD: $P < 0.01$), with crated gilts having higher levels of cortisol than penned gilts. There was no effect of straw availability.
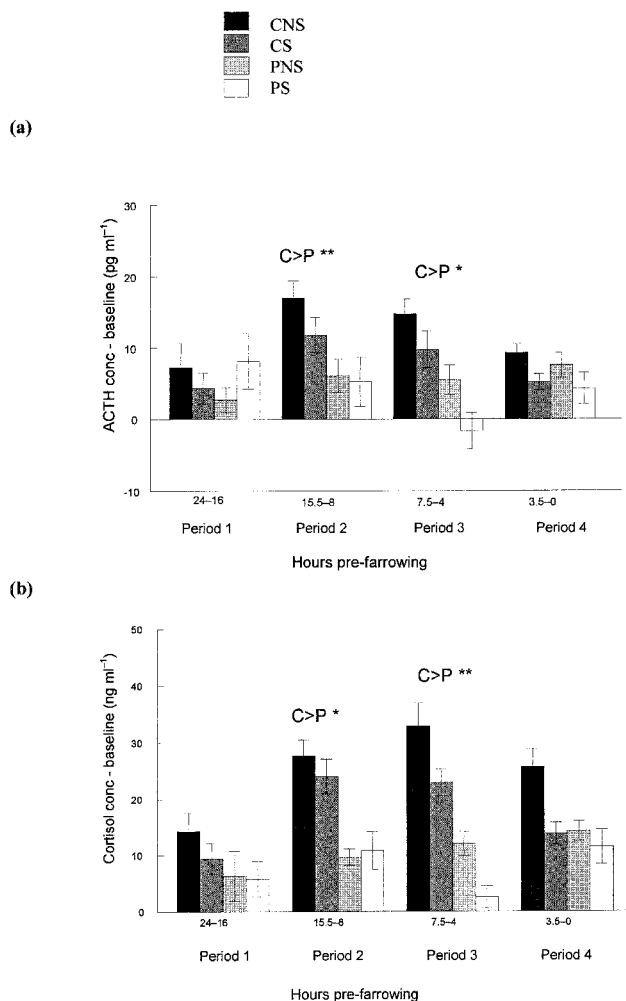

Figure 3 **Plasma concentrations of (a) ACTH and (b) cortisol during the 24 h pre-parturition period in gilts housed in crates, no straw (CNS, n = 8); crates with straw (CS, n = 9), pens, no straw (PNS, n = 9) and pens with straw (PS, n = 8). Significance levels and direction of effects are shown for each of the periods (*$P < 0.05$, **$P < 0.01$).**

Discussion

There is growing evidence that pre-parturient nesting in the sow is triggered by the endocrine cascade that prepares the sow for delivery and perhaps specifically the release of PGF2α (eg

Burne *et al* 2000). By varying the provision of space and substrate, we effectively manipulated the expression of this strongly physiologically dependent behaviour. In terms of behavioural effects, we found that increased space, rather than substrate, had the greatest effect on pre-parturient behaviour. Providing pigs with more space in the pen environment increased time spent standing and reduced time spent in lateral lying and sitting. This is consistent with other studies that found small narrow farrowing pens to decrease the amount of time spent standing during the nest-building period (Cronin *et al* 1998), and found farrowing crates to increase the amount of time spent sitting (Hartsock & Barczewski 1997; Jarvis *et al* 1997), an atypical posture suggested to reflect thwarting of nest-building behaviour (Jarvis *et al* 1997). In contrast to other work (Hansen & Curtis 1981; Cronin *et al* 1994; Hartsock & Barczewski 1997), we found that penned gilts changed posture more frequently than crated gilts, perhaps because we used a higher number of posture categories than in previous studies. We also found that penned gilts spent more time lying ventrally. As ventral lying is often a transitional posture between lying laterally and standing, the greater proportion of time spent in this posture may result from an increased frequency of posture changing in the penned gilts. Alternatively, lying behaviour may be carried out during nest-building as a way of resting and the more active penned gilts may have adopted this posture to rest as opposed to the extreme resting position of lateral lying.

There is evidence to show that where access to nesting substrates is restricted, pigs will 'redirect' their nesting behaviour to other substrates. In this and previous work (eg Widowski & Curtis 1990; Jensen 1993; Lawrence *et al* 1994; Jarvis *et al* 1997) where manipulable substrates (eg straw) are absent, gilts redirect their pre-parturient behaviour to inappropriate substrates (eg concrete floor, bars of the crate), indicating the relative independence of nesting behaviour from the quality of available stimuli.

However, whilst absence of a manipulable nesting substrate caused redirection of nesting behaviour, we only found a decrease in total substrate use when space allowance was restricted (see also Cronin *et al* 1994; Hartsock & Barczewski 1997 for similar results). The effect of restricted space on substrate use was not only reflected in the decreased use of all substrates in the crate environment, but also in the decreased use of the added substrate (straw) by crated gilts. The decreased activity and decreased substrate-directed behaviour seen in the crated gilts in this study may be separate behavioural responses to space restriction. Alternatively, these observations suggest that space facilitates the use of available nesting substrates, perhaps by permitting the gilts to walk and orientate during the nesting phase. We found that increased space led to a substantial increase in the proportion of time the gilts spent walking. Other work on feral (Stolba & Wood-Gush 1989) and indoor (non-crated) sows (Haskell & Hutson 1994) has illustrated the high levels of locomotion performed during the pre-parturient phase, indicating that walking is an important behavioural element of nesting in the pig.

Nesting behaviour in the pig is a set of coordinated behavioural activities involving gathering, carrying and nest construction (Gundlach 1968; Jensen 1989), and locomotion may be necessary to retain organisation of this behaviour pattern. In the pig, locomotion or the stimuli associated with locomotion (eg increased substrate novelty) may act to reinforce substrate use. Alternatively, the influence of locomotion on substrate use may be directly at a physiological ('hard-wired') level, for example by inducing neural changes that stimulate substrate-directed behaviour.

In the hours preceding parturition, basal oxytocin levels in the sow rise (Lawrence *et al* 1995) and uterine contractions increase (Taverne 1992), and we might expect decreased

nesting activity in anticipation of delivery. In this study, despite having higher absolute levels of substrate-directed behaviour, penned gilts showed a greater reduction in their total substrate-directed behaviour from Period 3 to Period 4 than gilts housed in crates. This greater reduction in substrate-directed behaviour could reflect greater ability to have performed nest-building and feedback from the nest-site. However, floor-directed behaviour is regarded as being part of the first phase of nest-building (Jensen 1993), and so the continuation of floor-directed behaviour in penned gilts without straw in this study may be a result of the concrete floor of the pen providing insufficient feedback to end nest-building. This is consistent with Damm *et al* (2000), who found that gilts with smaller amounts of available substrates terminated their nesting behaviour later. There may also be an element of maturity or experience involved, as in a study by Jarvis *et al* (2001) second-parity sows separated their nesting behaviour more distinctly into the two nesting phases identified by Jensen (1993) by performing more floor-directed behaviour in the early stages of nesting.

In this study we combined environmental manipulation of the expression of nesting behaviour with physiological measures of the pituitary–adrenal (PA) axis. Our aim was to provide a physiological perspective on the consequences for the sow of being constrained in her expression of nesting behaviour. The hypothalamo–pituitary–adrenal (HPA) axis is seen as one of the body's main stress axes and it has been shown to be activated in response to many psychological and physical stressors (eg Checkley 1996). The HPA axis has also been shown to be activated in relation to self-reported anxiety in women during labour (Lederman *et al* 1978) and so is a particularly appropriate measure of the psychological consequences of thwarting of behaviour during the parturient period. We found evidence of a general increase in HPA activation from Period 1 to a peak during Period 3 in crated and penned gilts. There is considerable evidence in many species that the foetal HPA axis has an important role in the initiation of parturition (eg Whittle *et al* 2001); however, there is evidence that this is not the case in the pig (Randall *et al* 1990). Although previous studies of sows (eg Killian *et al* 1973; Meunier-Salaun *et al* 1991) have reported increased concentrations of plasma maternal cortisol during the pre-parturient phase, it is thought that this is more likely to be a result rather than a cause of parturition (eg Lawrence *et al* 1994). However, in addition to activation of the HPA axis relating to parturition itself, we found an additional environment-induced PA activation, with space-restricted gilts having higher ACTH and cortisol levels particularly during the peak of nest-building behaviour. Exercise is known to activate the HPA axis (Petrides *et al* 1994); however, this study provides evidence that space-restricted gilts, although being less active during the pre-parturient phase, show greater activation of the PA axis. Taken together with our behavioural observations, these results suggest that space restrictions on locomotion and substrate-directed behaviour are also stress-inducing, perhaps because they invoke an intervening aversive psychological state. The lack of effect of straw availability on plasma ACTH and cortisol concentrations suggests that redirection of substrate-directed behaviour to the floor by the penned gilts without access to straw satisfies, to some extent, the nest-building needs of those gilts and reduces physiological stress.

Altering the expression of nesting behaviour may also have implications for later maternal behaviour and piglet survival. The availability of substrates during nesting can, through altering maternal behaviour, reduce piglet crushing (Thodberg *et al* 1999; Damm *et al* 2000) and increase responsiveness to piglet distress calls (Herskin *et al* 1999; Cronin & van Amerongen 1991). Appleyard *et al* (2000) reported that sows in crates that savage their piglets show greater evidence of disturbance of their nesting behaviour. Previous work (Jarvis *et al* 1999) has suggested that appropriate maternal behaviour in the sow is to lie passively during delivery, and that endogenous opioids released around parturition may be

partly involved in generating this state. Restrictions on expression of nesting behaviour may cause disturbance to the physiological changes necessary to result in a passive parturient sow.

One of the main concerns highlighted by the European Union Scientific Veterinary Committee (EUSVC 1997) relating to the use of crates to house farrowing sows was that they 'restrict the movements of the sow and usually sows are not given straw when in crates'. The EUSVC's recommendation for future research relating to farrowing crates was to investigate 'the extent to which acute pre-farrowing stress in sows in farrowing crates is attributable to confinement or to a lack of manipulable substrates'. Our study quite clearly demonstrates that confinement rather than nesting substrate has a greater impact on the welfare of pre-parturient pigs as characterised by a reduction in nesting behaviour and increased physiological stress.

Animal welfare implications

We have found that provision of space during the pre-parturient phase reduces physiological stress of gilts, with straw availability having little effect. This effect of space on physiological stress may be a result of increased activity and locomotion facilitating the performance of substrate-directed behaviour. Overall, these data suggest that space restriction, rather than lack of straw, has the greatest impact on the behaviour and welfare of pre-parturient gilts, which has major implications for animal welfare legislation relating to farrowing accommodation.

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References

Appleyard S, Hall A D and Lawrence A B 2000 Pre-farrowing behaviour distinguishes piglet-savaging gilts from non-piglet-savaging gilts. *Proceedings of the 34th International Congress of the International Society for Applied Ethology* p 62. Federal University of Santa Catarina: Florianopolis, Brazil

Arey D S 1992 Straw and food as reinforcers for prepartal sows. *Applied Animal Behaviour Science 33*: 217-226

Arey D S, Petchey A M and Fowler V R 1992 The pre-parturient behaviour of sows housed in pairs. *Applied Animal Behaviour Science 34*: 49-59

Boulton M I, Wickens A, Brown D, Goode J A and Gilbert C L 1997 Prostaglandin F2α-induced nestbuilding in pseudopregnant pigs. I. Effects of environment on behaviour and cortisol secretion. *Physiology & Behaviour 62*: 1071-1078

Brooks A N 1992 Prostaglandin E2 stimulates adrenocorticotrophin and cortisol secretion via a hypothalamic site of action in fetal sheep. *Journal of Developmental Physiology 18*: 173-177

Burne T J H, Murfitt P J E and Gilbert C L 2000 Deprivation of straw bedding alters PGF2a-induced nesting behaviour in female pigs. *Applied Animal Behaviour Science 69*: 215-225

Castren H, Algers B, de Passillé A M B, Rushen J and Uvnas-Moberg K 1993 Pre-parturient variation in progesterone, prolactin, oxytocin and somatostatin in relation to nest-building in sows. *Applied Animal Behaviour Science 38*: 91-102

Checkley S 1996 The neuroendocrinology of depression and chronic stress. *British Medical Bulletin 52*: 597-617

Cronin G M and van Amerongen G 1991 The effects of modifying the farrowing environment on sow behaviour and survival and growth of piglets. *Applied Animal Behaviour Science 30*: 287-298

Cronin G M, Schirmer B N, McCallum T H, Smith J A and Butler K L 1993 The effects of providing sawdust to pre-parturient sows in farrowing crates on sow behaviour, the duration of parturition and the occurrence of intra-partum stillborn piglets. *Applied Animal Behaviour Science 36*: 301-315

Cronin G M, Smith J A, Hodge F M and Hemsworth P H 1994 The behaviour of primiparous sows around farrowing in response to restraint and straw bedding. *Applied Animal Behaviour Science 39*: 269-280

Cronin G M, Dunsmore B and Leeson E 1998 The effects of farrowing nest size and width on sow and piglet behaviour and piglet survival. *Applied Animal Behaviour Science 60*: 331-345

Damm B I, Vestergaard K S, Schroder-Petersen D L and Ladewig J 2000 The effect of branches on prepartum nest building in gilts with access to straw. *Applied Animal Behaviour Science 69*: 113-124

Duncan W F, Lincoln D W and Naylor A M 1990 Plasma cortisol is increased during inhibition of LH secretion by central LHRH in the ewe. *Neuroendocrinology 51*: 705-712

European Union Scientific Veterinary Committee Report 1997 The welfare of intensively kept pigs. *Report of the Scientific Veterinary Committee of the European Union.* Available at http://europa.eu.int/comm/food/fs/sc/oldcomm4/out17_en.html

Gundlach H 1968 Brutfursorge, Brutpflege, Verhaltens-ontongense und Tagesperiodik beim Europaischen Wildschwein (*Sus scrofa*). *Zeitschrift fur Tierpsychologie 25*: 955-995

Hansen K E and Curtis S E 1981 Prepartal activity of sows in stall or pen. *Journal of Animal Science 51*: 456-460

Hartsock T G and Barczewski R A 1997 Prepartum behaviour in swine: effects of pen size. *Journal of Animal Science 75*: 2899-2904

Haskell M J and Hutson G D 1994 Pre-farrowing behaviour of sows and gilts with access to space for locomotion. *Australian Journal of Experimental Agriculture 34*: 1099-1105

Herskin M S, Jensen K H and Thodberg K 1999 Influence of environmental stimuli on nursing and suckling behaviour in domestic sows and piglets. *Animal Science 68*: 27-34

Jarvis S, Lawrence A B, McLean K A, Deans L, Chirnside J and Calvert S K 1997 The effect of environment on behavioural activity, ACTH, β-endorphin and cortisol in pre-parturient gilts. *Animal Science 65*: 465-472

Jarvis S, McLean K A, Calvert S K, Deans L A, Chirnside J and Lawrence A B 1999 The responsiveness of sows to their piglets in relation to the length of parturition and the involvement of endogenous opioids. *Applied Animal Behaviour Science 63*: 195-207

Jarvis S, van der Vegt B J, Lawrence A B, McLean K A, Deans L A, Chirnside J and Calvert S K 2001 The effect of parity and environmental restriction on behavioural and physiological responses of pre-parturient pigs. *Applied Animal Behaviour Science 71*: 203-216

Jensen P, Floren K and Hobroh B 1987 Peri-parturient changes in behaviour in free-ranging domestic pigs. *Applied Animal Behaviour Science 17*: 69-76

Jensen P 1989 Nest site choice and nestbuilding of free-ranging domestic pigs due to farrow. *Applied Animal Behaviour Science 22*: 13-21

Jensen P 1993 Nest building in domestic sows: the role of external stimuli. *Animal Behaviour 45*: 351-358

Jensen P, Vestergaard K and Algers B 1993 Nestbuilding in free-ranging domestic sows. *Applied Animal Behaviour Science 38*: 245-255

Killian D B, Garverick H A and Day B N 1973 Peripheral plasma progesterone and corticoid levels at parturition in the sow. *Journal of Animal Science 37*: 1371-1375

Lawrence A B, Petherick J C, McLean K A, Gilbert C L, Chapman C and Russell J A 1992 Naloxone prevents interruption of parturition and increases plasma oxytocin following environmental disturbance in parturient sows. *Physiology & Behaviour 52*: 917-923

Lawrence A B, Petherick J C, McLean K, Deans L, Chirnside J, Vaughan A, Clutton E and Terlouw E M C 1994 The effect of environment on behaviour, plasma cortisol and prolactin in parturient sows. *Applied Animal Behaviour Science 39*: 313-330

Lawrence A B, Petherick J C, McLean K A, Deans L A, Chirnside J, Vaughan A, Gilbert C, Forsling M L and Russell J A 1995 The effects of chronic environmental stress on parturition and on oxytocin and vasopressin secretion in the pig. *Animal Reproduction Science 38*: 251-264

Lederman R P, Lederman E, Work B A and McCann D S 1978 The relationship of maternal anxiety, plasma catecholamines and plasma cortisol to progress in labour. *American Journal of Obstetrics and Gynecology 132*: 495-500

Meunier-Salaun M C, Gort F, Prunier A and Schouten W P G 1991 Behavioural patterns and progesterone, cortisol and prolactin levels around parturition in European (Large White) and Chinese (Meishan) sows. *Applied Animal Behaviour Science 31*: 43-59

Noldus L P J J, Trienes R J H, Hendriksen A H M, Jansen H and Jansen R H 2000 The Observer Video-Pro: new software for the collection, management, and presentation of time-structured data from videotapes and digital media files. *Behaviour Research Methods, Instruments and Computers 32*: 197-206

Petrides J S, Mueller G P, Kalogeras K T, Chrousos G P, Gold P W and Deuster P A 1994 Exercise-induced activation of the HPA axis — marked differences in the sensitivity to glucocorticoid suppression. *Journal of Clinical Endocrinology and Metabolism 79*: 377-383

Phillips P A, Fraser D and Thompson B K 1992 Sow preference for farrowing crate width. *Canadian Journal of Animal Science 72*: 745-750

Randall G C B, Kendall J Z, Tsang B K, Taverne M A M 1990 Endocrine changes following infusion of fetal pigs with corticotropin in litters of reduced numbers. *Animal Reproduction Science 23*: 109-122

Stolba A and Wood-Gush D G M 1989 The behaviour of pigs in a semi-natural environment. *Animal Production 48*: 419-425

Taverne M A M 1992 Physiology of parturition. *Animal Reproduction Science 28 (Symposium 12 — Parturition)*: 422-440

Thodberg K, Jensen K H, Herskin M S and Jorgensen E 1999 Influence of environmental stimuli on nest building and farrowing behaviour in domestic sows. *Applied Animal Behaviour Science 63*: 131-144

Whittle W L, Patel F A, Alfaidy N, Holloway A C, Fraser M, Gyomorey S, Lye S J, Gibb W and Challis J R G 2001 Glucocorticoid regulation of human and ovine parturition: the relationship between fetal hypothalamic–pituitary–adrenal axis activation and intrauterine prostaglandin production. *Biology of Reproduction 64*: 1019-1032

Widowski T M and Curtis S E 1990 The influence of straw, cloth tassel, or both on the prepartum behaviour of sows. *Applied Animal Behaviour Science 27*: 53-71