

Peri-natal environmental effects on maternal behaviour, pituitary and adrenal activation, and the progress of parturition in the primiparous sow

S Jarvis^{*†}, BT Reed[‡], AB Lawrence[‡], SK Calvert[†] and J Stevenson[†]

[†] Animal Behaviour and Welfare, Sustainable Livestock Systems, Scottish Agricultural College, West Mains Road, Edinburgh EH9 3JG, UK

[‡] Institute of Ecology and Resource Management, University of Edinburgh, West Mains Road, Edinburgh EH9 3JG, UK

* Contact for correspondence and requests for reprints: s.jarvis@ed.sac.ac.uk

Abstract

Maternal behaviour in free-ranging sows is normally performed in an isolated nest that the sow has built during the pre-parturient period. Consequently there is much concern over the use of restrictive farrowing crates, in which manipulable substrates are often not provided, for parturient sows under commercial conditions. This study examined the impact of the provision of space and substrate on the performance of maternal behaviour by gilts (primiparous sows) on physiological indicators of stress and on the progress of parturition. Gilts had an indwelling jugular catheter implanted 12 days before their expected farrowing date. At 5 days before expected farrowing, 34 gilts were placed in one of four farrowing treatments: crate without straw (C, $n = 8$), crate with straw (CS, $n = 9$), pen without straw (P, $n = 9$) or pen with straw (PS, $n = 8$). Behavioural observations of gilts and piglets were made during an 8 h period after the expulsion of the first piglet. Blood samples were taken via a catheter extension to minimise disturbance throughout the parturition period. Gilts in all treatments were most active in the first 2 h: performing more standing/walking, substrate-directed and piglet-directed behaviour. This active phase was followed by inactivity and passivity, as has been seen in free-ranging sows. However, this temporal profile of behaviour was more pronounced in the penned gilts (P and PS), which were more active during the first 2 h than the crated gilts (C and CS). Gilts in crates spent longer sitting throughout the 8 h period and tended to show more savaging of their piglets. Savaging gilts were found to be more active and responsive to piglets. The provision of straw did not alter gilt behaviour but did alter piglet behaviour, with piglets that were born into environments with no straw (C and P) spending more time next to the gilt's udder. The provision of straw increased the length of parturition (CS and PS), but this did not have detrimental effects on piglet survival. Plasma cortisol was unaffected by space or substrate, however, plasma ACTH was found to be highest in C gilts during the second hour of parturition. Plasma oxytocin was unaffected by space or substrate, however, there was a positive relationship between plasma oxytocin and unresponsiveness to piglets. In conclusion, it appears that farrowing crates thwart interactions between the gilt and her piglets, and that the provision of space during parturition, irrespective of straw availability, facilitates the performance of maternal behaviour that more closely resembles that performed by free-ranging sows.

Keywords: animal welfare, environment, farrowing crate, maternal behaviour, parturition, pig

Introduction

Traditionally, intensive housing systems have usually concentrated on the elimination of litter or straw bedding with a concomitant attempt to increase the efficiency of space utilisation (Baxter 1974). These working practices can often be seen as having adverse effects on the behaviour and mental well-being of the animals (Harrison 1964). For the farrowing pig, recent decades have seen a reduction in the use of farrowing pens in favour of farrowing crates in which little or no straw is used (Fraser & Broom 1990). It is widely acknowledged that the main benefit to be gained from the use of farrowing crates, as opposed to larger pen-like or 'open' alternatives, is the ability to limit piglet losses by restricting sow movement (Brent 1986). With their introduction in the 1960s it was hoped to reduce the alarming and costly pre-weaning mortality rates, which were often up to 25% (Beynon 1990), and to this end the crates seem to be

relatively successful. Many studies show reduced mortality rates in the crate environments (Blackshaw *et al* 1994; Weary *et al* 1996), although the figure still stands at around 12% (MLC 2000). However, public concern has been voiced over the use of farrowing crates with regard to their potential to inhibit the sow's normal behaviour patterns associated with nesting and maternal care.

Previous research has shown that during each phase of peri-parturient behaviour there are a number of environmental conditions that are important to the sow, including the social environment, shelter, nesting material and offspring interaction (reviewed by Arey 1997). It is possible that restricting the sow's access to these conditions at the stage of pregnancy that they are desired may impact upon her future maternal behaviour (eg Thodberg *et al* 1999; Damm *et al* 2000), with subsequent effects on piglet welfare. In relation to this, environmental restriction around farrowing time in

the pig has been shown to cause increased activation of the hypothalamic–pituitary–adrenal (HPA) axis — the body's main stress axis (Lawrence *et al* 1994; Jarvis *et al* 1997, 2002). In addition, environmental disturbance during farrowing has been shown to decrease levels of plasma oxytocin (Lawrence *et al* 1992). Oxytocin is crucial to the progress of parturition through its role in inducing uterine contractions (Taverne 1992) and milk production (pigs: Algers *et al* 1990), and has been shown to be involved centrally in the control of maternal behaviour (rats: Pedersen *et al* 1982; Fahrback *et al* 1985).

In evolutionary terms, suitable maternal care in the sow is represented by those behaviours that give the piglets the greatest chance of survival. During the early stages of farrowing, turning, sniffing and nose-to-nose contact with the piglets are common in unrestrained conditions (Watson & Bertram 1983; Jarvis *et al* 1999) and in free-ranging conditions (Jensen 1986; Petersen *et al* 1990). This initial period of investigation and exploration of the first-born piglets then gives way to extended periods of lateral lying (Jones 1966; Randall 1972; Watson & Bertram 1983; Petersen *et al* 1990; Jarvis *et al* 1999). Since it is vital that the new-born piglets waste no time in sucking from the sow (Whittemore 1980), increased sow lateral lying with the teats exposed is advantageous to the piglets as it enables the transfer of colostrum to the piglets and also increases the availability of warmth (Fraser 1984).

As mentioned, sows normally investigate piglets in the early stages of farrowing; however, the farrowing crate would appear to restrict the sow's access to her piglets (Blackshaw & Hagelsø 1990). Abnormal maternal responses to piglets, such as savaging, have been shown to occur more frequently when sows are housed in farrowing crates than in more loose housing systems (Cronin *et al* 1996; Jarvis *et al* 1998). Savaging attempts tend to occur during the earlier stages of farrowing and so are often directed towards those piglets born first (English *et al* 1977). However, further research has found that crated savagers are more restless and more responsive to piglets across the whole of the expulsive phase of parturition and that they do not settle down into inactivity and passivity as do non-savagers (Ahlstrom *et al* 2002).

The aim of this investigation was to add to our understanding of sow requirements during the farrowing process by examining the effect of space allowance and straw availability during the peri-natal period. In this paper we will examine the consequences of these environmental manipulations on the performance of maternal behaviour, physiological stress responses (as measured by HPA axis activation), the progress of parturition and on a hormone vital to this process: oxytocin. In addition, we will investigate the effect of space and straw availability on the incidence of abnormal maternal responses and examine behavioural differences between savaging and non-savaging sows.

Methods

The study took place at the Scottish Agricultural College, Easter Howgate Pig Unit, Edinburgh, UK, and 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.

Animals and housing

Gilts were chosen as subjects because they had no previous experience of any farrowing environment or indeed of the farrowing process itself. Thirty-four Large-White × Landrace primiparous gilts (Cotswold Pig Development Co, Lincoln, UK) were purchased in groups of six at approximately 6 months of age. A straw-bedded pen (2.6 m × 4.1 m) was provided to house each group and they were fed 2.5 kg/day of a commercial diet providing 13 MJ DE/kg. The pens were cleaned as required and fresh bedding straw was provided twice each week.

A boar was introduced when the gilts were approximately 8 months of age and the gilts were served on two consecutive days. The day of expected parturition was calculated as 114 days after the first service date. Once pregnancy was confirmed (at around 32 days after service), the gilts were housed in their stable groups in a yard (9.6 m × 6 m) with straw, where they were floor-fed 2.5 kg/day of the same commercial diet. Once again, the pens were cleaned and straw for bedding was provided twice each week.

Catheterisation

All 34 gilts had a jugular catheter (silastic; internal diameter of 1.47 mm and external diameter of 1.93 mm; Osteotec Ltd, Christchurch, Dorset, UK) implanted under general anaesthesia at around 12 days before the expected day of parturition (for full details of the procedure see Lawrence *et al* 1992). Briefly, 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) until sampling began. After the operation, the gilts were housed in individual straw-bedded pens (2 m × 2 m). The same commercial feed (2.5 kg/day) was offered in two meals at 0800 h and 1600 h.

Experimental treatments

Five days before the expected day of parturition, gilts were transferred either to a conventional farrowing crate (2.25 m × 0.45 m and 1.05 m high) or to a pen (2.5 m × 3.0 m). The gilts in each of these two environment groups were then further sub-divided by substrate by either providing straw or not. This 2 × 2 factorial design provided the following number of animals in each treatment: crate without straw (C, n = 8), crate with straw (CS, n = 9), pen without straw (P, n = 9) and pen with straw (PS, n = 8).

The crate consisted of a solid floor with a slatted dunging area at the rear, while the pen had a solid floor that was

Table 1 Ethogram used to record gilt behaviour during the study period.

Gilt posture	
Standing	upright on all four legs
Sitting	front legs straight, back legs bent with hindquarters on floor ('dog-like')
Lying on belly (ventrally)	with neither shoulder touching the ground (udder not exposed)
Lying on side (laterally)	with one shoulder touching the ground (udder exposed)
Walking movement	'around' the pens or 'backwards and forwards' in crates
Substrate-directed (bars, floor or straw) and piglet-directed behaviour	
Rooting	forceful push with the snout
Pawing	a leg is raised and moved backwards or forwards directed at an object while gilt is stationary
Nosing	sniffing or gentle touch with the nose
Biting	or attempting to bite
No response	no response shown to any piglet that is in contact with, or very close to, the gilt's head
Other	where none of the above behaviours are occurring

sloped to allow drainage. The slatted areas of the crates and the pen floors were cleaned after the morning feed and straw was then provided in those experimental conditions that required it. Both the crate and the pen had a heated 'creep' area for piglets, outside the specified dimensions. The temperature of the farrowing rooms was controlled across both environments (mean [\pm standard error] crate temperature: minimum = $15.8^{\circ}\text{C} \pm 0.93$, maximum = $21.2^{\circ}\text{C} \pm 0.38$; pen temperature: minimum = $15.0^{\circ}\text{C} \pm 0.94$, maximum = $21.1^{\circ}\text{C} \pm 0.46$). Some natural lighting was provided and additional lighting was provided between 0800–1600 h. Dim lighting was used during the night to enable observation (1600–0800 h). The gilts were presented with 3 kg/day of a food that provided 13.75 MJ DE/kg and contained 18% protein in two meals at 0800 h and 1600 h. The food allowance was increased to appetite following parturition.

Behavioural observations

Continuous observations of gilt behaviour

Twenty-four hour time-lapse video equipment (Panasonic AG6124) was used to monitor the behaviour of the 34 gilts. Video cameras were permanently positioned above each pen or crate, and continuous recordings commenced on entry to the farrowing accommodation and continued until 2 days after parturition. From the videotapes a baseline observation period (1 h duration) was observed 2 days before parturition. Continuous behavioural observations were made from the birth of the first piglet (BFP) for 8 h. All data recorded via videotape were transferred using the Observer 3.0 behavioural recording program (Noldus Information Technology 1994). The ethogram described in Table 1 was used to record the frequencies/durations of the behaviours shown by the gilts.

Piglet information and progress of parturition

The length of gestation was calculated. For each piglet in the study, birth times were recorded as well as whether they were born alive, stillborn (fully formed but dead at birth) or

mummified. The mean piglet birth interval and duration of farrowing (time between the birth of the first and last piglet) were calculated.

Piglet location

Scans were undertaken at 10 min intervals throughout the 8 h observation period to record the location of each live piglet in the crate or pen. It was hoped that this would enable any potential relationship between the farrowing environment, the gilt's behaviour and the piglets' behaviour to be observed. Piglets were recorded as being in, or within at least one piglet body length of, the following locations: creep, head of the gilt (forward of the ears), inactive at the udder (lying still), active at the udder or elsewhere.

Blood sampling protocol

Following entrance to the farrowing house, blood samples were taken twice each day (1000 h and 1400 h) from the tap at the back of each gilt's neck. When the onset of nest-building was observed (increased activity and substrate-directed behaviour), a silastic extension tube was fitted to the tap so that samples (every 30 mins) could be taken from outside the pen or crate, thereby minimising disturbance. Approximately 2 h before the BFP, blood sampling frequency was increased to 10 min intervals. Once the first piglet was fully expelled by the gilt, sampling frequency increased to every 5 mins for the first hour, then dropped to every 10 mins in the second hour and then to every 15 mins until 4 h after the BFP. Samples were then taken every 30 mins until one hour after the placentas had been expelled. All blood samples were centrifuged at 3000 rpm for 20 mins at 4°C and were then stored in a -20°C freezer for future assay.

Radioimmunoassays

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 ng/l and the intra-assay and inter-assay coefficients of variation were 13.3% and 12.3% respectively.

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 minimum detectable level of the assay was 0.156 ng/ml and the intra-assay and inter-assay coefficients of variation were 8.9% and 15.6% respectively. Single samples were extracted and then assayed in duplicate.

Oxytocin

Oxytocin was extracted using Sep-Pak C-18 cartridges, and assayed in duplicate as previously described by Thornton *et al* (1986). Recoveries of standard synthetic oxytocin after extraction ranged between 85–96%. The minimum detectable level was 10.4 pg/ml and intra-assay and inter-assay coefficients of variation were 12.8% and 20.8% respectively.

Statistical analysis

Continuous observations of gilt behaviour

The behaviours recorded (see Table 1) were combined to give the following variables: duration of time spent i) standing and walking, ii) lateral and ventral (lying), iii) sitting, iv) performing all substrate-directed behaviour, v) performing all piglet-directed behaviour, and vi) performing 'no response' to piglets, and the frequency of i) posture changing and ii) nosing piglets. These variables were calculated for the 1 h baseline period and for each of the 8 h following the BFP.

To investigate effects of environment and substrate on these variables during the 1 h baseline period, data were analysed using ANOVAs (Genstat, Version 5). To determine the effects of environment (Env), substrate (Subs) and hour (Hour) during farrowing, data were analysed using repeated measures ANOVAs (Genstat, Version 5), with a randomisation test to check the significance level of the variance ratio.

Gilts were divided into non-savagers and savagers according to the incidence of biting at piglets. A chi-square analysis (χ^2) (Minitab 12.1) was carried out to determine whether savaging was affected by environment and by substrate separately. Since crated gilts tended to perform more savaging attempts, a more detailed analysis was carried out on the behaviour of the crated gilts. A Kruskal-Wallis test (Minitab 12.1) was employed to see if there was a significant difference in behaviour between non-savaging and savaging gilts in the first and third hours. These particular hours were chosen because savaging often occurs in the early stages of farrowing and because the sample as a whole showed increased activity in the first 2 h after the BFP, followed by increased inactivity and unresponsiveness from the third hour onwards.

Piglet information and progress of parturition

The number of live piglets was calculated as a percentage of the total number born, and environment and substrate effects were analysed using ANOVAs (Minitab 12.1). Gestation lengths, farrowing durations and piglet birth intervals were also calculated for each treatment and compared across environments and substrates using ANOVAs (Minitab 12.1).

Piglet location

The percentage of piglets recorded in each location was calculated for the 8 h of piglet scan data. The use of percentage data accounted for varying mean piglet birth intervals and therefore also accounted for differing numbers of piglets being present at any scan between gilts. The means of these percentages for the entire 8 h period were then compared using ANOVAs (Genstat, Version 5) to determine whether there were environment and/or substrate effects.

Hormone analysis

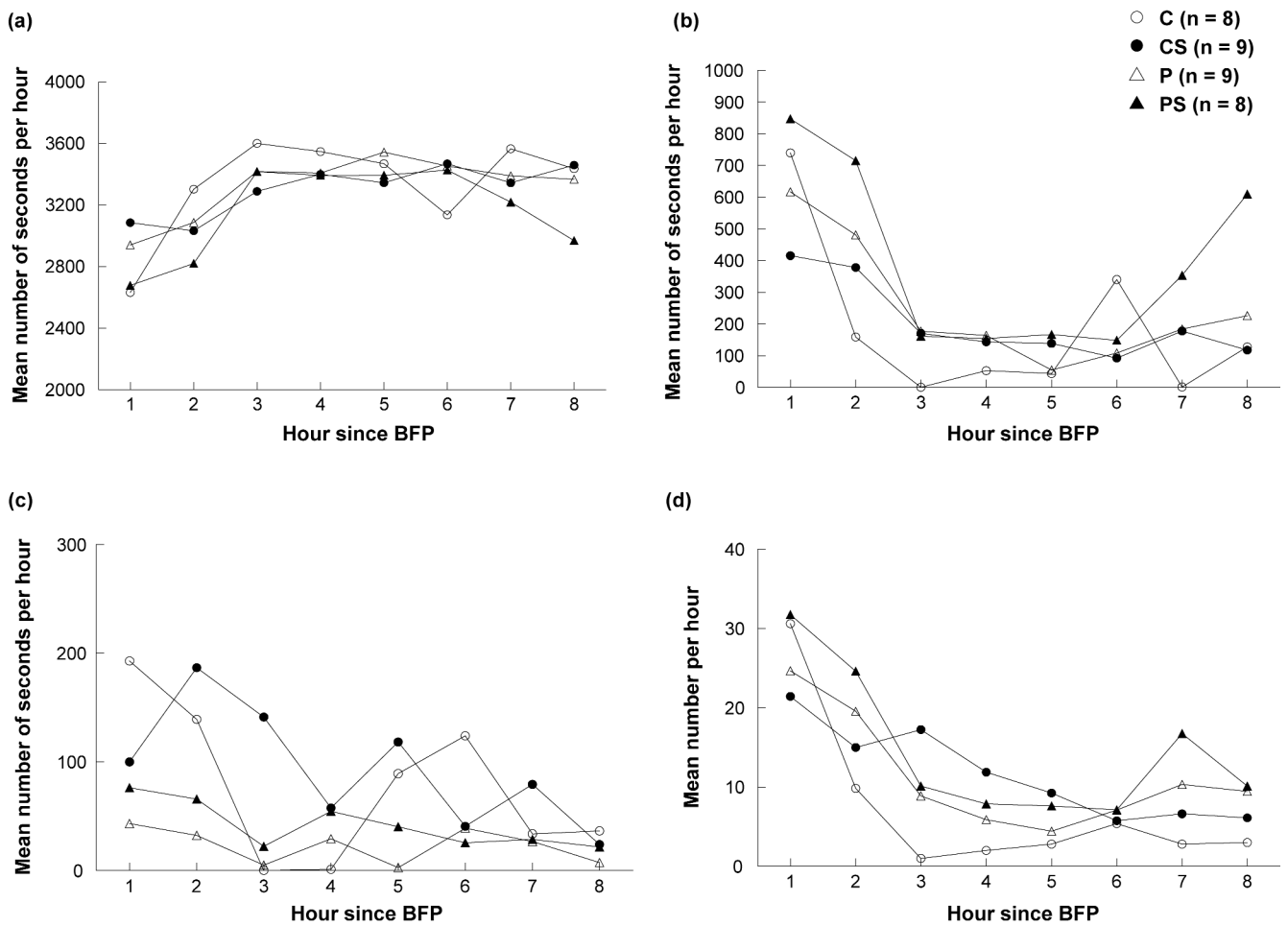
For cortisol and ACTH, a baseline value was calculated for each gilt from the mean of her 1000 h samples taken 3 and 4 days before farrowing. For oxytocin, the mean value of the samples taken during the 2 h prior to the BFP was used as a baseline; however, samples taken in the 5 mins before the BFP were excluded. The oxytocin baseline was taken closer to parturition because oxytocin does not increase until this time. There was a weak tendency for gilts without straw to have higher plasma oxytocin concentrations during the baseline period (Subs: $F_{1,25} = 2.78$; $P = 0.108$). Therefore, to account for this treatment difference, each gilt's baseline measure of each of the physiological variables was subtracted from its subsequent measures. The results following the BFP were then divided into three periods: Hour 1, Hour 2 and Hour 3-p (Hour 3, and all samples until the placentas were expelled). Data were checked for normality and log-transformed where required. Repeated measures ANOVAs (Genstat, Version 5) were used to investigate the effect of period (Hours 1, 2 and 3-p) and the effects of the environment and substrate within each of these periods on plasma cortisol, ACTH and oxytocin.

Relationships between variables

Variables were selected to investigate the relationships between the behavioural and physiological measures taken. A mean value for each gilt was calculated over the entire study period for each of the variables: inter-piglet birth interval; duration of sitting; duration of standing; frequency of posture changing; duration of substrate-directed behaviour; duration of piglet-directed behaviour; duration of not responding to piglets; cortisol; ACTH; and oxytocin. The data were checked for normality and log-transformed where required. A factor analysis was carried out using a correlation matrix and a varimax rotation (Minitab 12.1).

For all of the data presented, untransformed means are reported in the figures. Significance was taken as $P < 0.05$, although some tendencies are also reported.

Figure 1



Mean number of seconds per hour spent a) lying, b) standing/walking and c) sitting, and d) the mean number of posture changes made per hour by gilts.

Results

Continuous observations of gilt behaviour

Gilts housed in different environments and with differing substrate availability did not differ in any of the behavioural variables during the 1 h baseline period. Therefore, baseline was not accounted for in the subsequent analysis of the behavioural variables during the 8 h after the BFP. The following sections present the results of the data collected during the 8 h period after the BFP.

Posture

Across environments and substrates for all postures there was a significant effect of hour: lying was lowest in the first 2 h after the BFP (Hour: $F_{7,184} = 4.56$; $P < 0.001$; Figure 1a), while standing/walking (Hour: $F_{7,184} = 4.80$; $P < 0.001$; Figure 1b), sitting (Hour: $F_{7,184} = 1.82$; $P < 0.085$; Figure 1c) and the frequency of posture changing (Hour: $F_{7,184} = 7.27$; $P < 0.001$; Figure 1d) were highest in the first 2 h.

In terms of the effects of environment on posture, penned gilts spent more time standing/walking in the first 2 h after the BFP than did crated gilts, following which, gilts in both

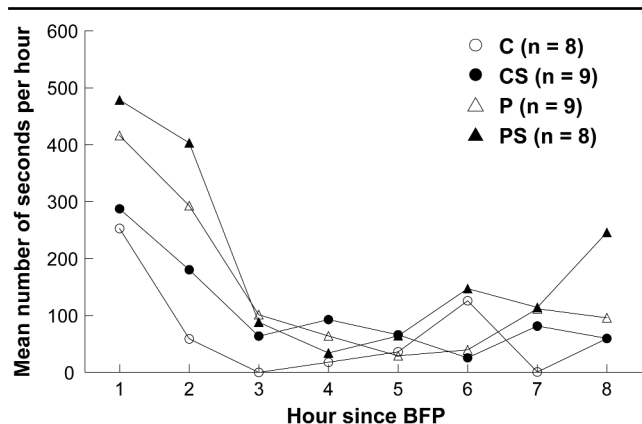
environments performed similar levels of this behaviour as parturition progressed (Hour*Env: $F_{7,184} = 2.14$; $P < 0.05$; Figure 1b). It was also found that crated gilts spent significantly more time sitting across the entire 8 h observation period than did penned gilts (Env: $F_{1,30} = 6.94$; $P < 0.05$; Figure 1c). No effects of substrate were found on any of the postural behaviours.

Substrate-directed and piglet-directed behaviour

The duration of time that the gilts spent performing substrate-directed behaviour was greatest in the first 2 h of the study period for all treatments (Hour: $F_{7,184} = 7.15$; $P < 0.001$; Figure 2), but was particularly increased during the first 2 h in the penned compared to the crated gilts (Env: $F_{7,184} = 2.28$; $P < 0.05$; Figure 2).

The penned gilts spent more time performing piglet-directed behaviour compared to the crated gilts (Env: $F_{1,30} = 8.00$; $P < 0.01$; Figure 3a), with the highest levels occurring within the first and second hours after the onset of parturition (Hour*Env: $F_{7,184} = 2.55$; $P < 0.05$; Figure 3a). A similar result was found for the frequency of nosing piglets: the penned gilts performed more nosing of piglets than did

Figure 2



Mean number of seconds per hour spent directing behaviour towards all substrates.

those in the crates (Env: $F_{1,30} = 6.94$; $P < 0.05$; Figure 3b), with most instances of nosing tending to occur in the first 2 h (Hour*Env: $F_{7,184} = 2.86$; $P = 0.07$; Figure 3b). Gilts housed in pens spent more time performing 'no response' to piglets that approached their heads than did those housed in crates (Env: $F_{1,30} = 11.35$; $P < 0.01$; Figure 3c); however, this tended to be later in the expulsive phase, particularly in hours 2–5 (Hour*Env: $F_{7,184} = 1.85$; $P = 0.081$; Figure 3c).

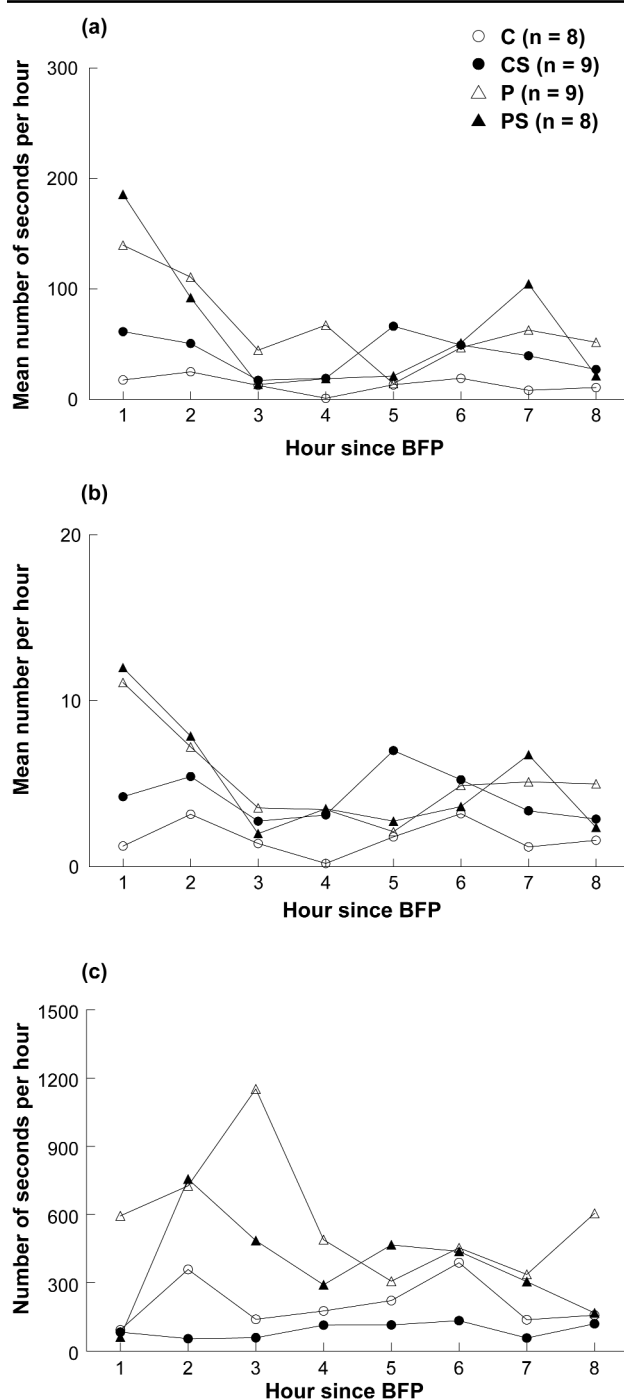
Savaging of piglets by gilts

There was a strong tendency for a greater than expected number of the gilts housed in crates to savage their piglets compared to those housed in pens ($\chi^2 = 3.78$; $df = 1$; $P = 0.052$). Of the 17 gilts in crates, seven (four in crates with straw and three in crates without straw) were savagers. Of the gilts in crates, those that exhibited savaging behaviour were more restless in the first and third hour of farrowing, compared to non-savaging gilts. The savagers spent significantly less time lying laterally (Hour 1: $H = 7.48$; $df = 1$; $P < 0.01$, Hour 3: $H = 9.59$; $df = 1$; $P < 0.01$), more time standing/walking (Hour 1: $H = 6.10$; $df = 1$; $P < 0.02$, Hour 3: $H = 6.14$; $df = 1$; $P < 0.02$), more time sitting (Hour 1: $H = 2.15$; $df = 1$; $P = 0.14$, Hour 3: $H = 9.59$; $df = 1$; $P < 0.01$), and performed a higher frequency of posture changes (Hour 1: $H = 5.99$; $df = 1$; $P < 0.02$, Hour 3: $H = 9.59$; $df = 1$; $P < 0.01$) than non-savagers. Savagers also performed more substrate-directed behaviour (Hour 1: $H = 3.44$; $df = 1$; $P = 0.064$, Hour 3: $H = 9.59$; $df = 1$; $P < 0.01$) and floor-directed behaviour (Hour 1: $H = 4.63$; $df = 1$; $P < 0.05$, Hour 3: $H = 9.59$; $df = 1$; $P < 0.01$), and in the first hour tended to spend less time not responding to piglets than did non-savagers (Hour 1: $H = 3.31$; $df = 1$; $P = 0.069$), indicating increased responsiveness to piglet approaches.

Piglet information and efficiency of farrowing

There was no effect of environment or substrate on the number of live-born piglets (number born alive [mean \pm standard error] = C: 12.0 ± 0.7 ; CS: 10.3 ± 1.0 ;

Figure 3



a) Mean number of seconds per hour spent directing behaviour towards piglets. b) Mean number of noses per hour towards piglets. c) Mean number of seconds per hour spent 'not responding' to piglets.

P: 11.8 ± 0.9 ; PS: 10.8 ± 1.4) or on the percentage of piglets born alive. Similarly, the length of gestation was not affected by space or straw availability (mean gestation length [days] = C: 113.9 ± 0.3 ; CS: 114.7 ± 0.5 ; P: 114.4 ± 0.5 ; PS: 114.0 ± 0.46). Environment (pen or crate) had no effect upon the duration of farrowing; however, gilts provided with straw experienced significantly

Table 2 Factor analysis loadings and the percentage of variation in the dataset explained. Bold numbers indicate a loading of more than ± 0.5 .

Variable	Factor 1 loadings	Factor 2 loadings
Inter-piglet birth interval	0.146	-0.654
Duration of sitting	0.685	-0.290
Duration of standing	0.909	0.089
Frequency of posture changing	0.962	-0.039
Duration of substrate-directed behaviour	0.934	-0.057
Duration of piglet-directed behaviour	0.539	0.394
Duration of not responding to piglets	-0.150	0.768
Cortisol	0.079	-0.061
ACTH	0.187	-0.052
Oxytocin	0.094	0.839
Variation explained (%)	34.7	19.8

longer farrowings than did those without (mean duration of farrowing [mins] = C: 174 ± 40 ; CS: 257 ± 44 ; P: 146 ± 15 ; PS: 207 ± 31 ; $F_{1,33} = 4.82$; $P < 0.05$). This resulted in a greater mean piglet birth interval in the 'with straw' treatments (Subs: $F_{1,33} = 8.83$; $P < 0.01$; Figure 4).

Piglet location

Over the 8 h observation period, piglets in the pen environment spent a significantly greater amount of time around the head of the gilt compared to those in the crate environment (Env: $F_{1,30} = 19.49$; $P < 0.001$). Piglets whose mothers had farrowed with straw in their surroundings spent significantly less time inactive at the gilt's udder (Subs: $F_{1,30} = 8.68$; $P < 0.01$). There was no significant effect of substrate or environment on the amount of time that piglets spent in the creep area, were active at the udder of the gilt, or on the incidence of piglets being recorded 'elsewhere' in the pen or crate.

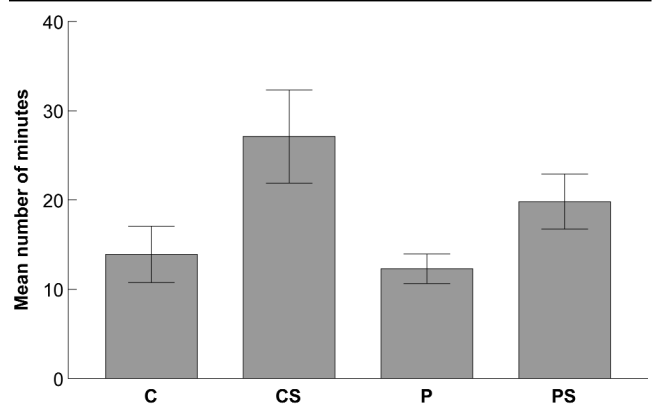
Hormonal analysis

ACTH

Overall, there was a tendency for ACTH concentrations to be lower in the first hour after the BFP compared to the other two periods (Period: $F_{2,64} = 3.06$; $P = 0.054$; Figure 5a). In this first hour, plasma ACTH concentrations were not affected by the environment or by the availability of straw (Figure 5a). During the second hour, however, both substrate (Subs: $F_{1,29} = 4.96$; $P < 0.05$; Figure 5a) and environment (Env: $F_{1,29} = 7.10$; $P < 0.05$; Figure 5a) affected plasma ACTH concentrations, with gilts in crates and those without straw having elevated levels. There was also a tendency for an interaction between environment and substrate, with C gilts having higher levels of plasma ACTH than gilts from the other three treatments (Env*Subs: $F_{1,29} = 3.25$; $P = 0.082$; Figure 5a). These differences had disappeared by Hour 3-p, mainly because of an increase in ACTH concentrations in PS gilts.

Cortisol

Plasma cortisol concentrations were highest during the second hour (Period: $F_{2,64} = 7.26$; $P = 0.001$; Figure 5b), but

Figure 4

The mean number of minutes between live-born piglets born to gilts in the four treatments.

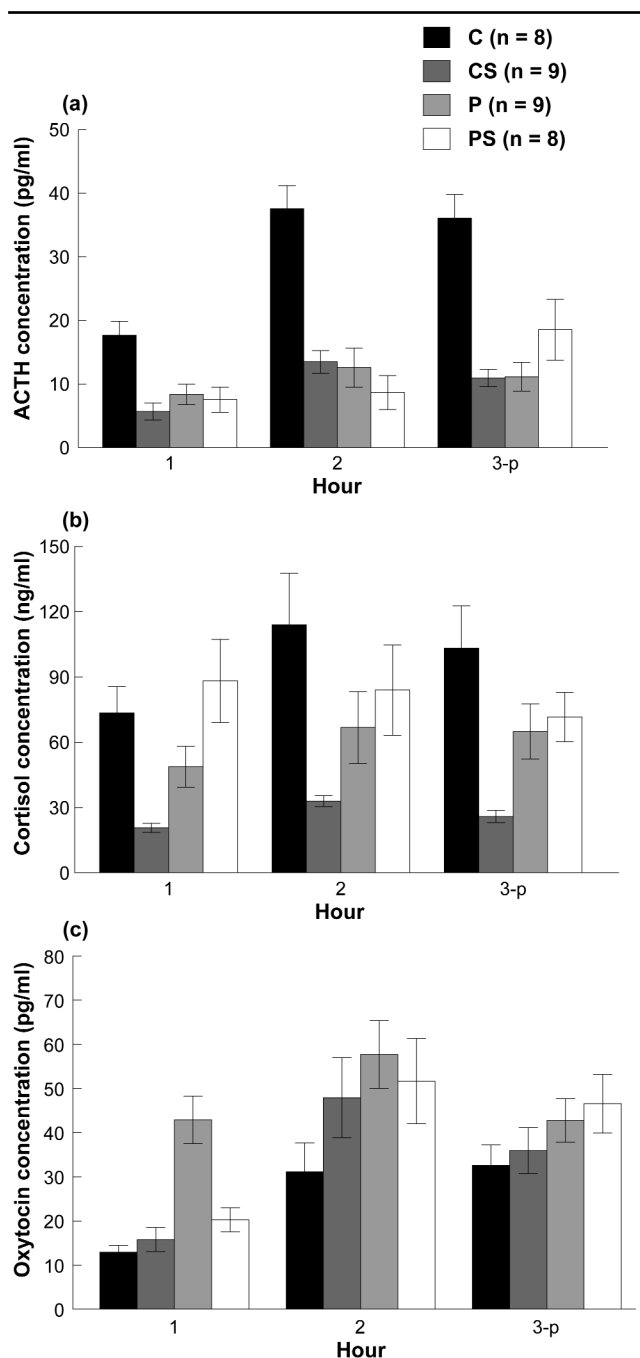
were unaffected by environment or substrate during Hours 1, 2 or 3-p.

Oxytocin

Plasma oxytocin concentrations were not affected by environment or by substrate during any of the three farrowing periods (Figure 5c). However, concentrations of oxytocin did increase across the three periods (Period: $F_{2,54} = 7.18$; $P < 0.05$).

Relationships between variables

Factor 1 (see Table 2) explained 34.7% of the variation in the dataset analysed and suggested that gilts that performed a lot of standing, sitting and posture changing also spent a lot of time directing behaviour towards their piglets and towards substrates. This indicated that pigs that were more restless over the entire period were less likely to show passivity. Factor 2 (see Table 2), which explained 19.8% of the variation, indicated that gilts that had a faster delivery (ie shorter inter-piglet birth intervals) had higher levels of plasma oxytocin and were less responsive to their piglets (ie they were more passive).

Figure 5

Mean (\pm standard error) plasma concentrations of a) ACTH, b) cortisol and c) oxytocin during parturition (pre-parturition baseline values have been removed).

Discussion

The environment in which gilts were housed in the days just prior to farrowing, and for the farrowing period itself, was found to have an effect upon their behaviour during the expulsive phase of parturition. While across all treatments there was a higher level of posture changing, substrate-directed behaviour and investigation of piglets in the first 2 h of the farrowing period, it was very clear that the availability of space, rather than of straw, facilitated these behaviours.

Thus, penned gilts performed more standing and walking, substrate-directed behaviour and piglet-directed behaviour in the first 2 h following the onset of parturition. In addition, gilts housed in pens, following the initial period of piglet investigation, became less responsive towards their piglets.

This temporal profile of activity and investigatory behaviour followed by inactivity and passivity has been observed in free-ranging and loose-housed sows during parturition (Watson & Bertram 1983; Jensen 1986; Petersen *et al* 1990; Jarvis *et al* 1999), as well as in crated sows (Jones 1966; Randall 1972; Fraser *et al* 1997). Indeed, the first factor of our principal components analysis demonstrates that in our study responsiveness was positively related to activity. This maternal strategy is somewhat unusual but has been suggested to be of adaptive relevance because lying inactive allows the piglets full access to the udder for warmth and nutrition during their very early life (Fraser 1984; Jarvis *et al* 1999). The transition from an active period to an inactive period was not as distinct in the crated gilts in this study. Although we found a general decrease in substrate-directed behaviour following the first 2 h after the BFP in the crated gilts, they performed fairly consistent levels of piglet-directed behaviour across the entire 8 h. In addition, we found that they spent significantly longer in a sitting posture and this also remained at a consistent level across the expulsive phase. Higher levels of sitting have been found in pre-parturient nesting gilts housed in crates (Cronin *et al* 1993; Jarvis *et al* 1997), and we now have evidence that this increased sitting persists into the expulsive phase of parturition and is further increased in savaging gilts. This sitting behaviour has been suggested to reflect motivational conflict during the nesting period (Jarvis *et al* 1999) because the gilt is motivated to nest-build but the behaviour is thwarted because of environmental restriction. It may be that the gilts in this study, during the expulsive phase of parturition, were also experiencing motivational conflict in that during the early stages there may have been a strong motivation to interact with and investigate piglets, which was thwarted by their inability to make contact.

It is possible that the effects of space restriction observed in this study are a result of a 'carry over' effect from the pre-parturient period when nest-building behaviour is performed. There is evidence that nesting behaviour is thwarted in farrowing crates, and that this results in increased physiological stress (Lawrence *et al* 1994; Jarvis *et al* 1997, 2002). In addition, it has been shown that the provision of various substrates for nesting in large pens can affect the maternal behaviour of sows (Thodberg *et al* 1999; Damm *et al* 2000). A cross-over study between environments in the pre-parturient and parturient periods would be required to investigate this.

The increased ability of gilts in pens to interact with their piglets, resulted in these piglets spending significantly more time around the head of the sow than did the piglets in crates. In crated gilts there was a tendency to show more abnormal maternal responses (eg biting) to piglets approaching their heads. This might have been due to the thwarting of nest-building, to the gilt's frustration at being unable to interact with piglets as she would like, or perhaps

to an initial inability to associate the process of farrowing with the piglets in her environment, of which she had no prior experience. Interestingly it was found that, of the gilts in the crates, those that were classified as savagers were more active, performed more substrate-directed behaviour and were more responsive to their piglets in the first hour after the BFP. Although this pattern in savaging gilts might appear to be similar to that of the penned gilts during this time period, we found that savaging gilts continued to be restless throughout the expulsive period, as has been found in other work (Harris *et al* 2001; Ahlstrom *et al* 2002).

The provision of straw to gilts in pens and crates in this study had very little effect on the gilts' behaviour during parturition. Surprisingly, this is also true of pre-parturient nest-building gilts: straw is the preferred substrate if available, but its presence does not increase substrate-directed behaviour or alter postural changes either in a pen or a crate (Jarvis *et al* 2002). As gilt lying was unaffected by the presence of straw in the present study, straw might not necessarily function to increase the sow's comfort when giving birth, but may instead have some other function. Straw in the farrowing environment did alter piglet behaviour, in that piglets without access to straw spent more time inactive at the gilt's udder. Therefore, it could be that a straw-like substrate has important thermoregulatory properties for piglets.

It has been previously indicated that extended farrowing durations can increase the risk of piglets being born dead (particularly for those born later in the farrowing) (Beynon 1990; Fraser *et al* 1997; Gordon 1997). The present study found that even though farrowing was extended by the provision of straw, the difference was not great enough to affect the percentage of piglets born alive. This suggests that the parturition environment can affect the length of farrowing but will not necessarily affect piglet mortality during parturition.

It is unclear why the presence of straw lengthens parturition. Previous work has found that the provision of additional manipulable substrates during the nesting and expulsive periods of parturition leads to increased substrate-directed behaviour during the expulsive period (Thodberg *et al* 1999; Damm *et al* 2000). However, we do not think that parturition was slower in the gilts that we provided with straw as a result of continued nesting behaviour during expulsion, because we did not find any effect of straw on substrate-directed behaviour. Straw, as well as providing warmth for piglets, may provide warmth for the sow. However, it is unlikely that any temperature differences between gilts with and without straw could account for differences in the length of parturition because previous work has shown that ambient temperature does not affect inter-piglet birth intervals (Biensen *et al* 1996). Another possible explanation for the extended farrowing durations of gilts with straw is the alteration in the behaviour of the piglets. We found that in the 'no straw' treatments, piglets spent a greater amount of time at the udder. Stimulation of the udder leads to the release of oxytocin from the posterior pituitary, which, by increasing uterine contractions (Taverne

1992), may lead to reduced inter-birth intervals. However, although we found a relationship between plasma oxytocin and inter-birth interval across all gilts, we did not find an effect of straw on circulating levels of plasma oxytocin.

The factor analysis showed there to be a relationship between increased plasma oxytocin, a faster delivery rate (ie shorter inter-birth intervals) and increased passivity (not responding to piglets). One might have expected higher plasma oxytocin levels to be related to faster delivery because of the influence of oxytocin on uterine muscle contractions (see above), however, the relationship between plasma oxytocin and passivity is a novel finding. Central oxytocin is known to be important in the control of maternal behaviour in rodents (rats: Pedersen *et al* 1982; Fahrback *et al* 1985), and by demonstrating a relationship in the pig between plasma oxytocin and maternal behaviour we suggest that there may be some relationship between central oxytocin and the control of maternal behaviour in the pig. Also, the relationship shown between plasma oxytocin and passivity further strengthens the suggestion made by some researchers (Fraser 1984; Jarvis *et al* 1999) that passivity is an important component of good maternal behaviour in the pig.

Significantly higher ACTH levels were found in the second hour of farrowing in gilts housed in crates without straw (C), compared to gilts in the other three treatments. This difference was not found for plasma cortisol, which may be due to differences in the clearance rate of ACTH or to alteration in ACTH receptor binding in the adrenal cortex. Exercise or physical activity is known to activate the HPA axis (Petrides *et al* 1994), however, this cannot explain the elevated levels of plasma ACTH in the C gilts because we have evidence that they were actually less active than, for example, the penned gilts. Instead, we suggest that the elevated levels of plasma ACTH during the second hour of parturition in the C gilts may be a result of the thwarting of interactions with piglets. We know from this study and many others that investigation of piglets occurs predominantly in the early stages of farrowing, however, we found that crated gilts spent significantly less time interacting with their piglets than did penned pigs. It was the C gilts specifically that had higher levels of plasma ACTH, and we suggest that the thwarting of piglet interactions by being in a crate is further accentuated in the gilts in this treatment as a result of the alteration of piglet behaviour when straw is not present: piglets were observed to spend more time at the udder when straw was unavailable and so reduced the opportunity for the gilt to interact with them. It may also be important to consider the role that thwarted mother-offspring interaction plays in the occurrence of subsequent abnormal maternal responses, such as the savaging of piglets by crated gilts.

In conclusion, we have found that the provision of space, irrespective of straw availability, allows gilts to perform maternal behaviour that is more similar to that reported in free-ranging sows. The provision of straw did lengthen the parturition process, but was not reflected in circulating oxytocin levels and did not have detrimental effects upon

piglet survival. In addition, we suggest that the provision of straw during the expulsive phase may provide a better thermal environment for piglets and subsequently facilitate mother–offspring interactions through encouraging piglet locomotion.

Animal welfare implications

We have shown here that the provision of space, rather than of straw, facilitates the performance of maternal behaviour that more closely resembles that reported in free-ranging sows: a more active period involving interactions with piglets, followed by a more inactive and passive period. The restrictive nature of the farrowing crate appears to increase the likelihood that a gilt will savage her piglets. Savaging gilts showed increased restlessness, which did not give way to inactivity as is seen in free-ranging and penned gilts. Overall, these findings suggest that space restriction, rather than a lack of straw, is detrimental to the performance of maternal behaviour in the pig, with potential consequences for sow and piglet welfare.

Acknowledgements

The authors would like to thank Jenny Ogg, Jacqui Mann and Robert Kendal for technical assistance; Peter Finnie and Philip O'Neil for their assistance with the care of the animals; Dave Allcroft for statistical advice; Ian Swanston for assistance with radioimmunoassays; James Mylne, Jon Hunton, Bill McKelvey and Eddie Clutton for carrying out the surgical procedures and anaesthesia; and Dr Rick D'Eath for commenting on the manuscript. This work was funded by the Ministry of Agriculture, Fisheries and Food and by the Meat and Livestock Commission. The Scottish Agricultural College also receives funding from the Scottish Executive Environment, Rural Affairs Department.

References

Ahlstrom S, Jarvis S and Lawrence A B 2002 Savaging gilts are more restless and more responsive to piglets during the expulsive phase of parturition. *Applied Animal Behaviour Science* 76: 83-91

Algers B, Rojanasthiens S and Uvnas-Moberg K 1990 The relationship between teat stimulation, oxytocin release and grunting rate in the sow during nursing. *Applied Animal Behaviour Science* 26: 267-276

Arey D S 1997 Behavioural observations of peri-parturient sows and the development of alternative farrowing accommodation: a review. *Animal Welfare* 6: 217-229

Baxter S H 1974 Intensive housing and its effects on farm animals. *South African Journal of Animal Science* 4: 259-264

Beynon N 1990 *Pigs — A Guide to Management*. The Crowood Press: Wiltshire, UK

Biensen N J, von Borell E H and Ford S P 1996 Effects of space allocation and temperature on periparturient maternal behaviours, steroid concentrations, and piglet growth rates. *Journal of Animal Science* 74: 2641-2648

Blackshaw J K, Blackshaw A W, Thomas F J and Newman F W 1994 Comparison of behaviour patterns of sows and litters in a farrowing crate and a farrowing pen. *Applied Animal Behaviour Science* 39: 281-295

Blackshaw J and Hagelso A M 1990 Getting-up and lying down behaviours of loose-housed sows and social contacts between sows and piglets during day 1 and day 8 after parturition. *Applied Animal Behaviour Science* 25: 61-79

Brent G 1986 *Housing the Pig*. Farming Press Ltd: Ipswich, UK

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

Cronin G M, Schirmer T H, McCallum T H, Smith J A and Butler K L 1993 The effects of providing sawdust to preparturient 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, Simpson J and Hemsworth P H 1996 The effects of the gestation and farrowing environments on sow and piglet behaviour and piglet survival and growth in early lactation. *Applied Animal Behaviour Science* 46: 175-192

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

English P, Smith W and MacLean A 1977 *The Sow — Improving Her Efficiency*. Farming Press Ltd: Ipswich, UK

Fahrbach S E, Morrell J I and Pfaff D W 1985 Possible role for endogenous oxytocin in estrogen-facilitated maternal behaviour in rats. *Neuroendocrinology* 40: 526-532

Fraser A F and Broom D M 1990 *Farm Animal Behaviour and Welfare*, 3rd Edition. Bailliere Tindall: London, UK

Fraser D 1984 The role of behaviour in swine production: a review of research. *Applied Animal Ethology* 11: 317-339

Fraser D, Phillips P A and Thompson B K 1997 Farrowing behaviour and stillbirth in two environments: an evaluation of the restraint–stillbirth hypothesis. *Applied Animal Behaviour Science* 55: 51-66

Gordon I 1997 *Controlled Reproduction in Pigs*. CAB International: Wallingford, UK

Harris M J, Bergeron R and Gonyou H W 2001 Parturient behaviour and offspring-directed aggression in farmed wild boar of three genetic lines. *Applied Animal Behaviour Science* 74: 153-163

Harrison R 1964 *Animal Machines*. Vincent Stuart: London, UK

Jarvis S, Calvert S K, Stevenson J, van Leeuwen N and Lawrence A B 2002 Pituitary–adrenal activation in pre-parturient pigs (*Sus scrofa*) is associated with behavioural restriction due to lack of space rather than nesting substrate. *Animal Welfare* 11: 371-384

Jarvis S, Lawrence A B, McLean K, Chirnside J, Deans L A and Calvert S K 1998 The effects of environment on plasma cortisol and beta-endorphin in the parturient pig and the involvement of endogenous opioids. *Animal Reproduction Science* 52: 139-151

Jarvis S, Lawrence A B, McLean K A, Deans L A, Chirnside J and Calvert S K 1997 The effect of farrowing environment on behavioural activity, ACTH, beta-endorphin and cortisol in pre-farrowing 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

Jensen P 1986 Observations on the maternal behaviour of free-ranging domestic pigs. *Applied Animal Behaviour Science* 16: 131-142

Jones J E T 1966 Observations on parturition in the sow. Part II: The parturient and post-parturient phases. *British Veterinary Journal* 122: 471-478

Lawrence A B, Petherick J C, McLean K, Deans L, Chirnside J, Vaughan A, Clutton E and Terlouw E M 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, Gilbert C, Chapman C and Russell J A 1992 Naloxone prevents interruption of parturition and increases plasma oxytocin following environmental disturbance in parturient sows. *Physiology and Behavior* 52: 917-923

MLC 2000 *Pig Yearbook* 1999. Meat and Livestock Commission: Milton Keynes, UK

Pedersen C A, Ascher J A, Monroe Y L and Prange A J 1982 Oxytocin induces maternal behaviour in virgin female rats. *Science* 216: 648-650

Petersen V, Recen B and Vestergaard K 1990 Behaviour of sows and piglets during farrowing under free-range conditions. *Applied Animal Behaviour Science* 26: 169-179

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

Randall G C B 1972 Observations on parturition in the sow I: Factors associated with the delivery of the piglets and their subsequent behaviour. *Veterinary Record* 90: 178-182

Taverne M A M 1992 Physiology of parturition. *Animal Reproduction Science* 28: 433-440

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

Thornton S N, Leng G, Bicknell R J, Chapman C and Purdew T 1986 Vasopressin, but not oxytocin is released in response to water deprivation in conscious goats. *Journal of Endocrinology* 110: 335-340

Weary D M, Pajor E A, Fraser D and Honkanen A M 1996 Sow body movements that crush piglets: a comparison between two types of farrowing accommodation. *Applied Animal Behaviour Science* 49: 149-158

Watson T S and Bertram J M 1983 Some observations on mother-infant interactions in the pig (*Sus scrofa*). *Applied Animal Ethology* 9: 253-261

Whittemore C 1980 *Pig Production — The Scientific and Practical Principles*. Longman Group Ltd: London, UK