Open Access
Asian Australas. J. Anim. Sci.
Vol. 28, No. 11 : 1519-1524 November 2015
http://dx.doi.org/10.5713/ajas.15.0174
www.ajas.info
pISSN 1011-2367 eISSN 1976-5517

Benefits of Prepartum Nest-building Behaviour on Parturition and Lactation in Sows — A Review

Jinhyeon Yun* and Anna Valros
Research Centre for Animal Welfare, Department of Production Animal Medicine,
Faculty of Veterinary Medicine, University of Helsinki, Helsinki 00014, Finland

ABSTRACT: It is well known that prepartum sows have an innate motivation to build a nest before parturition. Under commercial conditions, however, the farrowing crate, which is widely used in modern pig husbandry, inhibits this innate behaviour through the lack of space, materials, or both. Thus, restriction of nest-building behaviour could generate increased stress, resulting in a decrease in maternal endogenous hormones. Hence, it could lead to detrimental effects on farrowing and lactating performance. Here we review interactions between prepartum nest-building behaviour, stress and maternal endogenous hormone levels, and discuss their effects on parturition, lactation, and welfare of sows and offspring. (**Key Words:** Farrowing Environment, Nest-building, Pig Welfare, Maternal Behaviour, Farrowing Duration, Stillbirths)

INTRODUCTION

Prepartum sows exhibit natural patterns of nest-building (NB) behaviour, including rooting, pawing, and searching for suitable NB materials, all of which are expressions of the desire to build a farrowing and lactating nest to protect their offspring against predators and cold (Widowski and Curtis, 1990; Wischner et al., 2009). Although potential risk factors such as predators, nutrient deficiency, and rapid heat loss seem no longer to be of concern in modern pig husbandry, a number of studies have revealed that sows perform NB behaviour even when crated in conventional farrowing crates with no possibility to build a nest (Jensen, 1993; Lawrence et al., 1994; Yun et al., 2014a), or even where a completed nest was already provided (Arey et al., 1991). Moreover, Gustafsson et al. (1999) found that frequency and forms of NB behaviour of domesticated sows were similar to those of wild type sows.

NB behaviour is initiated by endogenous hormonal reactions (Widowski and Curtis, 1990; Castrén et al., 1993; Algers and Uvnas-Moberg, 2007), and activated by exogenous environmental factors until completion of the nest (Jensen, 1993; Algers and Uvnas-Moberg, 2007; Chaloupkova et al., 2011). In modern pig husbandry, however, due to lack of space, nesting materials, or both, there is little possibility to perform these natural activities, resulting in an increase in stress levels in sows (Lawrence et al., 1994; Jarvis et al., 1997; Lawrence et al., 1997; Jarvis et al., 2001). As a result, detrimental effects of inhibiting the expression of prepartum NB behaviour on parturition, lactation, and welfare in sows have been reported in numerous studies. This review, therefore, investigated interactions of prepartum maternal behaviour, physiological stress, and lactating endocrinology, and their effects on parturition and lactation performance of sows.

ENVIRONMENTAL FACTORS AFFECTING NEST-BUILDING BEHAVIOUR

In nature, sows leave the herd and move up to almost 6.5 km a day prior to parturition to find a place to build a nest (Jensen, 1986). Typically the sows excavate the ground using their forelegs and snouts, and collect nesting materials around the pits. The radius of the nest varies depending on

* Corresponding Author: Jinhyeon Yun. Tel: +358-50-3112550, Fax: +358-9191-57300, E-mail: jinhyeon.yun@helsinki.fi
Submitted Feb. 27, 2015; Revised Apr. 16, 2015; Accepted Apr. 25, 2015

the age of the sow (Jensen, 1989; Mayer et al., 2002) and the proximal environment (Mayer et al., 2002). As long as the neonatal piglets stay close to the sow within the nest, they are able to thermoregulate and occupy space for suckling milk properly (Wischner et al., 2009). The nest also offers a hiding place for the piglets against potential predators (Wischner et al., 2009).

Farrowing crates have been widely used in modern pig husbandry, mainly to reduce piglet mortality rate due to crushing. Weber et al. (2007) and Pedersen et al. (2011); however, showed that the farrowing crate can reduce piglet losses due to crushing, but increase deaths due to other causes, and thus the crate system makes no contribution to reducing total piglet losses compared with non-crated systems. The farrowing crate, mainly due to lack of space, disturbs choice of a nest site and performance of natural prepartum activities of sows. Thus, sows in crates necessarily farrow without the possibility to build a nest, resulting in an increase in stress levels and welfare issues. Sows housed in farrowing crates showed more active standing and lying down (Hansen and Curtis, 1980; Heckt et al., 1988), and performed more NB-like behaviour, interacting with the steel bar and concrete floor, compared with sows housed in pens (Lawrence et al., 1997; Damm et al., 2003). In contrast, sows in pens performed more NB behaviour, including pawing, rooting and arranging, than did crated sows.

Jarvis et al. (2002) found no effects of providing nesting materials, such as straw, in the farrowing crates on stress reaction induced by the inhibition of the desire for NB behaviour in prepartum gilts. However, higher frequency of NB behaviour was associated with sows housed in pens provided with straw than in pens without straw (Burne et al., 2000). Irrespective of the provision of straw, providing space per se in gilts could encourage the performance of NB behaviour during parturition (Jarvis et al., 2004). In addition, Yun et al. (2014a) reported more vigorous and intensive NB behaviour in sows housed in an opened crate and provided with abundant nesting materials, compared with sows housed in a closed crate or in an open crate, but with only minimal nesting materials. Consequently, this could indicate that the provision of nesting materials can increase the expression of prepartum NB behaviour, even in addition to the effect of increased space allowance. However, freedom of movement in prepartum sows is also important for the motivation of NB behaviour when not having access to nesting materials.

DETRIMENTAL EFFECTS OF RESTRICTING NEST-BUILDING ON PREPARTUM SOWS

Sows housed in crates showed NB-like behaviour, such as rooting and biting at steel bars, and frequently changed their body positions, which is known to be associated with inability to express NB behaviour. Due to frequent contact with the ground, this can provoke an increase in skin damage. In addition, sows in the farrowing crate had greater difficulties in lying down during the first day, and this damaging motion, i.e., pressure and sliding, was related to higher frequency of limb lesions (Boyle et al., 2002).

Inhibiting the expression of prepartum NB behaviour in crated sows has been shown to lead to increased plasma cortisol and ACTH concentrations (Lawrence et al., 1997; Jarvis et al., 2002) and heart rates in. In addition, continued confinement resulted in an increased opioid receptor density in sows (Zanella et al., 1996). Endogenous opioids were reported to be negatively correlated with oxytocin (Bicknell and Leng, 1982; Douglas et al., 1995), and might thus influence parturition (Oliviero et al., 2008), or early lactation performance (Yun et al., 2013). In addition, it has also been shown that the aversive psychological state and stress induced by the interference of prepartum NB behaviour can result in an increase in stereotypic bar-biting (Jensen, 1988; Lawrence et al., 1997; Yun et al., 2015). Incidence of bar-biting behaviour in crated sows can also be considered to be redirected NB behaviour to cope with unfavourable farrowing environments (Lawrence et al., 1994; Lawrence et al., 1997). Considering all the results of crating sows during the periparturient period, i.e., an increase in physiological injuries and stereotypic behaviour, as well as an increased stress reaction (Jarvis et al., 2001), it can be assumed that the thwarting of natural behaviour during the prepartum period results in impaired welfare of sows.

INTERRELATIONS BETWEEN NEST-BUILDING BEHAVIOUR AND ENDOGENOUS MATERNAL HORMONES

A rise in plasma concentrations of prolactin is known to initiate NB behaviour in prepartum sows (Widowski and Curtis, 1990; Castrén et al., 1993; Algers and Uvnas-Moberg, 2007), while the onset of prepartum NB behaviour has not been directly related to plasma oxytocin concentrations in the sow (Boulton et al., 1997; Gilbert et al., 2002). In contrast, several studies have suggested that prolactin concentrations in prepartum sows might not be correlated with the degree of NB behaviour (Lawrence et al., 1994), and played only a limited role in preparturient activity of sows (Rushen et al., 2001). Yun et al. (2014a) also suggested that prolactin concentrations might be correlated with oxytocin concentrations, rather than with performance of NB behaviour per se. However, this finding does not preclude the preliminary works (e.g., Wischner et al., 2009) showing that a rise in prolactin concentrations could affect motivation for NB behaviour in sows.

Moreover, a prostaglandin (F2α) injection is known to stimulate nest-building behaviour coupled with an increase in prolactin concentrations in prepartum sows (Blackshow and Smith, 1982).

Castrén et al. (1993) suggested that the end of NB behaviour could be related to a rise in oxytocin concentrations in prepartum sows. However, it is still unclear whether oxytocin plays a role in ending NB behaviour. Damm et al. (2002) established a tendency towards correlation between plasma oxytocin concentrations and NB, such as arranging, behaviour in crated gilts with access to nesting materials. In addition, Yun et al. (2014b) also demonstrated that vigorous NB behaviour induced by the provision of abundant nesting materials and space was accompanied with an increase in plasma oxytocin concentrations in prepartum sows. Results from trials with primiparous rats showed that central endogenous oxytocin played a crucial role in the expression of postpartum maternal behaviour, including NB.

INFLUENCES ON PARTURITION AND LACTATION SUCCESS

Farrowing performance

Piglet stillbirths represent both economic loss and welfare issues, and are a major concern in the pig industry. It is suggested that the rate of stillbirths in pigs is associated with duration of farrowing. Many studies have shown that restricted conditions or lack of materials for NB behaviour in prepartum sows resulted in prolonged farrowing duration, whereas some suggested no confinement effect on farrowing progress (Hales et al., 2015). This relationship between prepartum NB restriction and farrowing duration might be linked with the endocrine system in sows (Baxter and Petherick, 1980). It has been suggested that inhibiting the expression of prepartum NB behaviour in crated sows due to a lack of space or substrates increases endogenous opioids (Zanella et al., 1996; Jarvis et al., 1997), which are known to impede oxytocin secretion during farrowing (Bicknell and Leng, 1982; Douglas et al., 1995). A number of studies demonstrated that oxytocin, as a modulator of uterine or other muscle contractions during the parturition period (Taverne et al., 1979; Higuchi et al., 1985), can influence piglet birth intervals (Castrén et al., 1993; Lawrence et al., 1997; Jarvis et al., 2004; Oliviero et al., 2008). Circulating oxytocin concentrations during early parturition tended to be greater than during the prepartum period, and were positively associated with levels of prepartum oxytocin in sows (Yun et al., 2015). As described previously, inhibiting the expression of prepartum NB behaviour could provoke a decrease in oxytocin concentrations in prepartum sows (Yun et al., 2013; Yun et al., 2014a). Hence, restricted conditions for NB behaviour, with lower concentrations of oxytocin in prepartum sows, might affect a lengthened duration of farrowing. The link between the provision of a prepartum NB environment and piglet stillbirths, however, remains unclear. For instance, Weber et al. (2007) showed that a similar number of piglets were stillborn for crated and non-crated sows. In addition, Jarvis et al. (2004) revealed inconsistent results for stillbirth rate when nesting materials, space, or both were provided for prepartum sows, while Oliviero et al. (2010) found that piglet stillbirth was more highly correlated with farrowing duration in crated sows than in penned sows.

Lactating performance

Due to the absence of a milk reservoir in the sow, mammary gland growth is particularly important to develop a significant volume of secretory tissue and to maintain this tissue during lactation in order to achieve a high milk yield, and hence optimal piglet survival and growth (Herly, 2001). Mammary gland development prior to parturition can be affected by mammogenic hormones such as prolactin, while oxytocin plays a key role in postpartum mammary growth. Therefore, it can be speculated that prepartum NB behaviour in sows might contribute to mammary gland development. Yun et al. (2014a) suggested that elevated oxytocin and prolactin concentrations could be associated with NB behaviour in prepartum sows. Yun et al. (2014a) found that active NB behaviour in prepartum sows was positively correlated with nursing performance, and tended to be correlated with post-natal piglet weight gain in early lactation. Moustsen and Poulsen (2004) also reported that piglet weights at weaning from penned sows were higher than from crated sows. The release of oxytocin, as a crucial factor for milk production and ejection, might be the potential explanation for the link between duration of NB prior to parturition and nursing performance during early lactation (Yun et al., 2014a). Consequently, elevated levels of oxytocin and prolactin in sows induced by active NB behaviour during the prepartum period could lead to improved nursing performance in early lactation (Yun et al., 2014a).

Sows convert their body composition from anabolic to catabolic status to meet nutrient requirements for increasing milk demand during lactation (Valros et al., 2003; Valros et al., 2004). The level of metabolic status can be measured by analysing the products of nutrient metabolism, such as glucose (Boyd et al., 1995) or NEFA (Valros et al., 2003). The catabolic status has been shown to be associated with circulating oxytocin concentrations (Valros et al., 2004; Yun et al., 2014b). In addition, the release of oxytocin increases pancreatic hormones, such as insulin and glucagon, affecting metabolic processes (Algers and Uvnas-Moberg, 2007), and thus stimulates the body metabolism towards supplying nutrients for milk synthesis. Accordingly, it can

be speculated that activating NB behaviour in prepartum sows with an increase in circulating oxytocin concentrations and metabolic processes, could improve milk yield and nursing performance.

Colostrum intake by the newly born piglets plays a crucial role in transferring the innate immune system (Bourne, 1973). Prolactin is essential for lactose synthesis and for colostrum production by mammary epithelial cells (Foisnet et al., 2010), and thereby might lead to overall increase in colostrum yield in early lactating sows. Studies have shown that IgG concentrations in neonatal piglet serum were lower when prepartum sows had no possibility to build a nest due to lack of space or materials (Tuchscherer et al., 2002; Yun et al., 2014b). Consequently, this could be explained by an increase in colostrum and milk yields through elevated endogenous maternal hormones when sows had more chance to perform NB behaviour during the prepartum period.

Maternal characteristics

Piglet safety and the avoidance of crushing may depend on carefulness, such as rolling behaviour and the speed of lying down (Damm et al., 2005), or caring response of sows (Wechsler and Hegglin, 1997). Indeed, carefulness behaviour of sows, through lower crushing incidence, affected piglet survival rate (Wechsler and Hegglin, 1997; Herskin et al., 1998). Valros et al. (2003) also suggested that sows with a low litter mortality rate performed more rooting behaviour before lying down than sows with a high mortality rate in their litters. Hence, in order to reduce a major cause of piglet loss, sow carefulness behaviour towards their litters while standing and lying down should be considered. Herskin et al. (1998) showed that careful reactivity of sows towards piglets could be improved by provision of NB opportunities. Moreover, Yun et al. (2014a) also established a correlation between the duration of prepartum NB behaviour and carefulness of sows towards their offspring during early lactation, and suggested that the release of oxytocin, as a modulator of maternal characteristics, might be the explanation for the link. Oxytocin is known to modulate maternal nurturing behaviour, including the parent-child relationship in human (Ross and Young, 2009), and also encourage maternal reactivity of sows towards their offspring. In addition, oxytocin also plays a role in decreasing stress hormone levels, blood pressure, and heart rate, and thus contributes to stabilizing the condition of postpartum sows (Uvnas-Moberg and Petersson, 2005). It has therefore been suggested that active NB behaviour of prepartum sows, possibly due to elevated circulating oxytocin concentrations, could improve maternal carefulness behaviour in early lactation (Yun et al., 2013; Yun et al., 2014a).

CONCLUSION

The expression of NB behaviour in prepartum sows coupled with its consequences for sows and offspring has been discussed in numerous studies over recent decades. This paper summarizes interactions of prepartum NB behaviour with stress and maternal endocrinology, and their effects on parturition and lactation success. In summary, sows can experience frustration or injuries when having difficulties in moving or expressing prepartum NB behaviour, resulting in an increase in stress levels and a decrease in maternal endogenous hormones. Inadequate levels of those hormones induced by thwarting prepartum NB behaviour might have a detrimental effect on farrowing performance due mainly to prolonged birth intervals. In addition, it might also result in decreases in nursing performance and maternal characteristics, and thus, potentially, an increase in post-natal mortality. Therefore, it is suggested that activating prepartum NB behaviour, coupled with elevated levels of maternal endogenous hormones, might beneficially affect farrowing and nursing performance, maternal characteristics, and welfare of sows and offspring.

CONFLICT OF INTEREST

We certify that there is no conflict of interest with any financial organization regarding the material discussed in the manuscript.

REFERENCES

Algers, B. and K. Uvnas-Moberg. 2007. Maternal behavior in pigs. Horm. Behav. 52:78-85.

Arey, D. S., A. M. Petchey, and V. R. Fowler. 1991. The preparturient behaviour of sows in enriched pens and the effect of pre-formed nests. Appl. Anim. Behav. Sci. 31:61-68.

Baxter, M. R. and J. C. Petherick. 1980. The effect of restraint on parturition in the sow. In: Proceedings of the International Pig Veterinary Society. Vol. 6:84.

Bicknell, R. J. and G. Leng. 1982. Endogenous opiates regulate oxytocin but not vasopressin secretion from the neurohypophysis. Nature 298:161-162.

Blackshaw, J. K. and I. D. Smith. 1982. Behavioural effects of PGF2α in the non-pregnant sow. Appl. Anim. Ethol. 8:581-583.

Boulton, M. I., A. Wickens, D. Brown, J. A. Goode, and C. L. Gilbert. 1997. Prostaglandin F2alpha-induced nest-building in pseudopregnant pigs. II. Space restriction stress does not influence secretion of oxytocin, prolactin, oestradiol or progesterone. Physiol. Behav. 62:1079-1085.

Bourne, F. J. 1973. The immunoglobulin system of the suckling pig. Proc. Nutr. Soc 32:205-215.

Boyd, D. R., R. S. Kensinger, R. J. Harrell, and D. E. Bauman. 1995. Nutrient uptake and endocrine regulation of milk synthesis by mammary tissue of lactating sows. J. Anim. Sci. 73:36-56.

Boyle, L. A., F. C. Leonard, P. B. Lynch, and P. Brophy. 2002. Effect of gestation housing on behaviour and skin lesions of sows in farrowing crates. Appl. Anim. Behav. Sci. 76:119-134.

Burne, T. H., P. J. Murfitt, and C. L. Gilbert. 2000. Deprivation of straw bedding alters PGF(2alpha)-induced nesting behaviour in female pigs. Appl. Anim. Behav. Sci. 69:215-225.

Castrén, H., B. Algers, A. M. de Passillé, J. Rushen, and K. Uvnäs-Moberg. 1993. Preparturient variation in progesterone, prolactin, oxytocin and somatostatin in relation to nest building in sows. Appl. Anim. Behav. Sci. 38:91-102.

Chaloupkova, H., G. Illmann, K. Neuhauserova, M. Simeckova, and P. Kratinova. 2011. The effect of nesting material on the nest-building and maternal behavior of domestic sows and piglet production. J. Anim. Sci. 89:531-537.

Damm, B. I., M. Bildsøe, C. Gilbert, J. Ladewig, and K. S. Vestergaard. 2002. The effects of confinement on periparturient behaviour and circulating prolactin, prostaglandin F2a and oxytocin in gilts with access to a variety of nest materials. Appl. Anim. Behav. Sci. 76:135-156.

Damm, B. I., B. Forkman, and L. J. Pedersen. 2005. Lying down and rolling behaviour in sows in relation to piglet crushing. Appl. Anim. Behav. Sci. 90:3-20.

Damm, B. I., L. Lisborg, K. S. Vestergaard, and J. Vanicek. 2003. Nest-building behavioural disturbances and heart rate in farrowing sows kept in crates and Schmid pens. Livest. Prod. Sci. 80:175–187.

Douglas, A. J., I. Neumann, H. K. Meeren, G. Leng, L. E. Johnstone, G. Munro, and J. A. Russell. 1995. Central endogenous opioid inhibition of supraoptic oxytocin neurons in pregnant rats. J. Neurosci. 15:5049-5057.

Foisnet, A., C. Farmer, C. David, and H. Quesnel. 2010. Relationships between colostrum production by primiparous sows and sow physiology around parturition. J. Anim. Sci. 88:1672-1683.

Gilbert, C. L., T. H. Burne, J. A. Goode, P. J. Murfitt, and S. L. Walton. 2002. Indomethacin blocks pre-partum nest building behaviour in the pig (Sus scrofa): effects on plasma prostaglandin F metabolite, oxytocin, cortisol and progesterone. J. Endocrinol. 172:507-517.

Gustafsson, M., P. Jensen, F. H. de Jonge, G. Illmann, and M. Spinka. 1999. Maternal behaviour of domestic sows and crosses between domestic sows and wild boar. Appl. Anim. Behav. Sci. 65:29-42.

Hales, J., V. A. Moustsen, A. M. Devreese, M. B. F. Nielsen, and C. F. Hansen. 2015. Comparable farrowing progress in confined and loose housed hyper-prolific sows. Livest. Sci. 171:64-72.

Hansen, K. E. and S. E. Curtis. 1980. Prepartal activity of sows in stall or pen. J. Anim. Sci. 51:456-460.

Heckt, W. L., T. M. Widowski, S. E. Curtis, and H. W. Gonyou. 1988. Prepartum behavior of gilts in three farrowing environments. J. Anim. Sci. 66:1378-1385.

Herskin, M. S., K. H. Jensen, and K. Thodberg. 1998. Influence of environmental stimuli on maternal behaviour related to bonding, reactivity and crushing of piglets in domestic sows. Appl. Anim. Behav. Sci. 58:241-254.

Herley, W. L. 2001. Mammary gland growth in the lactating sow. Livest. Prod. Sci. 70:149-157.

Higuchi, T., K. Honda, T. Fukuoka, H. Negoro, and K. Wakabayashi. 1985. Release of oxytocin during suckling and parturition in the rat. J. Endocrinol. 105:339-346.

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

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

Jarvis, S., B. T. Reed, A. B. Lawrence, S. K. Calvert, and J. Stevenson. 2004. Peri-natal environmental effects on maternal behaviour, pituitary and adrenal activation, and the progress of parturition in the primiparous sow. Anim. Welf. 13:171-181.

Jarvis, S., B. J. Van der Vegt, A. B. Lawrence, K. A. McLean, L. A. Deans, J. Chirnside, and S. K. Calvert. 2001. The effect of parity and environmental restriction on behavioural and physiological responses of pre-parturient pigs. Appl. Anim. Behav. Sci. 71:203-216.

Jensen, P. 1986. Observations on the maternal behaviour of free-ranging domestic pigs. Appl. Anim. Behav. Sci. 16:131-142.

Jensen, P. 1988. Diurnal rhythm of bar-biting in relation to other behaviour in pregnant sows. Appl. Anim. Behav. Sci. 21:337-346.

Jensen, P. 1989. Nest site choice and nest building of free-ranging domestic pigs due to farrow. Appl. Anim. Behav. Sci. 22:13-21.

Jensen, P. 1993. Nest building in domestic sows: the role of external stimuli. Anim. Behav. 45:351-358.

Lawrence, A. B., K. A. McLean, S. Jarvis, C. L. Gilbert, and J. C. Petherick. 1997. Stress and parturition in the pig. Reprod. Domest. Anim .32:231-236.

Lawrence, A. B., J. C. Petherick, K. A. McLean, L. A. Deans, J. Chirnside, A. Gaughan, E. Clutton, and E. M. C. Terlouw. 1994. The effect of environment on behaviour, plasma cortisol and prolactin in parturient sows. Appl. Anim. Behav. Sci. 39:313-330.

Mayer, J. J., F. D. Martin, and I. L. Brisbin Jr. 2002. Characteristics of wild pig farrowing nests and beds in the upper Coastal Plain of South Carolina. Appl. Anim. Behav. Sci. 78:1-17.

Moustsen, V. A. and H. L. Poulsen. 2004. Comparison of production results in traditional farrowing crates and farrowing pens for loose housed sows. Meddelelse 679. Videnscenter for Svineproduktion, Copenhagen, Denmark. http://vsp.lf.dk/Publikationer/Kilder/lu_medd/2004/679.aspx. Accessed Dec. 6, 2004.

Oliviero, C., M. Heinonen, A. Valros, O. Halli, and O. A. Peltoniemi. 2008. Effect of the environment on the physiology of the sow during late pregnancy, farrowing and early lactation. Anim. Reprod. Sci. 105:365-377.

Oliviero, C., M. Heinonen, A. Valros, and O. Peltoniemi. 2010. Environmental and sow-related factors affecting the duration of farrowing. Anim. Reprod. Sci. 119:85-91.

Pedersen, L. J., P. Berg, G. Jorgensen, and I. L. Andersen. 2011. Neonatal piglet traits of importance for survival in crates and indoor pens. J. Anim. Sci. 89:1207-1218.

Ross, H. E. and L. J. Young. 2009. Oxytocin and the neural mechanisms regulating social cognition and affiliative behavior. Front. Neuroendocrinol. 30:534-547.

Rushen, J., S. Robert, and C. Farmer. 2001. Evidence of a limited role for prolactin in the preparturient activity of confined gilts. Appl. Anim. Behav. Sci. 72:309-319.

Taverne, M. A., C. Naaktgeboren, F. Elsaesser, M. L. Forsling, G. C. van der Weyden, F. Ellendorff, and D. Smidt. 1979. Myometrial electrical activity and plasma concentrations of progesterone, estrogens and oxytocin during late pregnancy and parturition in the miniature pig. Biol. Reprod. 21:1125-1134.

Tuchscherer, M., E. Kanitz, W. Otten, and A. Tuchscherer. 2002. Effects of prenatal stress on cellular and humoral immune responses in neonatal pigs. Vet. Immunol. Immunopathol. 86:195-203.

Uvnas-Moberg, K. and M. Petersson. 2005. Oxytocin, a mediator of anti-stress, well-being, social interaction, growth and healing. Z. Psychosom. Med. Psychother. 51:57-80.

Valros, A., M. Rundgren, M. Špinka, H. Saloniemi, and B. Algers. 2003. Sow activity level, frequency of standing-to-lying posture changes and anti-crushing behaviour—within sow-repeatability and interactions with nursing behaviour and piglet performance. Appl. Anim. Behav. Sci. 83:29-40.

Valros, A., M. Rundgren, M. Špinka, H. Saloniemi, F. Hultén, K. Uvnäs-Moberg, M. Tománek, Krejcı, amp, x, P., and B. Algers. 2004. Oxytocin, prolactin and somatostatin in lactating sows: associations with mobilisation of body resources and maternal behaviour. Livest. Prod. Sci. 85:3-13.

Weber, R., N. M. Keil, M. Fehr, and R. Horat. 2007. Piglet mortality on farms using farrowing systems with or without crates. Anim. Welf. 16:277-279.

Wechsler, B. and D. Hegglin. 1997. Individual differences in the behaviour of sows at the nest-site and the crushing of piglets. Appl. Anim. Behav. Sci. 51:39-49.

Widowski, T. M. and S. E. Curtis. 1990. The influence of straw, cloth tassel, or both on the prepartum behavior of sows. Appl. Anim. Behav. Sci. 27:53-71.

Wischner, D., N. Kemper, and J. Krieter. 2009. Nest-building behaviour in sows and consequences for pig husbandry. Livest. Sci. 124:1-8.

Yun, J., K.-M. Swan, C. Farmer, C. Oliviero, O. Peltoniemi, and A. Valros. 2014a. Prepartum nest-building has an impact on postpartum nursing performance and maternal behaviour in early lactating sows. Appl. Anim. Behav. Sci. 160:31-37.

Yun, J., K.-M. Swan, C. Oliviero, O. Peltoniemi, and A. Valros. 2015. Effects of prepartum housing environment on abnormal behaviour, the farrowing process, and interactions with circulating oxytocin in sows. Appl. Anim. Behav. Sci. 162:20-25.

Yun, J., K.-M. Swan, K. Vienola, C. Farmer, C. Oliviero, O. Peltoniemi, and A. Valros. 2013. Nest-building in sows: effects of farrowing housing on hormonal modulation of maternal characteristics. Appl. Anim. Behav. Sci. 148:77-84.

Yun, J., K. M. Swan, K. Vienola, Y. Y. Kim, C. Oliviero, O. A. T. Peltoniemi, and A. Valros. 2014b. Farrowing environment has an impact on sow metabolic status and piglet colostrum intake in early lactation. Livest. Sci. 163:120-125.

Zanella, A. J., D. M. Broom, J. C. Hunter, and M. T. Mendl. 1996. Brain opioid receptors in relation to stereotypies, inactivity, and housing in sows. Physiol. Behav. 59:769-775.